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Comparison of the biology, ecology and potential pest impacts of the eucalypt-defoliating leaf beetles *Paropsisterna cloelia* and *Paropsis charybdis* (Coleoptera: Chrysomelidae) in New Zealand

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Abstract

Background: Eucalypt species are grown in New Zealand for a variety of purposes. Paropsine leaf beetles (Coleoptera: Chrysomelidae) impact eucalypt plantations in Australia and other countries where eucalypts have become established. Six eucalypt-feeding paropsines from Australia have established in New Zealand to date. *Paropsis charybdis* Stål is currently regarded as the worst eucalypt pest. *Paropsisterna cloelia* (Stål) established in New Zealand in 2016 and it remains uncertain whether its potential impacts will exceed those caused by *P. charybdis*.

Methods: In this review, we provide an update on eucalypt insect invasions in New Zealand, summarise available literature on *Pst. cloelia*, and compare its ecology to *P. charybdis*, including distribution, host preferences, phenology, and natural enemies. Finally, we identify key areas for future research and give recommendations for integrated pest management.

Results: The number of specialist eucalypt-feeding insects has increased to approx. 36 species. The largely overlapping distributions of *P. charybdis* and *Pst. cloelia* in Australia indicate a similar climate tolerance; hence *Pst. cloelia* is likely to spread throughout New Zealand over time. Life history traits and behaviour of *Pst. cloelia* suggest it has a higher reproductive output and higher survival rate of immature stages than *P. charybdis*. This could potentially lead to severe defoliation from more frequent population outbreaks of *Pst. cloelia*, particularly under climatic conditions that induce growth stress in trees. Both species seem to prefer eucalypt species from different sections within the subgenus *Symphyomyrtus*, indicating a degree of niche separation. *Paropsisterna cloelia* larvae feed on both flush juvenile and adult leaves of heteroblastic eucalypt species (i.e., producing morphologically different juvenile and adult leaves), which would be of particular concern if it were to invade *Eucalyptus nitens* Maiden plantations.

Conclusions: We believe that *Pst. cloelia* has the potential to exceed the observed impacts from *P. charybdis* in New Zealand and cause growth losses in its most preferred eucalypt species. An integrated pest management approach that employs strategies, such as breeding for resistance, choice and siting of species, biological control, and/or pesticide use at set damage thresholds could result in significant economic benefits and resilience. As biocontrol is a long-term solution, other strategies need to be investigated and implemented without delay for the industry to be pre-emptive.

Keywords: Biological control, defoliation, *Eucalyptus*, growth impact, host preferences, insect pest, integrated pest management, invasive species, paropsine, production forestry

Introduction

Most eucalypts (genus *Eucalyptus*) are indigenous to Australia; however, a large number of species have been planted for commercial or aesthetic purposes in urban and rural landscapes throughout New Zealand. Eucalypts are known to support many herbivorous insects and numerous species have subsequently established on plantings in New Zealand. This includes some particularly problematic species, such as paropsine leaf beetles (Coleoptera: Chrysomelidae: Paropsini), or paropsines. Here, we summarise current knowledge on a recently established paropsine species, *Paropsisterna cloelia* (Stål), and compare its ecology to that of the current most damaging eucalypt-defoliating paropsine in New Zealand, *Paropsis charybdis* Stål*,* including distribution, host preferences, phenology, and natural enemies, to estimate its potential impacts. Finally, we identify key areas for future research and give recommendations for integrated pest management.

Eucalypt forestry in New Zealand

The genus *Eucalyptus* L'Hér. belongs to the family Myrtaceae (order Myrtales) and has approximately 850 species, primarily native to Australia. *Eucalyptus* is a versatile genus as different species grow naturally under a wide range of climates, some withstanding harsh environmental conditions. The fast-growing species, generally originating from the wetter regions in eastern Australia, are utilised globally for production forestry (Brooker 2002; Paine et al. 2011). Eucalypts were brought to New Zealand by Australian goldminers in the 1860's and have been present in the country for approximately 150 years (Poole et al. 2017). Eucalypts are hardwoods, but their wood properties, growth characteristics, site requirements, and pest tolerance and resistance vary between species (Page & Singh 2014; Poole et al. 2017; Shelbourne et al. 2002).

In New Zealand, Radics et al. (2018) estimated the total area planted with eucalypts in 2018 was 27,598 ha with a total asset value of NZ$671 million. *Eucalyptus nitens* Maiden currently occupies the largest area of any eucalypt species with approximately 15,300 ha (Radics et al. 2018) in the North and South Island due to its suitability for high quality short fibre pulp, high yields, and tolerance for frost and snow (Miller et al. 1992). However, *E. nitens* suffers severe defoliation caused by the eucalypt tortoise beetle *Paropsis charybdis* and high susceptibility to fungal leaf disease especially at low-altitude sites in the North Island, which cause growth reduction and death (Hood et al. 2002; Miller et al. 1992; Shelbourne et al. 2002). As these effects are smaller in colder temperatures, this species has subsequently been planted more extensively in the South Island (Miller et al. 1992; Shelbourne et al. 2002). Research is also investigating the use of *E. nitens* for solid (Lausberg et al. 1995) and engineered wood products, including laminated veneer lumber (LVL) (Gaunt et al. 2003). Ash eucalypts, e.g., *E. fastigata* Deane & Maiden and *E. regnans* F.Muell., are also increasingly planted for pulp in the North Island and for carbon sequestration (Kennedy et al. 2011; Miller et al. 2000).

There are plans for a substantial expansion of eucalypt plantings in New Zealand. The New Zealand Dryland Forests Innovation (NZDFI) is promoting an expanded multi-regional eucalypt industry focussed on naturally ground-durable eucalypt species such as *E. bosistoana* F.Muell.*, E. globoidea* Blakely*,* and *E. quadrangulata* Deane & Maiden (Millen et al. 2018). According to calculations by Radics et al. (2018), the NZDFI should achieve their aim of 100,000 ha of viable planted eucalypts by 2050 (Millen et al. 2018), and this resource would be valued at approx. NZ$2.4 billion. The rationale for this expansion is based on the vision of the NZDFI that New Zealand grown naturally ground-durable eucalypt timber can replace chromated copper arsenate (CCA) treated *Pinus radiata* D.Don (Millen et al. 2019). On optimal sites, some eucalypt species achieve faster growth rates and produce significantly stiffer and more durable wood compared to *P. radiata* (radiata pine) (Millen et al. 2018). Growing naturally durable eucalypts could diversify the New Zealand forestry sector that currently relies heavily on radiata pine (Millen et al. 2019). Eucalypt species could also satisfy the domestic lumber market that currently relies on imported sawn hardwood lumber, which amounted to approximately NZ$50 million in 2017 (Millen et al. 2018). However, this growth of eucalypt plantings is contingent upon the absence or at least successful management of major pests of these tree species.

Insects feeding on eucalypts in New Zealand and establishments since 2000

The entomological fauna associated with eucalypts in Australia is highly diverse. It is estimated that 15,000–20,000 species of herbivores, pollinators, predators, and parasitoids are dependent on eucalypts (Majer et al. 1997). New Zealand has no native eucalypts, and the closest relatives are from the genera *Leptospermum* Forster & Forster (mānuka), *Kunzea* Reichenb. (kānuka), *Metrosideros* Banks ex Gaertn. (pōhutukawa and rātā) and *Lophostemon* Schott, which belong to the same subfamily (Myrtoideae) as *Eucalyptus* (Salmon 2001). Only a small number of polyphagous native insects, including the puriri moth (*Aenetus virescens* (Doubleday), Lepidoptera: Hepialidae), bronze beetle (*Eucolaspsis* sp. (Fabricius), Coleoptera: Chrysomelidae), various leafrollers and wood borers, have colonised eucalypts in New Zealand, but generally with negligible impacts (Withers 2001). It is hypothesised that this is due to the lack of closely related host species in New Zealand (Ridley et al. 2000).

Australian insect herbivores have spread throughout the world following the establishment of their host plants, including eucalypts (Paine et al. 2011). Worldwide, New Zealand has the most successful establishments of eucalypt-feeding insects originating from Australia (Hurley et al. 2016; Mansfield 2016), with the first exotic herbivores establishing in the 1860s (Withers 2001). Withers (2001) reported 57 Australian eucalypt-feeding insects established in New Zealand, which included 31 polyphagous insects that are seldom considered pests impacting tree health. However, 26 eucalypt-feeding specialists established, of which some cause economically relevant damage to trees. Here, we provide an update of this list by collating new species that have established since 2000 based on records in the Forest Health Database (maintained by Scion and the New Zealand Forest Owners Association), in the 'Surveillance' magazine (e.g., Ministry for Primary Industries 2016), and published in the scientific literature (Hoare &

Hudson 2018). By 2023, an additional ten eucalypt-feeding specialist insects are known to have established in New Zealand (Table 1, Figure 1). Between 1980 and 2000, Withers (2001) reported that specialist insects were arriving at a rate of one per 17 months, but between 2000 and 2023, this rate has dropped to one every two or three years (Figure 1). Sap suckers (Hemiptera) remain the most common invaders (Mansfield 2016); however, defoliators (primarily Lepidoptera, Coleoptera, Hymenoptera) can also cause significant impacts (Withers 2001). The scale of damage from each pest varies between eucalypt hosts and between regions; however, most reports of impacts are anecdotal rather than systematically documented (Murray & Lin 2017).

Paropsine leaf beetles in New Zealand

Paropsine leaf beetles are considered the most damaging pests of plantation eucalypts in Australia (Elek & Wardlaw 2013) and they cause impacts in other countries where eucalypts have been introduced (Fanning & Baars 2014; Paine et al. 2011). Paropsines are a diverse group of leaf-feeding beetles within the Coleoptera subfamily Chrysomelinae, comprising 12 genera with more than 450 described species and many still awaiting description (Reid 2006). We are most interested in the paropsines that feed on eucalypts during both their larval and adult stages, which gives them the common name eucalypt leaf beetles.

New Zealand has six native genera of Chrysomelinae (Leschen et al. 2020) but no paropsines; however, six species from three genera of eucalypt-feeding paropsine leaf beetles native to Australia have established in New Zealand to date. *Paropsis charybdis*, first recorded in New Zealand in 1916, has historically been the most damaging defoliator of eucalypt species and is currently regarded as the number one eucalypt pest (Withers & Peters 2017). *Trachymela sloanei* (Blackburn) was first recorded in New Zealand in 1976 and *T. catenata* (Chapuis) in 1992. Both are considered minor pests, although *T. sloanei* can have localised outbreaks. However, as feeding damage by different paropsine species cannot be distinguished (Mann 2023), *T. sloanei* damage may be underestimated as contributing to the total damage due to all damaging life stages being nocturnal (Murray & Lin 2017). *Paropsisterna beata* (Newman), first recorded in New Zealand in 2012, was believed to have been eradicated in 2013 (Yamoah et al. 2016). The species was subsequently observed in 2016 (Ministry for Primary Industries 2016; New Zealand Farm Forestry Association 2016) but it has not been seen since, leaving its status uncertain. *Paropsisterna cloelia* (Stål) (*Paropsisterna* henceforth abbreviated to *Pst.*) was first detected in 2016 in the Hawke's Bay (Lin et al. 2017; Rogan 2016). Most recently, a third species of *Trachymela*, which is awaiting identification, was detected in June 2021 in Nelson (Ministry for Primary Industries 2021); however, its impacts are uncertain at this time (B. Rogan, personal communication[1]).

