Current and potential threat of psyllids (Hemiptera: Psylloidea) on eucalypts

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Abstract: The introduction of Australian psyllids to non-native ranges across the globe is continually increasing. This is due to an increase of global trade and human movement, exacerbated by climate change. Several psyllids have been recorded as pests of eucalypts in the native range of these trees. With the current trend of eucalypt pest introductions, there is a concern that many more eucalypt-feeding psyllids in Australia will in time be introduced and become pests in eucalypt growing regions of other continents. Here we examine the current and potential threat of psyllids on eucalypts. Specifically, we consider the diversity of eucalypt psyllids in their native range and those eucalypt psyllids that have been introduced outside Australia and become pests in their new ranges. In addition, the potential pathways and characteristics of these invasive psyllids are discussed.

Keywords: plantation forests; insect pests; invasive species; pathways

1 Introduction

Psyllids or jumping plant-lice are minute (1–10 mm) phloem-feeding insects of the superfamily Psylloidea (Hollis 2004). Immatures can be free-living or develop in galls they induce or under lerps they build. Rarely, they can develop under lerps from other species or live under bark, and there is one species known to be an inquiline in galls induced by other species (Hodkinson 1974, 1984; Yang et al. 2001; Hollis 2004; Burckhardt 2005). Psyllids have generally narrow host ranges, i.e. the immatures can complete their development only on a single or a few related plant species (Hollis 2004; Burckhardt 2005; Hodkinson 2009). Plants are often reported as 'hosts' based on the presence of adult psyllids, which, however, may represent casual associations (Burckhardt et al. 2014). Psyllids are closely related to whiteflies, aphids and scale insects, and collectively they form the monophyletic suborder Sternorrhyncha (Hemiptera) (Gullan and Martin 2003). Within Psylloidea, currently eight families (Aphalaridae, Calophyidae, Carsidaridae, Homotomidae, Liviidae, Phacopteronidae, Psyllidae and Triozidae) and 20 subfamilies are recognised (Burckhardt and Ouvrard 2012; Ouvrard 2020). Around 4000 psyllid species have been described but more than twice this number can be expected globally (Burckhardt and Queiroz 2020).

Forty psyllid species have been reported of economic relevance worldwide, mostly in agriculture (Burckhardt 1994; Percy 2014). There is an increasing focus on psyllids given their serious threat to agriculture as vectors of plant pathogens, as economically important agricultural and forestry pests and as potential control organisms of invasive weeds (Burckhardt and Ouvrard 2012). Psyllids can harm their hosts directly or indirectly. The feeding sometimes physically damages plant tissue, resulting in necrosis or leaf distortion, defoliation and die back. The removal of large quantities of plant sap furthers these effects and weakens the plant making it more susceptible to attack from other pests. When population levels are high, the secreted honeydew can damage leaves and fruits. The induction of galls by physical and/or biochemical stimuli can further harm the plant. Indirect effects are the growth of sooty mould on the secreted honeydew and the transmission of bacterial plant pathogens (Hodkinson 1974, 2009; Burckhardt 1994; Hollis 2004; Munyaneza 2010; Hall et al. 2013). The economically most devastating psyllid vectors are *Diaphorina citri* Kuwayama (Liviidae), vectoring *Candidatus* Liberibacter spp. causing Huanglongbing (HLB, citrus greening) on citrus (Halbert and Manjunath 2004; Hall et al. 2013), *Bactericera cockerelli* (Šulc) (Triozidae), vectoring *Candidatus* Liberibacter solanacearum causing zebra chip disease on potato (ZC) (Liefting et al. 2009; Munyaneza 2010) as well as *Cacopsylla pyricola* (Foerster) and related species, vectors of *Candidatus* Phytoplasma spp., responsible for pear decline (Burckhardt and Hodkinson 1986; Cho et al. 2017).

The economic impact of psyllids can be enormous. For example, HLB was responsible for the destruction of more than 14.8 million plants in the State of São Paulo, Brazil and for the increase in production costs that can vary from US$ 97.40/ha/year to US$ 472.12/ha/year (Fukuda et al. 2010; Kleffmann 2012). In addition, losses equivalent to US$ 4.5 million were realised in Florida and 8000 jobs were lost due to HLB (Hodges and Spreen 2012). In New Zealand, the potato industry lost US$ 96 million since the arrival of ZC in 2006 (Ogden 2011), while in the southwestern and central United States, cost of production to manage *B. cockerelli* averaged US$ 300 per acre (Guenthner et al. 2011). Henceforth, some species are listed and recommended for regulation as quarantine pests (EPPO 2018).