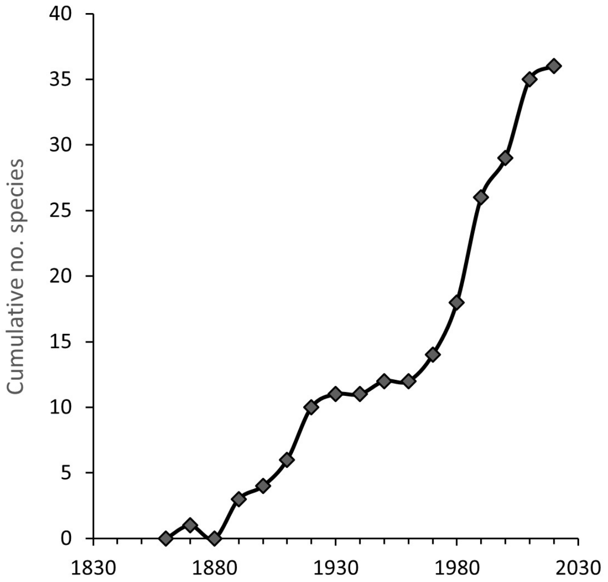

FIGURE 1: Cumulative establishment of specialist eucalypt-feeding insects in New Zealand by decade.

TABLE 1: Specialist eucalypt-feeding insects established in New Zealand since 2000.

Year	Species (Authority)	Order: Family	Place of first detection
2002	*Creiis lituratus* (Froggatt)	Hemiptera: Aphalaridae	Auckland
2009	*Anoeconeossa communis* Taylor	Hemiptera: Aphalaridae	Auckland
2009	*Stericta carbonalis* (Guenée)	Lepidoptera: Pyralidae	Banks Peninsula, Canterbury
2012	*Thaumastocoris peregrinus* Carpintero and Dellapé	Hemiptera: Thaumastocoridae	Auckland
2012	*Paropsisterna beata* (Newman)	Coleoptera: Chrysomelidae	Wellington
2014	*Phellopsylla formicosa* (Froggatt)	Hemiptera: Aphalaridae	Auckland
2016	*Paropsisterna cloelia* (Chapuis)	Coleoptera: Chrysomelidae	Napier
2017	*Glycaspis brimblecombei* Moore	Hemiptera: Aphalaridae	North Canterbury
2019	*Macarostola ida* (Meyrick)	Lepidoptera: Gracillariidae	Auckland
2021	*Trachymela* sp.	Coleoptera: Chrysomelidae	Nelson

Of these six species, it is the recent arrival of *Pst. cloelia* (previously known as *Pst. variicollis* (Nahrung et al. 2020)) that is causing fresh concern to eucalypt growers. This concern arises as *Pst. cloelia* appears to actively feed for a longer period during the year than other paropsines (Murray & McConnochie 2019; Rogan 2016) and may produce more generations per year than *P. charybdis* (Withers et al., 2018). Given these traits, *Pst. cloelia* may present a risk to the planned expansion of New Zealand's eucalypt industry, especially if it spreads into warmer regions.

Effects of beetle defoliation on eucalypt trees

Paropsine adults emerge in late spring after overwintering beneath bark or under leaf litter, or after periods of rain that trigger new growth in their host plants (Selman 1994). Paropsines characteristically chew inwards from the leaf margins towards the midvein (Whyte 2012) and are efficient exploiters of new leaf growth. Carnegie et al. (2005) observed that peak egg laying of *Paropsis atomaria* Olivier coincides with the availability of new foliage. Many paropsine species defoliate young trees (Selman 1994), while some only feed on older trees; however, the most severe defoliation generally occurs in younger age-classes (Carnegie et al. 2005). The effect of defoliation on the growth of plantation eucalypt species in New Zealand is poorly quantified and we rely heavily on research carried out in the southern parts of Australia on short-term effects of defoliation on saplings and young trees (≤3 years) of few key forestry species, such as *E. nitens, E. globulus* Labill., and *E. regnans.* It has been shown that the impact on tree growth is dependent on the severity, frequency, timing, and pattern of defoliation, as well as abiotic factors, such as nutrient and water availability that can constrain a plant's capacity to recover from defoliation.

Generally, studies agree that increases in defoliation severity result in decreased tree growth, but the level of defoliation at which noticeable effects on trees occur varies between studies (Eyles et al. 2009; Pinkard, Baillie, Patel, & Mohammed 2006; Quentin et al. 2011). For example, >10% defoliation by the *Eucalyptus* weevil *Gonipterus platensis* Marelli (formerly known as *G. scutellatus* Gyllenhal) resulted in short-term effects on the growth in young *E. globulus* plantation stands, whereas >20% defoliation altered the shape of the growth curve over time, suggesting longer-term effects on growth occurred (Pinkard, Baillie, Patel, & Mohammed 2006). Pinkard, Baillie, Patel, Paterson, et al. (2006) recorded defoliation levels of 25-38% of the total crown leaf area resulting in a decrease in stem growth of *E. globulus* seedlings by 17%. Conversely, Eyles et al. (2009) and Quentin et al. (2011) found that <50% defoliation of *E. globulus* did not impact growth of either height and diameter. Variability in the damage threshold that reduced growth may be explained by several factors. To begin with, eucalypt species as well as provenances within the same eucalypt species may vary in their tolerance and resistance to defoliation (Lin 2017; Mann 2023). Furthermore, studies use different methods to defoliate trees, e.g., natural versus artificial defoliation. Although the two methods show the same trend in tree responses, artificial defoliation may underestimate the impacts on trees (Quentin et al. 2010).

There is a general understanding that several defoliation events within one season and repeated defoliation in consecutive years will have a greater impact on tree growth than a single defoliation event within one season that is not repeated in consecutive years (Candy et al. 1992; Pinkard, Baillie, Patel, Paterson, et al. 2006). For example, a single defoliation event of 3-year-old *E. globulus* had no significant effect on growth, but triple defoliation within one season led to a 15% reduction in diameter and 26% reduction in height increment (Pinkard, Baillie, Patel, Paterson, et al. 2006). Likewise, 66% defoliation of current-season foliage of 3-year-old *E. regnans* only decreased height growth when repeated in two consecutive years (Candy et al. 1992).

The timing of defoliation can influence the ability to recover, e.g., late-summer and autumn defoliation has a larger negative effect than defoliation at other times of the year (Candy et al. 1992). For example, Candy et al. (1992) found that 100% late-season defoliation of 3-year-old *E. regnans* repeated for two consecutive years led to significantly higher mortality than repeated early-season defoliation. The pattern of defoliation may also play a role in the level of growth impact on trees. Pinkard, Baillie, Patel, Paterson, et al. (2006) found that artificial defoliation of the upper half of the tree had a bigger effect on stem growth (height and diameter growth increment) of 7month-old *E. globulus* seedlings than defoliation of the lower half.

Most studies are field-based and do not control for abiotic factors, e.g., temperature, water, and nutrient availability, which substantially affect tree growth (Costa e Silva et al. 2006; Wang et al. 2019). However, several studies assessed interactions between selected abiotic factors and defoliation. Eyles et al. (2009) examined the effect of defoliation and resource availability on biomass in *E. globulus* saplings and found that 40% artificial defoliation only reduced growth when water and nutrients were also limiting. In a study by Pinkard, Baillie, Patel, and Mohammed (2006), defoliation of >10% led to decreased growth of 3-year-old *E. globulus* after 12 months when no fertiliser was added. However, the addition of N and P fertiliser applied either separately or in combination increased height growth of trees defoliated to the same level as trees defoliated <10% (Pinkard, Baillie, Patel, & Mohammed 2006). As the interactions between different abiotic factors are not well understood, and defoliation impacts on eucalypts vary considerably between species and sites (Mann 2023; Pinkard et al. 2014), impact studies should be assessed on a regional or site-level scale. For a comprehensive review of the growth impacts of defoliation in eucalypts see Eyles et al. (2013).

Australian studies of defoliation impacts have not included key ground-durable eucalypt species of interest to the NZDFI (Millen et al. 2019). Two studies have investigated the effect of artificial defoliation on ground-durable eucalypt species in New Zealand. Lin (2017) found that severity, frequency, and timing of defoliation impacted *E. bosistoana* tree growth over two seasons, with a bigger effect on diameter than height growth. Although all defoliation treatments decreased diameter and height growth, only severely defoliated trees (90% of whole crown) and trees defoliated in late-summer showed a significant reduction in diameter growth of 13–21% compared to undefoliated control trees (Lin 2017). Trees with severe late-summer defoliation showed a significantly smaller increase in height (13% less height growth compared to undefoliated control trees) (Lin 2017). Repeated moderate defoliation (50% of whole crown) and severe defoliation in spring plus late summer had the biggest impact on both diameter and height growth with a reduction of 33–34% and 13–16%, respectively (Lin 2017). A comparative greenhouse study between *E. bosistoana* and *E. globoidea* suggested that both species cannot compensate for herbivory under water deficit stress. However, *E. globoidea* maintained a larger growth increase in the low-water treatment than did *E. bosistoana* (Mann 2023).

Although serious paropsine beetle outbreaks tend to occur on younger trees (pre-canopy closure) (Carnegie et al. 2005), economic losses due to defoliation on older trees post-canopy closure may be an important constraint on wood productivity. This is certainly the case in New Zealand grown *E. nitens* and *E. globulus* as *P. charybdis* only feeds on adult foliage that is present on 4+ year old trees that have transitioned from juvenile to adult leaf morphology (Withers & Peters 2017). Flush foliage also tends to be situated higher in the crown, where defoliation tends to have a bigger impact on growth, whereas senescing leaves dominate the lower crown (Eyles et al. 2013). Moreover, growth rates in temperate eucalypt plantations tend to be higher post-canopy closure (Beadle et al. 2008). However, the impact of defoliation on the growth of old versus young trees has not been directly compared in the same species in the same experiment. Such experiments would only be possible in homoblastic species (i.e., producing juvenile and adult leaves that are morphologically indistinguishable).

Nomenclature of *P. charybdis* and *Pst. cloelia*

In New Zealand, *P. charybdis* has been present for over 100 years and has been the subject of numerous research studies (e.g., Lin 2017; McGregor 1989; Murphy 2006; Murphy & Kay 2000; Murray 2010; Steven 1973; Styles 1970). It is not a major pest in Australia.

Historically, *Pst. cloelia* has been plagued with naming uncertainty, in part due to its variable colour polymorphisms (red, green, brown, and black morphs exist), and expanded geographic range. It has previously been known as *Pst. cloelia*, and incorrectly as *Pst. obovata* (Chapuis), and *Pst. variicollis* (Chapuis). Furthermore, all three species were previously known from the genus *Chrysophtharta* Weise until the genus was synonymised under *Paropsisterna* Motschulsky (Reid 2006). When the species established in New Zealand, it was incorrectly first referred to as *Pst. variicollis* (Lin et al. 2017). Peixoto et al. (2018) recommended a taxonomic revision and following Dr Chris Reid morphologically examining museum specimens from Australia, England, and New Zealand, Leschen et al. (2020) concluded that *Pst. variicollis* was a junior synonym of *Pst. cloelia*. To avoid future confusion, it should be noted that during the early 2000s, the emerging Western Australian pest issues were recorded as being caused by *Pst. variicollis* (Loch 2005), but later suggested as the identity being *Pst. obovata* (Matsuki & Tovar 2012). Similarly, in Tasmania, Murphy (2006) used the name *Pst. obovata* for the same species that had been referred to as *Pst. variicollis* by de Little (1979b). Finally, Nahrung et al. (2020) applied a combination of molecular and morphological analyses of specimens from multiple localities and concluded that the species known by these names are in fact one species, endemic to eastern Australia, that has since become invasive in Western Australia (WA), New Caledonia (Jolivet & Verma 2008), and New Zealand. This is supported by all previously known species sharing the same unique species of sexually transmitted mite, *Chrysomelobia captivus* Seeman & Nahrung (Acari: Podapolipidae) (Seeman & Nahrung 2005). The exact Australian geographic origin of New Zealand's invasive population remains unknown but is likely to be somewhere in mainland Australia (Nahrung et al. 2020). We therefore treat all literature referring to *Paropsisterna* (*Chrysophtharta*) *variicollis*, *Paropsisterna* (*Chrysophtharta*) *obovata*, and *Paropsisterna* (*Chrysophtharta*) *cloelia* as relating to the currently taxonomically accepted species *Pst. cloelia*.

Distribution

Paropsis charybdis

Paropsis charybdis was first recorded in New Zealand in 1916, in the Port Hills of Canterbury (Thomson 1922). It spread through the South Island in subsequent years, and was found for the first time in the North Island in 1956 (White 1973). By 1964, it was present in all areas of New Zealand with suitable host plants (White 1973) (Figure 2A).

Paropsisterna cloelia

Paropsisterna cloelia was initially discovered in March 2016 at Te Pohue in the Hawke's Bay (Lin et al. 2017; Rogan 2016). In January 2019 it was found in the South Island (Nelson and Marlborough regions) (Murray & McConnochie 2019; Withers 2019a). At the time of publication, the New Zealand distribution of *Pst. cloelia* spans the central North Island to central South Island, including the districts of Gisborne, Taupo, Hawke's Bay, Manawatu-Wanganui, Wellington, Nelson, Marlborough and North Canterbury (iNaturalist 2023b) (Figure 2B). However, these distributions are based on citizen-derived observations and not a systematic survey and thus are likely underestimating the true distribution of *Pst. cloelia*.

The Australian distributions of *P. charybdis* and *Pst. cloelia* overlap and extend from subtropical Queensland to cool temperate Tasmania (de Little 1989; iNaturalist 2023a, 2023b; Nahrung et al. 2020; Styles 1970) (Figure 2).

Host preferences in Australia

The genus *Eucalyptus* is divided into eight subgenera, of which *Symphyomyrtus* and *Eucalyptus* (previously *Monocalyptus*) are the most species rich, with approximately 470 and 130 species, respectively (Nicolle 2022). Both *P. charybdis* and *Pst. cloelia* prefer eucalypts from the subgenus *Symphyomyrtus* (Bain & Kay 1989; de Little 1979b).

Paropsis charybdis

Paropsis charybdis has become an occasional pest defoliating mature *E. nitens* in plantations in Tasmania (de Little 1989) and *E. cloeziana* Muell. In south-eastern Queensland (Nahrung 2006). This has occurred in plantations where species were grown outside their native distribution (Nahrung 2006) (Table 2). The species also feeds on other section Maidenaria species, such as

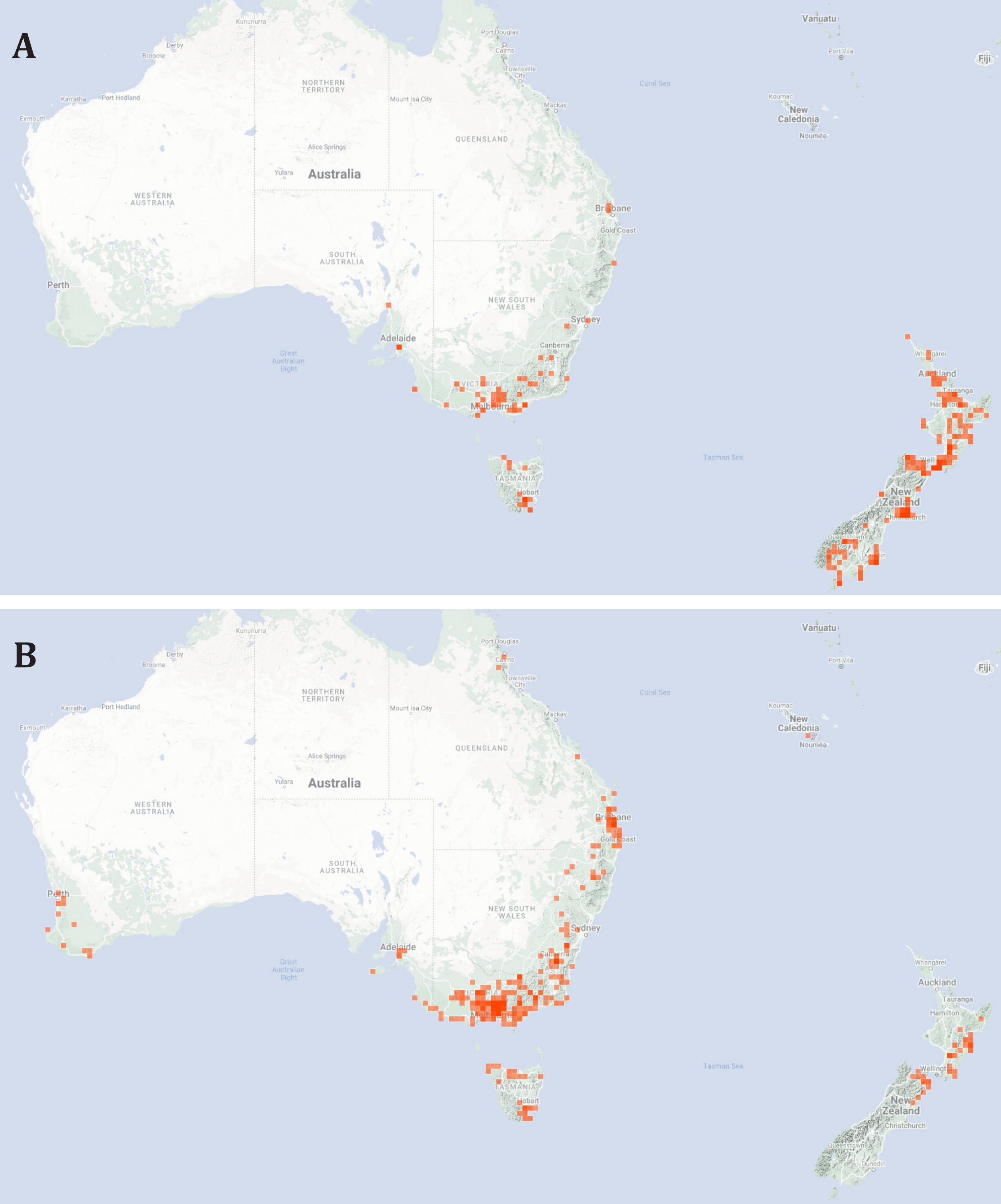

FIGURE 2: Australian and New Zealand geographic distributions of (A) *Paropsis charybdis* (iNaturalist 2023a) and (B) *Paropsisterna cloelia* (iNaturalist 2023b).

E. viminalis Labill., *E. ovata* Labill., *E. dalrympleana* Maiden, *E. rubida* Deane & Maiden (de Little 1979a).

Paropsisterna cloelia

This species has been recorded utilising *Angophora floribunda* Sweet as a host plant (Selman 1994) and as a pest of various *Symphyomyrtus* eucalypt species in different Australian regions. From the eucalypt section Latoangulatae it has been observed on *E. dunnii* Maiden in Queensland (Nahrung 2006) and New South Wales (NSW) (Carnegie et al. 2005; Elliott et al. 1998; Simmul & de Little 1999), *E. pellita* F.Muell., and *E. urophylla* S.T.Blake in Queensland (Simmul & de Little 1999), *E. grandis* W.Hill in Queensland (Simmul & de Little 1999) and NSW (Carne et al. 1974; Elliott et al. 1998; Selman 1994; Simmul & de Little 1999); and from the section Maidenaria it has been collected from *E. viminalis* in Victoria (Elliott et al. 1998; Simmul & de Little 1999), *E. globulus* in Victoria (Elliott et al. 1998; Ridenbaugh 2020), South Australia (Simmul & de Little 1999), and WA (Loch 2005, 2006), and *E. nitens* in Victoria (Elliott et al. 1998) and Tasmania (Simmul & de Little 1999). From the eucalypt subgenus *Idiogenes* it has been collected from *E. cloeziana* in Queensland (Nahrung 2006) (Table 2).

Host preferences in New Zealand

Paropsis charybdis

In New Zealand, *P. charybdis* has been recorded on 59 eucalypt species, but with a distinct preference for *Symphyomyrtus* species (White 1973). Susceptibility to defoliation varies considerably between species (Bain 1977), with the most preferred hosts belonging to the section Maidenaria, e.g., *E. globulus*, *E. viminalis*, *E. macarthurii* Deane & Maiden, *E. camaldulensis* Dehnh., *E. quadrangulata,* and *E. nitens* (Bain & Kay 1989; McGregor 1989; Murphy & Kay 2000; Withers & Peters

TABLE 2: Direct comparison of the biological and ecological characteristics of *Paropsisterna cloelia* and *Paropsis charybdis*.

Ecological trait	***Pst. cloelia***	***P. charybdis***
Eggs per batch	Average of 56.6 (lab);[a] 30-60 (field).[b]	Average of 17–23 (lab);[a] 20–50 (field).[b]
Fecundity	Average of 1428 (lab) per female lifetime.[a]	Average of 1045 (lab) per female lifetime.[a]
Oviposition rate	Average of 19.8 (lab) per day.[a]	Average of 14.9 (lab) per day.[a]
Generations	Australia: 2 generations in cooler regions (ACT, Tasmania, SE-Queensland),[b, c] 3-4,[b] potentially even 5 generations in warmer climates (NSW).[d] New Zealand: 2 generations in Marlborough,[e] unknown for other parts of the country.	Australia: 1–2 generations in SE-Queensland.[c] New Zealand: 2 generations in Nth Island.[f,g,h]
Oviposition	Flush foliage.[b]	Mature adult foliage.[f,h]
Food preferences	Larvae prefer flush foliage,[i] but feed on both adult and juvenile leaves in heteroblastic species (*E. globulus* and *E. nitens*).[j]	Larvae can only feed on flush adult foliage[f] and die on juvenile foliage of heteroblastic species.[j]
Distribution & host preference in Australia	Present from Queensland to Tasmania, Western Australia and SW Australia.[k] Wide host range but prefers species of subgenus *Symphyomyrtus* sections Maidenaria and Adnataria[b]: pest of *E. dunnii, E. pellita, E. urophylla, E. cloeziana, E. grandis, E. viminalis, E. globulus,* and *E. nitens* in several regions.[c,d,l,m,n,o,p,q]	Present from SE Queensland to Tasmania. Wide host range but prefers species of subgenus *Symphyomyrtus,* section Maidenaria: pest of *E. nitens* in Tasmania,[s] *E. cloeziana* in SE Queensland.[c]
Distribution & host preference in New Zealand	Nth Island: spreading; currently central North Island to central South Island.[k] Seems to prefer species of subgenus *Symphyomyrtus,* section Adnataria: e.g., *E. bosistoana* and *E. tricarpa;* among others *E. cladocalyx.*[t,u]	Main eucalypt defoliator, present throughout New Zealand.[v] Wide host range, but prefers species of subgenus *Symphyomyrtus,* section Maidenaria: e.g., *E. globulus, E. viminalis*, *E. macarthurii, E. camaldulensis, E. quadrangulata* and *E. nitens*.[f,g,w,x]

[a] Murphy (2006), [b] de Little (1979b), [c] Nahrung (2006), [d] Elliott et al. (1998), [e] Weser (unpublished observations), [f] McGregor (1989), [g] Murphy and Kay (2000), [h] Styles (1970), [i] Mo and Farrow (1993), [j] R. Ridenbaugh (personal communication)[5], [k] iNaturalist (2023b), [l] Carne et al. (1974), [m] Carnegie et al. (2005), [n] Loch (2005), [o] Ridenbaugh (2020), [p] Selman (1994), [q] Simmul and de Little (1999), [r] iNaturalist (2023a), [s] de Little (1989), [t] Lin (2017), [u] Tara Murray & Kuwabara (personal communication)[2,3], [v] White (1973), [w] Bain and Kay (1989), [x] Withers and Peters (2017).