Several psyllid species have been reported to inflict serious damage to forest plantations. Their economic importance is, however, generally geographically limited. A notable exception are the eucalypt psyllids. Eucalypts, which include *Angophora* (12 spp.), *Corymbia*

(~ 95 spp.) and *Eucalyptus* (~ 730 spp.) (Nicolle 2019) are native to Australia, Papua New Guinea, Timor-Leste, Indonesia and the Philippines, but are planted globally with multiple purposes, such as a source of hardwood timber, paper, pulp, bioenergy (firewood, charcoal, alcohol) as well as essential oils (Jacobs 1981; Eldridge et al. 1993; Turnbull 1999).

Around 400 species of Psylloidea have been recorded from Australia representing all eight currently recognised families. Of these, Aphalaridae with 280 species (= 69.7%) is by far the largest family followed by Triozidae with 62 species (= 15.4%) and Psyllidae with 44 species (= 10.9%). Australian Aphalaridae is mostly composed of Spondyliaspidinae (279 species) and only a single species representing the Rhinocolinae (Hollis 2004; Ouvrard 2020). The Spondyliaspidinae constitutes a predominantly Australian taxon of 24 genera and 308 species usually associated with Myrtaceae (exceptions are *Boreioglycaspis*, *Ctenarytaina* and *Eurhinocola*) (Burckhardt 1991). Currently, 268 species are known to develop on eucalypts: 257 Spondyliaspidinae and 11 Triozidae (Ouvrard 2020) (Table 1).

Several psyllid species have been recorded as pests of eucalypts in their native and, in particular, introduced ranges. There is some concern that additional Australian eucalypt psyllids may be introduced into other continents and become pests. Individuals of two *Ctenarytaina* species in Spain have been shown to carry *Candidatus* Phytoplasma mali but there was no evidence for transmitting the pathogen (Rosa García et al. 2013). Although they do not seem to transmit plant pathogens, eucalypt psyllids can be of major economic importance in forestry. The purpose of this review is to examine the current and potential threat of psyllids on eucalypts. We discuss the diversity of eucalypt psyllids in their native and introduced ranges, their pest status, as well as likely pathways and characteristics of these invasive psyllids.

Table 1. Psyllid genera (and number of species) associated with eucalypt genera (and subgenera) and type of immature life style (Hollis 2004; Ouvrard 2020 and publications cited therein). The species number per genus represents the species for which eucalypts are confirmed or likely hosts. *Aphalara tecta* Maskell, 1898, a lerp-builder on *Eucalyptus bridgesiana* is not included in the table, as its identity is uncertain (Hollis 2004).

Psyllid genus (# species)	Eucalypt host genus (subgenus)	Type of immature
Agelaeopsylla Taylor, 1990 (5)	*Angophora*, *Corymbia* (*Blakella*, *Corymbia*)	free-living
Anoeconeossa Taylor, 1987 (18)	*Eucalyptus* (*Eucalyptus*, *Eudesmia*, *Symphyomyrtus*)	free-living
Australopsylla Tuthill and Taylor, 1955 (2)	*Eucalyptus*. (*Eucalyptus*, *Symphyomyrtus*)	lerp-builder (1), gall-inducer (1)
Blastopsylla Taylor, 1985 (9)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	free-living
Blepharocosta Taylor, 1992 (7)	*Eucalyptus* (*Eucalyptus*, *Idiogenes*)	unknown
Cardiaspina Crawford, 1911 (24)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	lerp-builders
Creiis Scott, 1882 (8)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	lerp-builders
Cryptoneossa Taylor, 1990 (4)	*Corymbia* (*Blakella*), *Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	living under lerps of other species
Ctenarytaina Ferris and Klyver, 1932 (6)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	free-living
Dasypsylla Froggatt, 1900 (1)	*Eucalyptus* (*Symphyomyrtus*)	lerp-builder
Eucalyptolyma Froggatt, 1901 (5)	*Angophora*, *Corymbia* (*Blakella*, *Corymbia*)	lerp-builders
Glycaspis Taylor, 1960 (137)	*Corymbia* (*Blakella*), *Eucalyptus* (*Eucalyptus*, *Eudesmia*, *Symphyomyrtus*)	lerp-builders (119), gall-inducers (18)