2017). *Paropsis charybdis* can also defoliate species in the section Latoangulatae, such as *E. deanei* Maiden*, E. resinifera* J.White, and occasionally species in the section Adnataria, such as *E. leucoxylon* F.Muell*.* (Bain 1977; Styles 1970; White 1973) (Table 2).

Young larvae of *P. charybdis* feed exclusively on flush foliage (McGregor 1989). Late-instar larvae are also able to feed on expanding leaves and new shoots (Styles 1970). Heteroblastic eucalypt species produce juvenile (glabrous and waxy surface) and adult leaves with distinct morphological differences depending on the development phase of the tree (Potts & Wiltshire 1997), such as *E. globulus. E., quadrangulata,* and *E. nitens.* In these species, larvae of *P. charybdis* can only feed on the flush adult leaves. Adults beetles are more adaptable and, if needed, can feed on non-preferred species of eucalypts (Bain & Kay 1989), such as species of the subgenus *Eucalyptus,* like *E. fastigata*.

Paropsisterna cloelia

Based on information from Lin (2017) and T. Murray & S. Kuwabara (personal communication[2,3]) , *Pst. cloelia* has been recorded in New Zealand on 21 eucalypt species to date but seems to have a distinct preference for species in the *Symphyomyrtus* section Adnataria, such as *E. bosistoana* and *E. tricarpa* (L.A.S.Johnson) L.A.S.Johnson & K.D.Hill. Eggs and larvae have been recorded on 17 of these species, indicating that they are suitable hosts for reproduction. During the initial survey following its detection in the Hawke's Bay, the species was found feeding on numerous species, with high numbers of larvae and damage on several species in the section Maidenaria (*E. globulus, E. nicholii* Maiden & Blakely, *E. cinerea* F.Muell. ex Benth.) and of the subgenus *Eucalyptus* (*E. delegatensis* R.T.Baker), and low incidence on species in the section Latoangulatae (*E. botryoides* Sm.*, E. saligna* Sm.). It was also found on *E. nitens* but it was not possible to distinguish feeding by *Pst. cloelia* from damage by other established species (B. Rogan, personal communication[1]). Lin (2017) surveyed 11 eucalypt species for paropsine defoliation at three sites in the Hawke's Bay and recorded *Pst. cloelia* life stages when present (i.e., adults, larvae, and eggs). Adult *Pst. cloelia* were recorded on all these species with the highest numbers on *E. bosistoana* and *E. tricarpa*, two species in the section Adnataria. Immature stages (eggs and larvae) were recorded on seven *Symphyomyrtus* species (i.e., *E. quadrangulata, E. longifolia* Lindl. (section Maidenaria), *E. cladocalyx* F.Muell. (section Sejunctae), *E. camaldulensis* (section Exsertaria), *E. bosistoana, E. tricarpa, E. argophloia* Blakely (section Adnataria)) with the highest numbers on *E. bosistoana* and *E. tricarpa*. No immature stages were found on species from the subgenus *Eucalyptus* section Renantheria (*E. eugenioides* Sieber ex Spreng.*, E. globoidea* and *E. macrorhyncha*) and section Tranversaria (*E. notabilis* Maiden). However, counts of individuals of all life stages were low, suggesting that sampling at the end of January may have missed peak numbers of immature stages. Moreover, there was considerable variation in the numbers of different life stages present on the trees between the three study sites. The presence of defoliation in this study cannot be solely attributed to *Pst. cloelia* as *P. charybdis* was also present at all sites (Lin 2017; H. Lin, personal communication[4]) and feeding damage cannot be distinguished between paropsine species (Mann 2023).

In addition, T. Murray & S. Kuwabara (personal communication[2,3]) assessed ten eucalypt species at four sites in the Hawke's Bay (Woodville, Tutira, Waimarama, Omahu) in November and December 2017 when the first generation of *Pst. cloelia* was present. Larvae were again in the highest abundance on species in the *Symphyomyrtus* section Adnataria (*E. bosistoana,* and *E. tricarpa,* although to a lesser extent on *E. argophloia*). Some larvae were also recorded on *E. camaldulensis, E. longifolia,* and *E. quadrangulata.* Larvae were never found on *E. eugenoides, E. globoidea, E. macrorhyncha* (all subgenus *Eucalyptus*) or *E. cladocalyx* (*Symphyomyrtus* section Sejunctae, Table 2)*.* Three of the assessed sites were the same as those assessed by Lin (2017), which highlights the limited sites and regions within New Zealand that have been the subject of systematic surveys to date.

The only comparative study of paropsine defoliation from the South Island, specifically in Marlborough (Mann & Pawson 2022), was carried out at sites where both *P. charybdis* and *Pst. cloelia* were present. Results are consistent with those from the North Island sites, with *E. bosistoana* and *E. tricarpa* being the most defoliated species (Mann & Pawson 2022). *Eucalyptus bosistoana* and *E. tricarpa* are two of the most promising tree species in the NZDFI breeding programme for ground-durable eucalypt forestry in New Zealand (Millen et al. 2018). Larvae have been recorded during delimitation surveys on the subgenus *Eucalyptus* species *E. laevopinea* R.T.Baker, and subgenus *Symphyomyrtus* species *E. cinerea* F.Muell. ex Benth, *E. globulus,* and *E. nitens* (Forest Health Database, Scion and the Forest Owners Association).

Like *P. charybdis,* early-instar *Pst. cloelia* larvae are limited to feeding on flush foliage (Mo & Farrow 1993), whereas late-instar larvae feed on expanding leaves and shoots (Lin 2017). However, in heteroblastic eucalypt species, *Pst. cloelia* larvae of all ages can feed and develop fully on both flush waxy juvenile leaves as well as adult leaves (R. Ridenbaugh, personal communication[5]). Adults have been recorded on more eucalypt species than larvae (H. Lin, personal communication[4]), suggesting they can also feed on species that do not support juvenile stages.

Ecology, life cycle and phenology

Paropsis charybdis

Paropsis charybdis adults are ca. 11 mm long (de Little 1979b) and a reddish brown/marbled sandy colour (Figure 3). They are sexually dimorphic with adult males generally darker in colour and smaller than females (Steven 1973). Adults emerge from diapause in spring to feed, mate, and oviposit (McGregor 1989). *Paropsis charybdis* is highly fecund; Murphy (2006) reported an average fecundity (number of eggs a female lays in its lifetime) of 1044.7 eggs and an average oviposition rate of 14.9 eggs per day in the laboratory (Table 2). Eggs are pale yellow, ~2.6 mm long, and neatly arranged in two or three rows that are laid from the tip along the length of mature leaves adjacent to flush foliage, but never on flush foliage itself (Figure 3) (McGregor 1989; Styles 1970). The number of eggs recorded per batch varies considerably between studies, but averages ~20 eggs per batch (de Little 1979b; McGregor 1989; Murphy 2006; Styles 1970).

There are four larval instars. Young first-instar larvae are almost black (de Little 1979b) and feed gregariously. Older larvae are deep yellow with a dark head capsule (de Little 1979b) and feed solitarily or in small groups (Figure 3). Mature larvae (pre-pupae) turn pinkish and drop from the leaves to the ground to pupate in leaf litter (Styles 1970) or in chambers within the soil, with teneral adults emerging two to three weeks later (McGregor 1989). The full lifecycle from egg to adult takes 7–9 weeks; however, this varies with eucalypt species, quality of foliage (Steven 1973; Styles 1970), and temperature (Lin 2017; McGregor 1989). There are two generations per year in the central and lower North Island (McGregor 1989; Styles 1970) and in the upper South Island (Weser, unpublished observations) of New Zealand (Table 2). In Palmerston North (lower North Island), the first generation starts in late September with oviposition of eggs and finishes mid-December with emergence of new-generation teneral adults,

FIGURE 3: Life stages of *Paropsisterna cloelia* (left) and *Paropsis charybdis* (right): egg batch, larvae (L1-4), adult (from top to bottom).

and oviposition of the second generation occurs from January, emergence of teneral adults in mid-February (McGregor 1989). In Marlborough (upper South Island), the first generation (eggs to teneral adults) has been observed between late October to mid-December and the second generation from mid-January to late February (Weser, unpublished observations). Lin (2017), however, recorded only one generation in two consecutive years in Marlborough, possibly due to drought and the resulting limited abundance of flush foliage that is needed for reproduction and larval feeding. McGregor (1989) suggested that more generations are possible in warm climates where eucalypts continuously produce new foliage, and only one generation in cold areas that have a short growing season. However, this has not been confirmed. Certainly, generations do overlap due to the longevity of the adults and their extended egg-laying. Generational overlap of adults results in the sexual transmission of species-specific phoretic mites of *P. charybdis* in Australia (Seeman & Nahrung 2013). Young adults of the second generation may not mate or oviposit, but may feed vigorously to build fat reserves (McGregor 1989) before diapausing under loose bark or in leaf litter (Styles 1970).

Paropsisterna cloelia

Adult *Pst. cloelia* are approximately 8 mm long (de Little 1979b; Elliott et al. 1998) (Figure 3). The species lives up to its common name (*Eucalyptus* variegated beetle) and displays adult colour polymorphism. Teneral adults are bright orange-red, whereas mature adults can be red, green, or brown (Weser, unpublished observations). The melanistic form (orange with black or dark brown elytra) is restricted to eastern Australia and is not present in WA or New Zealand (Nahrung et al. 2020).

Adults of *Pst. cloelia* are even more fecund than *P. charybdis*. In laboratory trials, females produced an average of 1,428 eggs in their lifetime with an average oviposition rate of 19.8 eggs per day (Murphy 2006). Eggs are pale yellow, about 2 mm long and laid in loosely aggregated batches on flush foliage (de Little 1979b) (Figure 3). Batch sizes of between 30 and 60 eggs have been observed in the field (de Little 1979b) and an average of 56.6 eggs per batch under laboratory conditions (Murphy 2006) (Table 2).

The species follows the basic life history shared with other paropsines (Selman 1994), including four larval instars (Moore 1967) (Figure 3). First-instar larvae are covered with many tiny black dots that make them appear almost entirely black. Second and third instar larvae are creamy yellow with a black head capsule, black legs, and black last abdominal segments. Fourth instar larvae are distinctive with their aposematic colouration: they are yellow with a distinctive black middle line along the back (de Little 1979b) (Figure 3). All larval stages show strong aggregation behaviour and feed gregariously during the day (de Little 1979b). Like some other *Paropsis* and *Paropsisterna* species, larvae of *Pst. cloelia* perform cycloalexy, meaning that larvae feed in groups comprising different instars (monospecific aggregation) much more strongly than *P. charybdis*, and sometimes groups consist of different species (heterospecific aggregation) (Mo & Farrow 1993; Tan et al. 2017). This aggregation behaviour as well as their aposematic colouring presumably serves as protection against predation or parasitism (Tan et al. 2017). When not feeding, larvae position themselves in defensive circles with their heads pointing towards the middle and the end of their abdomens outwards (Tan et al. 2017). Larvae on the outer line of the circle raise their abdomens and evert their defensive vesicles when threatened (de Little 1979b), perform erratic movements with their abdomens, and excrete a defensive secretion containing hydrogen cyanide, benzaldehyde, and glucose (Moore 1967). Mature larvae develop into a pre-pupal stage, drop to the ground, and pupate within a chamber in the soil over seven to ten days (Elliott et al. 1998). In Australia, *Pst. cloelia* adults are known to disperse, seeking areas less populated by conspecifics in late summer (Selman 1994). Adult *Pst. cloelia* do not feed or overwinter gregariously (Nahrung & Clarke 2007) and have been found overwintering in leaf litter in Tasmania (de Little 1979b). No overwintering sites or dispersal behaviour have been recorded for this species in New Zealand.

According to Australian records, *Pst. cloelia* has varying numbers of generations per year depending on climatic conditions. In cooler regions, such as the Australian Capital Territory (ACT), Tasmania (de Little 1979b), and south-eastern Queensland (Nahrung 2006), *Pst. cloelia* undergoes two generations per year. However, three, potentially four generations per year are possible in warmer climates, such as NSW (de Little 1979b). Elliott et al. (1998) even suggested there may be up to five generations in NSW, with beetles remaining active for eight to nine months of the year (adult emergence in early spring to adults entering overwintering stage in late autumn).

In New Zealand, recent systematic sampling revealed that *Pst. cloelia* produces two full generations in Marlborough, with the first generation from late September (egg stage) to late December (emergence of teneral beetles) and the second generation from early January to mid-March (Weser, unpublished observations). In the North Island, larvae and adults of *Pst. cloelia* have been found in late April, at a time when the other two major defoliators (*P. charybdis* and *T. sloanei*) had already entered diapause (Rogan 2016). However, the phenology of the three species has not been compared or studied quantitatively in this area and the presence of *Pst. cloelia* may be a result of its higher conspicuousness and/or higher abundance at the site.

Paropsine control in Australia

Natural enemies

In their native range, natural, low-level fluctuations of paropsine beetle populations are quite effectively controlled by predators and parasitoids (de Little et al. 1990; Nahrung & Allen 2004). Coccinellids (ladybird beetles), reduviid (assassin) bugs, and pentatomid (shield and soldier) bugs are the main generalist predators of eggs and young larvae (Selman 1994). Tachinid flies and pteromalid wasps are the main parasitoids (Colless 2012; Cumpston 1939; Naumann 1991; Tanton & Khan 1978) and can, together with braconid wasps and nematodes, result in parasitism levels close to 100%, especially in years with high population levels of hosts (Selman 1994).

Paropsis charybdis

The diversity of *P. charybdis* natural enemies in Australia has been studied in Queensland and Tasmania, but not all parasitoids have been described. Peixoto et al. (2018) and Ridenbaugh et al. (2018) identified the braconid wasps *Eadya daenerys* Ridenbaugh, *E. paropsidis* Ridenbaugh, and *E. spitzer* Ridenbaugh (Hymenoptera: Braconidae) as larval parasitoids of *P. charybdis*. The average parasitism of *P. charybdis* by *E. daenerys* collected at four sites across Tasmania was 18%, with *P. charybdis* incurring between 3–6% parasitism in 72-hour sentinel larval trials (Peixoto et al. 2018). At least two species of tachinid flies dominate the larval parasitoid fauna, tentatively identified as *Froggattimyia tillyardi* Malloch (Diptera: Tachinidae) and *Paropsivora* spp. Malloch (Diptera: Tachinidae) (Bain & Kay 1989). Unidentified tachinids were responsible for variable (0–30%) larval parasitism on *P. charybdis* in the same sentinel trials in Tasmania (Peixoto et al. 2018). The parasitoid wasps *Neopolycystus insectifurax* Girault (Hymenoptera: Pteromalidae) and *Enoggera nassaui* (Girault) (Hymenoptera: Pteromalidae) parasitise *P. charybdis* eggs (Murphy 2006). In laboratory trials, *Enoggera nassaui* collected from Tasmanian locations parasitised eggs of New Zealand-collected and Tasmanian-collected *P. charybdis* at a rate of 9 and 11 eggs per hour, respectively (Murphy 2006). *Paropsis charybdis* adults are known to host three species of sexually transmitted mite species (Acari: Podapolipidae), *Chrysomelobia alleni* Seeman & Nahrung, *C. intrusus* Seeman & Nahrung (Seeman & Nahrung 2013), and *C. pagurus* Seeman (Seeman 2008). Mites are unlikely to cause death, but are thought to negatively impact reproduction in infested individuals (Withers & Peters 2017). New Zealand populations lack these mites (Seeman & Nahrung 2013; Withers & Peters 2017).

Paropsisterna cloelia

In Australia, the adult assassin bug *Pristhesancus plagipennis* Walker (Hemiptera: Reduviidae) feeds on adult *Pst. cloelia* (Whyte 2012). Adult *Pst. cloelia* are also frequently infected by entomophagous fungi towards the end of the summer when population levels are high (Selman 1994). Bacterial infections of late instar larvae do occur as well, but the mortality rate is generally low (Selman 1994). Like other paropsines, adult *Pst. cloelia* can be infested with sexually transmitted mites, which are found beneath the elytra (Seeman & Nahrung 2005). Infection by *C. captivus* mites increases overwintering adult mortality. However, no other aspects of fitness are affected. Females and larger individuals of both sexes are more often infected (Nahrung & Clarke 2007). *Chrysomelobia captivus* is absent from New Zealand populations of *Pst. cloelia* (Nahrung et al. 2020). In Australia, eggs of *Pst. cloelia* are eaten by generalist predators, such as *Harmonia conformis* (Boisduval) (Coleoptera: Coccinellidae), which can cause up to 23% mortality rate in the field (Mo & Farrow 1993). Larvae are parasitised by the tachinid fly *Froggattimyia tillyardi*, different *Paropsivora* species (Selman 1994), and the braconid wasp *Eadya annleckieae* Ridenbaugh (Hymenoptera: Braconidae) (Peixoto et al. 2018; Ridenbaugh et al. 2018). Field-collected *Pst. cloelia* larvae from Tasmania incurred an overall parasitism rate by *E. annleckieae* of 30% (Peixoto et al. 2018), and approximately 50% of 76 field-collected larvae were parasitised across sites in Victoria (Ridenbaugh 2020). Eggs are parasitised by the parasitoid wasps *N. insectifurax* and *E. nassaui* (Mo & Farrow 1993; Murphy 2006), which can cause mortality rates up to 23% in the field (Mo & Farrow 1993). In laboratory trials, *E. nassaui* parasitised *Pst. cloelia* eggs at a rate of 3 eggs per hour, which was significantly lower than parasitism rates of *P. charybdis* (Murphy 2006).

Pest management

There are considerable differences between eucalypt plantations in subtropical and temperate regions (Carnegie et al. 2005). In subtropical Australia, more than half of the eucalypt plantations are grown for long-rotation timber products and the remainder for short-rotation pulp (Carnegie et al. 2005). Plantation forestry is less established in Australian subtropical regions compared to temperate regions, and management is hampered by a lack of research (Carnegie et al. 2005). Due to the warmer climate, pests have more generations, are actively feeding for most of the year, and consequently can cause more damage (Carnegie et al. 2005). A range of pests have been identified, with paropsine beetles being the most frequent defoliators (Carnegie et al. 2008). However, detailed knowledge on the life cycle of pests is limited (Carnegie et al. 2005; Duffy 2007; Nahrung 2006; Nahrung, Duffy, et al. 2008; Nahrung, Schutze, et al. 2008). Presently, pest management in subtropical plantation forests utilises forest health monitoring, tree improvement, site-species matching, and limited use of pesticides, compared to plantation forests in temperate Australia (Carnegie et al. 2005).

Eucalypt forestry in temperate Australia is well-established and usually relies on one main species (e.g., *E. globulus* or *E. nitens*) grown in short-rotation stands for short-fibre pulp production (Carnegie et al. 2005). Forest managers can draw on more than two decades of research on silviculture, breeding, and pest management (Wardlaw et al. 2018). Paropsines remain one of the key pests in these plantations and require monitoring and management (Elek & Wardlaw 2013). Some forest companies have developed integrated pest management (IPM) strategies and are certified under a forest certification scheme either by the Forest Stewardship Council (FSC) or the Programme for the Endorsement of Forest Certification (PEFC) (Carnegie et al. 2005). The pest and disease control strategies include silvicultural methods (e.g., matching species and site), tree improvement measures for growth improvement and pest tolerance and resistance, pest monitoring and surveillance, and targeted control with chemical insecticides according to pre-set damage thresholds (Candy 1999; Elliott et al. 1992). This has led to a reduced and more targeted use of chemical pesticides in line with stated goals of minimising harm from the use of pesticides (Carnegie et al. 2005; Wardlaw et al. 2018). Biological insecticides (e.g., *Bacillus thuringiensis*) have fewer impacts on natural enemies but have limited effect on the target as they only kill young larvae and not late instars or adults (Elliott et al. 1992). Hence, the most common practice to control periodic paropsine and Lepidoptera outbreaks in eucalypt plantations in Australia remains targeted application of broad-spectrum pyrethroid insecticides (e.g., α-cypermethrin) within guidelines to maintain riparian buffer zones (Elek & Wardlaw 2013). These pesticides are very effective in killing all life stages of target pests, e.g., autumn gum moth (*Mnesampela privata* Guenée, Lepidoptera: Geometridae), gum leaf skeletoniser (*Uraba lugens* Walker, Lepidoptera: Nolidae), and paropsines (often *Paropsisterna bimaculata* (Olivier) and *Paropsisterna agricola* (Chapuis)). However, they also affect most beneficial insects and natural enemies, and have high aquatic toxicity (Elek & Wardlaw 2013). Moreover, pest insects may evolve resistance against insecticides, which limits their effect (Davies et al. 2007). In Tasmania, for example, FORICO manages more than 174,000 hectares of eucalypts, both planted and natural (Forico Pty Limited 2022) and has a pest monitoring programme every spring and summer to assess intervention needs. Often, natural enemies and weather events combine to reduce pest loads, but if defoliation and pest populations are above defined economic damage thresholds, then targeted aerial spraying with α-cypermethrin is undertaken using drones or helicopters (L. Cannon, personal communication[6]). This IPM programme has been estimated to prevent losses of more than two million m^3 merchantable wood volume (Wardlaw et al. 2018) with a benefit cost ratio of 7.5:1 of the expenditure on research (Cameron et al. 2018). Elek and Wardlaw (2013) showed that research into environmentally friendly biological pesticides has not identified a suitable alternative, and we contend that landscape scale management options (i.e., tree improvement, conservation/augmentative biocontrol with natural enemies, silvicultural practices, and the use of attract-and-kill traps, attractants, and repellents) remain insufficient to always protect the tree resource from impacts.

Paropsine control in New Zealand

Predators

In New Zealand, several native and exotic generalist predators are known to prey on different life stages of paropsines. The native ladybird beetle *Harmonia antipoda* (Mulsant) (Coleoptera: Coccinellidae) has been observed preying on *P. charybdis* eggs in laboratory trials (Alma 1980) but this has not been confirmed in the field. Two native predatory hemipteran species, the brown soldier bug *Cermatulus nasalis* (Westwood) (Hemiptera: Pentatomidae) and Schellenberg's soldier bug *Oechalia schellenbergii* (Guérin) (Hemiptera: Pentatomidae) have been observed preying on larvae of *Pst. cloelia* (Satchell et al. 2017) and *P. charybdis* (Ramsay 1963; Styles 1970) in the field. *Oechalia schellenbergii* is also known to feed on eggs of *P. charybdis* (Edwards & Suckling 1980). Edwards and Suckling (1980) studied predation by the polyphagous *C. nasalis* and *O. schellenbergii* on different species, including *P. charybdis* in the laboratory. Both hemipteran species showed no particular prey preference under controlled conditions. One complete generation of both hemipteran species could be reared by feeding only on *P. charybdis* larvae. Adult hemipterans had a daily consumption of 14–20 small larvae, or 1–8 big larvae, and hemipteran nymphs ingested circa one big larva per day. *Oechalia schellenbergii* also fed on eggs of *P. charybdis*. At overabundance, prey may only be consumed in parts (Edwards & Suckling 1980). Nevertheless, Edwards and Suckling (1980) conclude that both predators are not expected to greatly impact *P. charybdis* in the field because they do not consume enough, their life cycle is not synchronised with that of the pest, and they most likely only produce one generation per year. Recent observations in *E. nitens* plantations in Southland have concluded that the common starling (*Sturnus vulgaris* Linnaeus, Passeriformes: Sturnidae) is the main predator of adult *P. charybdis* in this region (J. Rope, personal communication[7]). In Marlborough, tauhou/silvereyes (*Zosterops lateralis* (Latham), Passeriformes: Zosteropidae) have been repeatedly observed feeding on *Pst. cloelia* larvae in the field (C. Weser, unpublished observations). In laboratory feeding trials, both larvae and adults of the Australian ladybird beetles (Coleoptera: Coccinellidae) *Harmonia conformis*, *Halmus chalybeus* (Boisduval), and *Rhyzobius ventralis* (Erichson) fed on *P. charybdis* eggs (Alma 1980). Additionally, the German wasp *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae), and sparrows (*Passer domesticus* (Linnaeus), Passeriformes: Passeridae), are reportedly predators of *P. charybdis* in New Zealand (Styles 1970). However, information on predators of paropsines in New Zealand are only derived from occasional field observations or laboratory studies and their impact on *Pst. cloelia* and *P. charybdis* populations in the field remains unquantified.

Biological control

Substantial effort has been spent attempting to establish known natural enemies (classical biological control) of the most damaging defoliator, *P. charybdis,* in New Zealand. Nevertheless, success has been limited, and the biological control agents introduced from Australia have been unable to consistently control paropsine populations to date. Since the 1930s, different parasitoids from Australia have been imported into New Zealand for the control of *P. charybdis*. Several attempts were made over the decades to introduce the braconid larval parasitoid *Aridelus* sp. Marshall (Hymenoptera: Braconidae) and the tachinid fly *F. tillyardi*, but rearing was challenged by hyperparasitism and low emergence rates (Bain & Kay 1989; Kay 1990). Consequently, *Aridelus* sp. was never released, and two releases of a total of 750 adult *F. tillyardi* at one site in the central North Island did not result in establishment, and further attempts were abandoned (Bain & Kay 1989; Kay 1990). In the 1970s and 1980s, the ladybird beetle *Cleobora mellyi* (Mulsant) (Coleoptera: Coccinellidae) was repeatedly introduced to New Zealand over several decades (Bain et al. 1979; Satchell et al. 2004). Initial releases were unsuccessful and did not lead to establishment in most regions of the country (Murray et al. 2008; Withers & Bain 2009), which was attributed to a lack of available psyllids/scale insects, as these are an essential part of *C. mellyi* diet to facilitate oviposition (Bain et al. 1984). Only in 2010, following extensive re-releases from collections made in the Marlborough Sounds in 2005 and 2006 into *Acacia melanoxylon* R.Br. (Fabales: Fabaceae) plantations in both islands, where psyllids were now plentiful, was establishment achieved throughout New Zealand (Withers & Berndt 2010). Field studies from Australia (S. C. Baker et al. 2003; Bashford 1999; de Little 1979b; de Little et al. 1990; Mensah & Madden 1994) and laboratory predation trials from New Zealand (Bain et al. 1984; de Little 1979b; Elliott & de Little 1980; Mansfield 2019) led to the conclusion that *C. mellyi* can have a significant impact on paropsine populations in the field through egg and, to a lesser extent, larval predation. Under laboratory conditions, *C. mellyi* adults showed a mean consumption rate of about 19 *Pst. bimaculata* eggs per day (de Little 1979b; Elliott & de Little 1980) and about 11 *P. charybdis* eggs per day (de Little 1979b). The effectiveness of *C. mellyi* as a predator in the field has been studied in Tasmania on *Pst. bimaculata*, a species of comparable size to *Pst. cloelia* (de Little 1989). de Little (1979b) observed *C. mellyi* as the main predator of *P. bimaculata* eggs in the field, causing egg mortality of up to 74%. de Little et al. (1990) found that predation of *P. bimaculata* eggs could reach 78% in the field, and *C. mellyi* was suspected to be the main predator. In New Zealand, *C. mellyi* feeds on both *Pst. cloelia* and *P. charybdis* eggs (Bain et al. 1979; Murray & McConnochie 2019; Satchell et al. 2004; Satchell et al. 2017; Withers & Bain 2009) and larvae (Satchell et al. 2017; Withers et al. 2018; Withers & Peters 2017) in the field, but its quantitative impact on population levels remains unknown (Withers et al. 2018). It would be very beneficial to understand the role of *C. mellyi* in regulating paropsine populations in New Zealand.

The two specialist egg parasitoids *E. nassaui* and *N. insectifurax* are effective agents against *P. charybdis* in New Zealand. Both *E. nassaui* and *Neopolycystus* sp. were introduced to New Zealand and released at several sites between 1987 and 1988 (Bain & Kay 1989). Initially, only *E. nassaui* successfully established in warmer parts of the country (Kay 1990) but after the release of a ‘cold-resistant’ strain from Tasmania (Murphy et al. 2004), it also established in cooler regions (Murray et al. 2008). Initial attempts to establish *Neopolycystus* sp. failed (Kay 1990). However, in 2002 *N. insectifurax* was detected in *P. charybdis* eggs collected in the Bay of Plenty (Berry 2003). These specimens differed morphologically from the only specimens kept from the original 1988 breeding colony, indicating that the presence of *N. insectifurax* in New Zealand is likely due to self-introduction (Berry 2003). On *P. charybdis*, both species readily parasitise 100% of eggs supplied to them in laboratory trials (Bain & Kay 1989) and are regularly reared from field-collected eggs (Berry 2003; Jones & Withers 2003; Mansfield et al. 2011; Murphy 2002). Although the two parasitoids reach high parasitism levels above 80% of the second late-summer generation of *P. charybdis* eggs in the North Island, they are generally not able to control the first appearance of the spring generation of the beetle (parasitism <20% prior to December) (Jones & Withers 2003; Mansfield et al. 2011; Murphy & Kay 2000; Pugh et al. 2020). *Enoggera nassaui* has also been reared from *Pst. cloelia* eggs collected in the field in New Zealand (T. Murray & S. Kuwabara, personal communication[2,3]; Withers & Pugh, unpublished observations). However, parasitism of *Pst. cloelia* by *N. insectifurax* in New Zealand is rare and has only been recorded once (Withers & Davy, unpublished observations). Moreover, parasitism rates by *E. nassaui* are generally low and *Pst. cloelia* seems to be a low-quality host, most likely due to its smaller size. Emerging adult wasps are smaller (approx. by one third) compared to those emerging from *P. charybdis* eggs (Murray & McConnochie 2019; Withers 2019b).

Murphy (2006) found that *Pst. cloelia* and *P. charybdis* were both hosts of *E. nassaui* in the field in Tasmania. However, in no-choice tests in the laboratory, rejection of *Paropsisterna* species as hosts happened repeatedly and parasitism rates were significantly lower compared to that of *Paropsis* species (Murphy 2006). Similarly, recent laboratory trials in New Zealand showed that both species have a strong oviposition preference for *P. charybdis* over *Pst. cloelia*, but both can fully develop in *Pst. cloelia* eggs as a host (Withers & Davy, unpublished observations). *Enoggera nassaui* can produce viable, fertile offspring in *Pst. cloelia* eggs. However, *N. insectifurax* offspring emerging from *Pst. cloelia* eggs were small and could not produce offspring, potentially representing a population sink (Withers & Davy, unpublished observations). To date, only two unpublished field studies of *Pst. cloelia* egg parasitism have been undertaken (T. Murray & S. Kuwabara, personal communication[2,3]; Withers & Pugh, unpublished observations), both in the Hawke’s Bay, and results are based on small sample sizes. This means the impact of these egg parasitoids on *Pst. cloelia* egg survival in the field is largely unknown, but is not expected to be significant. Egg parasitism of *Pst. cloelia* in the field in New Zealand remains a topic of current research.

In 2002, a hyperparasitoid of *E. nassaui*, *Baeoanusia albifunicle* Girault (Hymenopetra: Encyrtidae), was first detected in New Zealand (Murphy 2002). It is an obligate hyperparasitoid, which means it can only emerge from parasitised primary host eggs (Murray 2010). Hyperparasitism of *E. nassaui* by *B. albifunicle* still leads to mortality of *P. charybdis* eggs, but it reduces the abundance of *E. nassaui* in the field (Jones & Withers 2003) and hence subsequent parasitism of paropsine eggs. *Neopolycystus insectifurax* is not hyperparasitised by *B. albifunicle* in the field and, consequently, *E. nassaui* may decrease in abundance due to hyperparasitism, whereas *N. insectifurax* may increase (Jones & Withers 2003). Before the arrival of *N. insectifurax* and *B. albifunicle*, *E. nassaui* on its own achieved low parasitism (<20%) of *P. charybdis* eggs early in the season (October and November), but could reach >80% in March (Murphy & Kay 2000). At field sites with both primary parasitoids and the hyperparasitoid present, early-season parasitism (mostly by *E. nassaui*) was still low. At mid-season (December), *B. albifunicle* was overtaking *E. nassaui* and by late season, parasitism and emergence of *E. nassaui* were reduced to zero by the hyperparasitoid. Overall, late-season parasitism rates are high and dominated by *N. insectifurax* (Jones & Withers 2003; Mansfield et al. 2011; Pugh et al. 2020). While *N. insectifurax* does compensate for the reduced *E. nassaui* populations caused by the hyperparasitoid *B. albifunicle* (Mansfield et al. 2011), it is not present in all eucalypt growing areas. Murray et al. (2008) showed *E. nassaui* and *B. albifunicle* are well-established in all eucalypt growing areas throughout the country. *Neopolycystus insectifurax* has not been confirmed in Southland to date despite 1600 individuals being released there in 2003/04 (T. Withers, personal communication). The results of these field studies demonstrated the need for additional biological control agents to target the spring generation of *P. charybdis* (Pugh et al. 2020).

The larval parasitoid *Eadya daenerys* has been released into *E. nitens* plantations in Southland and in the central North Island in December and January, 2022/23 and 2023/24 (Withers 2023; T. Withers, personal communication) as an additional biocontrol agent to target the first (spring) generation of *P. charybdis* (Pugh et al. 2018; Pugh et al. 2020; Withers 2019a). At the time of the releases and writing these *E. nitens* plantations contain *P. charybdis* and not *Pst. cloelia* (Withers 2023). In laboratory choice trials, *E. daenerys* were significantly less attracted to larvae of *Pst. cloelia* than *P. charybdis* (i.e., four times more oviposition in *P. charybdis*), and the small number of *Pst. cloelia* larvae stung died as larvae (Davy, Todoroki & Withers, unpublished observations). Researchers do not expect *Pst. cloelia* will be targeted nor lower the parasitism of *P. charybdis* in the field by acting as a non-host for *E. daenerys* (T. Withers, personal communication).

Other control methods

Aerial spraying with chemical insecticides, such as DDT and Gusathion 50, was common practice in the 1960s and 1970s to control *P. charybdis* (Styles 1970). This proved effective for a short time in reducing pest populations and let the defoliated trees recover (Styles 1970). Nevertheless, applications did not prevent re-infestation from surrounding untreated areas. The high cost of repeated spray operations was seen as the main disadvantage (R. Baker & de Lautour 1962; Styles 1970). Silvicultural practices, such as the planting of less palatable species (e.g., *E. fastigata*, *E. delegatensis*, *E. pilularis* Sm., and *E. regnans* instead of *E. globulus, E. obliqua* L'Hér., *E. viminalis,* and *E. macarthurii*) were also used (Styles 1970). Currently, mass outbreaks of paropsines are generally controlled with aerial application of broad-spectrum synthetic pyrethroids such as α-cypermethrin, using ultra-fine droplets to assist canopy penetration, in an oil-based carrier to assist with retention (Rolando et al. 2016). Unfortunately this method has the negative side effect of also killing non-target insects, including predators and parasitoids (Withers et al. 2013). For the last two decades, the FSC has granted temporary derogations (permissions) to New Zealand companies for emergency control of *P. charybdis* outbreaks with α-cypermethrin in certified forests (FSC 2019). Derogations were granted while companies needed to demonstrate research was underway on alternative control options, such as biological control, alternative insecticides, and breeding for pest resistance (FSC 2019; Rolando et al. 2016). Consequently, different alternative options have been investigated over the years. Several biological and alternative insecticides were trialled with promising results against *P. charybdis* larvae (Jackson & Poinar Jr 1989; Pugh et al. 2015; Withers et al. 2013), but they would require multiple applications or greater volumes and are therefore more expensive to apply compared to current insecticides (Withers & Peters 2017). Since 2021, New Zealand has moved to a group scheme requiring each company, and for each pesticide spray operation, to undertake and document their own environmental and social risk assessment (ESRA). This risk-based approach has the advantage that forest management practices can meet both PEFC and FSC requirements for international markets. It now covers solid wood, sawn wood products and wood chips (Brett Gilmore Consulting 2020). Alongside the insecticide applications, NZDFI and the Specialty Wood Products Partnership (incorporating the previous New Zealand Eucalyptus Breeding Co-op) undertake research and development of tree breeding for various traits, including resistance and tolerance to pests and diseases (Altaner et al. 2016, Klápště, unpublished observations; Mann & Pawson 2022; Millen et al. 2019; Millen et al. 2018).

Discussion

Globally, the detection rate of specialist eucalypt-feeding insects drastically increased between 1986 and 2014, which corresponded with an increase in eucalypt plantings and worldwide trade and travel (Hurley et al. 2016). We show that the detection rate of potential eucalypt pests into New Zealand has continued to slow since the early 2000s. New Zealand is uniquely positioned with respect to eucalypt-feeding insect invasions and was the country with the first insect introductions, the highest number of first detections outside of Australia, and the highest number of total introductions compared to other regions in the world (Hurley et al. 2016). This has been attributed to its geographic proximity to Australia that facilitates natural dispersal (Pretorius et al. 2023) and the trade and travel connections between the two countries (Ridley et al. 2000). Although pathways of introduction are poorly understood on a global scale

(Hurley et al. 2016), imported wood (packaging, logs, sawn timber), used vehicles, machinery, containers, ships, plant material, and oversees travellers have been identified as general pathways for insects and pathogens (Meurisse et al. 2019; Ridley et al. 2000). The higher likelihood of detecting introduced eucalypt species in Auckland city suggests that the human-assisted invasions via trade and travel were historically the main introduction pathway (Withers 2001). However, for individual introductions the pathway remains speculative. For example, *Uraba lugens* and the paropsine beetle *Dicranosterna semipunctata* (Chapius) (Coleoptera: Chrysomelidae) were potentially moved as hitchhikers by tourists playing golf on Australian and then New Zealand golf courses, where they were first detected (Ridley et al. 2000). Another potential pathway for paropsine beetles was via the import of untreated eucalypt foliage for the cut flower industry from Australia into New Zealand, although this pathway was officially closed in 1999 (Withers 2001). However, it is possible that species discovered after 1999 had arrived via the foliage pathway as there is a well-recognised lag phase between first introduction and the build-up of populations before they are detected (Brockerhoff & Liebhold 2017). Trans-Tasman wind dispersal has been recorded for pathogens, small insects (such as aphids), and large moths and butterflies (Close et al. 1978; Fox 1978; Pretorius et al. 2023), but not for beetles. However, Coleoptera have been caught at substantial distances offshore, up to 800 km from the nearest land mass (Yoshimoto & Gressitt 1960). Consequently, although an unlikely pathway, we cannot completely rule out travel via long distance wind dispersal as a mode of entry into New Zealand for paropsine beetles. Realistically, we can expect further invasions into New Zealand of specialist eucalypt insects due to trade, travel, and natural dispersal between Australia and New Zealand despite strict biosecurity measures (Close et al. 1978; Fox 1978; Hurley et al. 2016; Pretorius et al. 2023; Ridley et al. 2000; Withers 2001).

Paropsisterna cloelia was first detected in New Zealand in 2016 and there remains much uncertainty regarding its potential negative impacts, compared with those of *P. charybdis*. The largely overlapping distributions of *P. charybdis* and *Pst. cloelia* in Australia suggest both species will show a similar climate tolerance; hence we assume *Pst. cloelia* will eventually spread throughout New Zealand. Adult *Pst. cloelia* have been observed dispersing with strong wind conditions up to 40 kilometres into previously uninfested eucalypt stands (B. Rogan, personal communication[1]). We cannot predict when *Pst. cloelia* will reach the *E. nitens* plantations in Southland and the central North Island due to uncertainty regarding its dispersal rate and method. Quantitative field studies of *P. charybdis* phenology have occurred in the Bay of Plenty and Manawatū-Whanganui regions (McGregor 1989; Styles 1970) and one comparative study of the two species in New Zealand from Marlborough (Weser, unpublished observations), which is also the first study of *Pst. cloelia* phenology in New Zealand. Preliminary data suggests that both *Pst. cloelia* and *P. charybdis* will produce two relatively concurrent generations in the moderate climates of the Marlborough region. For other areas of the country, we can speculate, based on studies from Australia, that *Pst. cloelia* may undergo three generations per annum in warmer regions, and potentially more where winter temperatures are mild, such as in Northland (de Little 1979b; Elliott et al. 1998). McGregor (1989) suggests a similar phenology for *P. charybdis*; however, phenology in warmer and colder areas, such as Northland and Southland, respectively, has not been quantified.

Life history traits and behaviour of *Pst. cloelia* suggest it may have competitive advantages over *P. charybdis*. Murphy (2006) proposed that species with a fecundity >600 eggs per female lifetime and an oviposition rate >10 eggs per day have pest potential. Incidentally, Murphy (2006) listed *Pst. cloelia* (alongside *Pst. agricola* and *Pst. bimaculata*) as one of the Australian paropsine species with the highest potential of becoming a serious pest in New Zealand based on its high reproductive output, exactly a decade prior to its establishment. As a comparison, the two *Trachymela* species that are not significant pests in New Zealand have relatively low reproductive outputs with a fecundity of ~400 and an oviposition rate of 12 and 7.5 eggs per day, for *T. catenata* and *T. sloanei,* respectively (Murphy 2006). Additionally, gregarious feeding and aposematic colouration may give *Pst. cloelia* larvae more protection against predation compared to solitarily feeding *P. charybdis* larvae. Larval gregariousness may also facilitate the successful initiation of feeding and increase survival of neonate paropsine larvae, especially on older leaves, due to prior damage to the leaf (Nahrung et al. 2001). It is also possible that the choice of oviposition sites has an effect. *Pst. cloelia* adults lay eggs on fresh foliage, which allows the larvae to start feeding immediately, whereas *P. charybdis* oviposits on old/mature leaves and, consequently, initiation of larval feeding requires neonates to disperse to the tips of branches to locate flush adult foliage and this may lead to higher mortality rates of young *P. charybdis* larvae, especially when new foliage is scarce (McGregor 1989).

Moreover, field and laboratory trials suggest that biological control agents introduced to New Zealand for the control of *P. charybdis* cannot currently control the first generation of *P. charybdis* (Pugh et al. 2020) and these parasitoids may have an even smaller effect on *Pst. cloelia*, which is not their preferred host. Time will tell whether *E. daenerys* will fill this gap for *P. charybdis*. Various generalist predators have been observed feeding on different life stages of both *Pst. cloelia* and *P. charybdis*, but the effect on populations of either species has not been quantified in the field. The two currently established egg biocontrol agents, the parasitoid wasps *E. nassaui* and *N. insectifurax,* attack *Pst. cloelia* eggs but significantly prefer *P. charybdis* (Withers & Davy, unpublished observations). The newly released larval parasitoid *E. daenerys* for the control of *P. charybdis* does not utilise *Pst. cloelia* as a host (Withers & Davy, unpublished observations). Altogether, it appears that natural enemies currently present in

New Zealand are unlikely to be sufficient to suppress *Pst. cloelia* populations.

Current knowledge of host preference indicates a degree of niche separation where *Pst. cloelia* and *P. charybdis* seem to prefer eucalypt species from different albeit closely related sections within the subgenus *Symphyomyrtus*, thus limiting direct competition to some extent. *Paropsis charybdis* and *Pst. cloelia* may co-occur in Australia on common hosts, such as *E. viminalis* in Tasmania and *E. cloeziana* in Queensland (Nahrung 2006; H. Nahrung, personal communication[8]); however, it is unknown how they might compete. In New Zealand, both species co-occur on common host trees at the same time, but *Pst. cloelia* is more abundant than *P. charybdis* on *E. bosistoana* and *E. tricarpa*, whereas *P. charybdis* is more abundant on *E. quadrangulata* (Lin 2017; T. Murray & S. Kuwabara, personal communication[2,3]; Murray & McConnochie 2019). Moreover, due to its limited current geographic range (Figure 2B), host preferences of *Pst. cloelia* in New Zealand are not yet certain and only a limited number of eucalypt species in plantations in two regions (Hawke's Bay and Marlborough) have been investigated. *Eucalyptus nitens*, a short fibre pulp species, is not grown in these two regions, as this species is planted in colder sites. Until *Pst. cloelia* reaches these plantations, the extent of impacts it may have in comparison to *P. charybdis* will not be known. The most concerning aspect for *E. nitens* pulp plantations is that *Pst. cloelia* can feed on both the waxy juvenile foliage of the heteroblastic species as well as the adult flush. Therefore, *Pst. cloelia* may damage these species while they are establishing (up to four years old) as well as when they are in their adult foliage.

In Tasmania, de Little (1979b) rarely observed niche overlap, and paropsines sharing the same host trees were generally temporally or spatially separated. An example of spatial or temporal niche separation can be seen in *Pst. agricola* and *Pst. cloelia* in Tasmania. Both species feed on the same hosts, but it is thought that *Pst. agricola* prefers wetter climates and *Pst. cloelia* drier areas (de Little 1979b). In sites with intermediate or varying climates, the species can avoid direct competition through phenological adaptation, where *Pst. agricola* defoliates trees in the wet spring, followed by *Pst. cloelia* later in the dry summer (de Little 1979b). In Tasmanian sites, the more extreme r-strategists (i.e., species with extremely high reproductive output and extremely gregarious larvae) were always locally more abundant than comparatively 'mild' r-strategists. These extreme r-strategists dominated new regrowth in unstable, disturbed sites and were considered potential pests in plantations (de Little 1979b). Two very abundant species, *Pst. bimaculata* and *Pst. agricola,* exhibit different host preferences when co-occurring in the same sites, resulting in spatial niche separation. However, when reared under competition in the laboratory, *Pst. bimaculata* (the more extreme r-strategist) displaced *Pst. agricola* on the more favourable host (de Little 1979b). Following the theory of competitive advantage due to life strategies, *Pst. cloelia* as a more extreme r-strategist with higher fecundity and extremely gregarious larvae (compared to *P. charybdis*) may outcompete *P. charybdis* on more preferred host species in New Zealand. However, this hypothesis requires further study across a greater range of host species and bioclimatic areas.

Implications for future research and management

We believe that an integrated management approach is needed to ensure the sustainability of an expanded eucalypt plantation forest industry in New Zealand. To mitigate potential risks from the presence of two serious defoliators (*P. charybdis* and *Pst. cloelia*), we suggest a four-pronged approach is needed:

1. Appropriate choice and siting of species

Research suggests that some eucalypts grown in unfavourable environments (e.g., low water and nutrient availability) may have a reduced ability to compensate for defoliation (Eyles et al. 2009; Mann 2023; Pinkard, Baillie, Patel, & Mohammed 2006; Pinkard, Baillie, Patel, Paterson, et al. 2006). Some of the eucalypt species currently trialled for dryland areas (Millen et al. 2018) may not be as drought resistant as previously assumed, which may lead to increased susceptibility to defoliation under drought stress (e.g., *E. bosistoana* (Mann 2023)) while trees might only be moderately affected when grown under more favourable conditions. Therefore, we hypothesise that paropsine damage will be worse when trees are drought stressed. In warmer/wet regions, e.g., Northland/ Bay of Plenty, damage may or may not be as severe as sufficient water might enable trees to compensate for herbivory. Hence, research is needed to test this hypothesis and define appropriate growth regions for individual species, and/or model tree responses under future climate scenarios.

2. Breeding for enhanced resistance and/or tolerance

Substantial variation in the resistance and/or tolerance to defoliation between and within eucalypt species has been observed (Mann 2023; Rapley et al. 2004). However, to fully capitalise on this genetic resource, two issues must be solved. Firstly, a standardised and comparable method for damage assessments of trees that is not entirely observer-biased (Withers et al. 2017) is needed to help screen seedlots at scale for desirable traits and assess their heritability. An initial assessment of paropsine damage using LiDAR imagery showed promising results (Mann 2023) and could be investigated further, including additional sensors, e.g., hyper-spectral tools. Current visual assessment tools, e.g., the Crown Damage Index (CDI), are limited in their accuracy, particularly above a certain tree height (Withers et al. 2017). Hence, aerial sensors may enable more accurate defoliation measurements of taller trees such as mature *E. nitens*. Secondly, potentially resistant or tolerant genotypes must be assessed in a range of controlled abiotic conditions (e.g., moisture, fertility) to quantify genotype × environment interactions. This overlaps with aspects of point one above.

3. Biological control (conservation and classical)

A range of generalist predators are known to feed on paropsine life stages and two established parasitoids attack paropsine eggs in New Zealand. The presence, abundance, and seasonal dynamics of generalist predators and existing egg parasitoids and their potential impact on populations of *Pst. cloelia* and *P. charybdis* is the subject of current research. Gaining insight into the current status of natural enemies of *P. charybdis* and *Pst. cloelia* will inform us whether natural enemies present in New Zealand have the potential to control *Pst. cloelia* and where the gaps in this control lie. Potentially, if there are times of the year when egg parasitoids are unable to control the pests, this could be compensated by improving the efficacy of natural enemies of paropsines that are already present in eucalypt plantations in New Zealand, e.g., through supplementary feeding (Mensah & Madden 1994), provision of over-wintering sites, or inundative releases (S. C. Baker et al. 2003). Additionally, several studies suggest that, besides other beneficial effects on ecosystem services (see Brockerhoff et al. 2017), increasing forest biodiversity by moving away from monocultures can decrease pest impacts and increase the effectiveness of natural enemies (e.g., Castagneyrol et al. 2014; Guyot et al. 2015; Klapwijk et al. 2016). In Australian eucalypt plantations, Steinbauer et al. (2006) found that increased habitat complexity (i.e., vegetational structure and diversity) tends to increase diversity and abundance in native parasitoid wasps. Hence, it would be worth investigating the effect of mixed tree species in eucalypt stands and considering a shift from current silvicultural practices of monoculture clear-cut towards mixed-species stands or mosaics of stands of several species.

If required, research to investigate the presence of additional classical biocontrol agents for possible future introductions to New Zealand should concentrate on host-specific agents. Sexually transmitted mites are known to specialise on certain paropsine species, but their impacts are expected to be relatively modest, such as increasing mortality during overwintering or lowering fecundity (Nahrung & Clarke 2007). Certainly, there are other natural enemies present in Australia that could be investigated for their potential as classical biological control agents of *Pst. cloelia* (Nahrung et al. 2020). *Eadya annleckieae* is one potential larval biocontrol agent, although like *Eadya daenerys*, it is assumed to undergo just one generation per annum (Pugh et al. 2020), creating delays until it could be effective and increasing the difficulty of completing the importation and host range testing phases of the classical biological control program. Encouragingly, there are more than one species of the parasitic tachinid flies, such as *F. tillyardi,* yet to be assessed in detail in Australia. While there is potential for classical biological control using Tachinidae that are already known to achieve high parasitism on *Pst. cloelia* and *P. charybdis* in the field in Australia (Colless 2012; Peixoto et al. 2018; Selman 1994; Tan et al. 2017), tachinids have a reputation for being extremely difficult to rear in containment (e.g., *Trichopoda giacomellii* (Blanchard), *Froggattimyia tillyardi*) (Bain & Kay 1989; Sands & Coombs 1999)) and establish in a new country (e.g., *Trichopoda pilipes* (Fabricius), *T. pennipes* (Fabricius), *Bogosia antinorii* Rondani) (Waterhouse 1998). Moreover, many tachinid species have a much broader host range than endoparasitic Hymenoptera (which tend to be highly host-specific), giving tachinids a reputation as being risky with respect to the safety of non-target species. Several species with broad host ranges across multiple families were introduced as biological control agents prior to current host specificity guidelines and some species have resulted in unacceptable non-target impacts (e.g. *Trigonospila brevifacies* (Hardy), *Compsilura concinnata* (Meigen)) (Boettner et al. 2000; Kellogg et al. 2003; Munro 1997, 1998; Munro & Henderson 2002; Stamp & Bowers 1990). Nevertheless, host-specific tachinids have also been utilised effectively as biological control agents elsewhere (e.g., *Myiopharus doryphorae* (Riley) and *M. aberrans* (Townsend) (López et al. 1997)). Tachinidae are one of the largest families of Diptera and, as an extremely diverse group, have posed a challenge to taxonomists (O'Hara 2013), leaving the potential for cryptic species (O'Hara & Cerretti 2016). Therefore, currently described tachinid parasitoids of Australian paropsines do hold promise as biological control agents for New Zealand in the future, but will require investment in taxonomic revision and understanding of host range and biology for rearing to support effective risk assessments and, potentially, releases.

Understanding *Pst. cloelia* phenology, temperature-dependent development and biology is crucial for the selection of appropriate and effective biological control agents. A number of studies have now concluded that biological control effectiveness relies on matching the parasitoid with its target species (Gerard et al. 2021; Rowbottom et al. 2013; Schröder et al. 2021; Zilahi-Balogh et al. 2012). As shown above, there are some prospects for advancing classical biological control of *Pst. cloelia*, but the eucalypt growing industry in New Zealand will first need to prioritise investment as research to support regulatory approval for the release of beneficial new organisms takes time, during which *Pst. cloelia* will continue to spread and cause damage.

4. Alternative pesticides and appropriate management thresholds

In Tasmania, IPM of paropsine pests in young plantations is based on a regression model that quantifies the relationship between pest abundance and level of defoliation in relation to defined action thresholds, i.e., the size of a 'damaging population' above which insecticide treatment is required to prevent significant damage (Carnegie et al. 2005; Elliott et al. 1992). To establish such a regression model, paropsine population levels were assessed by counting eggs and larvae on young trees early in the season to predict subsequent late-season defoliation (Elliott et al. 1992). Following the Tasmanian example, damage thresholds should ideally be determined for different economically relevant eucalypt species in New Zealand, below which growth impacts are acceptable, and action thresholds for paropsine population management be set. Objective measurement of population densities followed by quantification of defoliation (e.g., with LiDAR), then tree growth, is required to obtain these thresholds. A number of challenges exist that complicate these relationships, including separating the relative impacts of multiple pests present on the trees as well as leaf pathogens, genetic variation in the tree, and site-specific factors, on the subsequent defoliation and growth relationships. If multiple pest species are present, such damage thresholds would need to be combined. For example, two species present at levels below the threshold may together cause sufficient damage to warrant treatment. Once more, knowledge of the target species' phenology is essential for the right timing of pest abundance assessments and will also inform the timing of management interventions, especially of some biopesticides whose effectiveness may be restricted to particular life stages (Elek & Beveridge 1999). Any promising pesticide interventions will also need to be tested for efficacy against both paropsine species, dose-response thresholds should be obtained, and application methods need to be determined in relation to efficacy, environmental risk, and cost-benefit. We recommend the eucalypt industry be involved from the outset in any development of new pesticide applications for paropsine pest management, as these will need to meet both regulatory body approvals as well as the requirements of individual companies' risk-based assessments for maintaining PEFC/FSC status for their forest products.

In the interim it would be advantageous for the forest industry to monitor and report the distribution and hosts being attacked by *Pst. cloelia* to inform the risk it poses to different eucalypt species growing in different regions (Weser et al. 2022). Reporting the life stages present during these observations will help scientists understand how climate and regional characteristics alter *Pst. cloelia* phenology, defoliation, and impacts on productivity. This would be especially important should the pest reach warmer northern regions where three or more generations may cause several defoliation events during one season. Existing tools such as iNaturalist New Zealand (https://inaturalist.nz/) are suitable for such reporting and we continue to encourage this (Weser et al. 2022).

Conclusions

We believe that *Pst. cloelia* has the potential to become as damaging in New Zealand as *P. charybdis* and may significantly reduce growth rates of preferred eucalypt species, such as the *E. bosistoana* and *E. tricarpa* in the *Symphyomyrtus* section Adnataria. Niche separation may well limit direct competition between the two species, with *P. charybdis* preferring species in the Maidenaria section. Collectively, a higher reproductive output plus a higher survival rate of immature stages due to advantageous life strategies and a lack of host-specific natural enemies could lead to more frequent population outbreaks and consequently higher damage potential of *Pst. cloelia* compared to *P. charybdis.* This outcome may be more likely to occur under climatic conditions that induce growth stress in the trees. As *Pst. cloelia* larvae are known to feed on both flush juvenile and adult leaves of heteroblastic eucalypt species, *Pst. cloelia* could create additional damage to *E. nitens* plantations beyond what is currently occurring from *P. charybdis*. An integrated management approach that employs multiple strategies, such as biological control agents, breeding trees for resistance, choice and siting of species, and/or use of new pesticides applied at set damage thresholds could result in significant economic benefits and resilience to the impacts posed by these paropsines. Research is needed in areas where we lack sufficient knowledge. We recommend the eucalypt forest industry does not delay taking the necessary steps towards supporting an integrated pest management project against *Pst. cloelia.*

Endnotes

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Competing interests

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Authors' contributions

CW carried out the main part of the work, including establishing the concept and design of the review, collating and reviewing the literature, and writing and editing the manuscript. TMW updated numbers of eucalypt-feeding species established in New Zealand to date and added knowledge on eucalypts, pest species, pesticide application, and biocontrol agents. TMW and SMP critically improved and edited the manuscript.

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