Hyalinaspis Taylor, 1960 (5)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	lerp-builders
Kenmooreana Taylor, 1984 (3)	*Eucalyptus* (*Eudesmia*, *Symphyomyrtus*)	lerp-builders
Lasiopsylla Froggatt, 1900 (4)	*Corymbia* (*Blakella*), *Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	lerp-builders
Phellopsylla Taylor, 1960 (5)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	under bark (2), under sticky secretion on bark (1)
Phyllolyma Scott, 1882 (5)	*Eucalyptus* (*Symphyomyrtus*)	lerp-builders
Platyobria Taylor, 1987 (10)	*Corymbia* (*Corymbia*), *Eucalyptus* (*Acerosae, Eucalyptus, Eudesmia, Idiogenes*, *Symphyomyrtus*)	free-living (3), gall-inducer (1)
Schedotrioza Tuthill and Taylor, 1955 (12)	*Eucalyptus* (*Eucalyptus*, *Symphyomyrtus*)	gall-inducers
Spondyliaspis Signoret, 1879 (5)	*Eucalyptus* (*Symphyomyrtus*)	lerp-builders

2 Psyllids on eucalypts

2.1 Native range

Australia has a diverse psyllid fauna associated with eucalypts (Table 1), reflecting the species richness of the eucalypt flora. Eucalypts are confirmed (by the presence of immatures) or likely hosts of 275 psyllid species from 20 genera (Table 1). Of the 275 species only three have not been reported from Australia. *Blastopsylla degluptae* Taylor is native to Papua New Guinea (Taylor 1985), and *Ctenarytaina peregrina* Hodkinson and *Platyobria biemani* Burckhardt, Queiroz and Malenovský are currently known only from Europe but most likely represent introductions from Australia (Hodkinson 2007; Burckhardt et al. 2014). With 137 species, *Glycaspis* is, by far, the most species rich genus of eucalypt psyllids followed by *Cardiaspina* (24), *Anoeconeossa* (18) and *Schedotrioza* (12). The enormous diversity of *Glycaspis* compared to that of the other genera is above all the result of the very comprehensive collections made by the late K.M. Moore in 1966–1967, 1972 and 1974, covering the whole of Australia, and his taxonomic papers based on the material (cf. Hollis 2004 for references). Similar, intensive field work will be necessary to assess the diversity of the other genera. Spondyliaspidinae species are generally oligophagous. It is, therefore, not surprising that there are no clear host patterns at the generic level. Most genera of Spondyliaspidinae are associated with more than one genus/subgenus of eucalypts (Table 1). *Agelaeopsylla* and *Eucalyptolyma* are restricted to the genera *Angophora* and *Corymbia*. *Blepharocosta* is reported from the subgenera *Eucalyptus* and *Idiogenes* but not much is known about these, and the host range may be broader. All the other genera are associated with eucalypts of *Symphyomyrtus* and often also other subfamilies.

Of the 275 species of eucalypt psyllids, information on the biology of immatures is known for 261 species. Of these 69% are lerp-builders, 16% free-living, 12% gall-inducers, 2% live under vacated lerps of other species and 1% develop under or on bark (Table 1). Free-living immatures feed on actively growing shoots and foliage and are usually covered in flocculent waxy secretions, a protection against desiccation and natural enemies (Hollis 2004). Free-living immatures can be found in five genera of eucalypt psyllids (Table 1).

Over two thirds of the known eucalypt psyllids are lerp-builders, hence their name lerp insects. The lerp is a hard scale-like structure under which the immature feeds and develops. Lerps are a very characteristic feature of Australian Spondyliaspidinae (Burckhardt 1991; Hollis 2004) but they can be found also in other psyllid taxa, such as in the East Asian *Celtisaspis* (Aphalaridae, Pachypsyllinae), the Neotropical *Euphalerus* or the African *Retroacizzia* (both Psyllidae, Macrocorsinae). The first instar builds the lerp soon after it begins to feed by weaving the anal exudates to form the basic structure. The lerp can be attached to the leaf or stem surface at one or more points. The size of the lerp is increased by the subsequent instars (Hollis 2004). Lerps display a large variety of shapes, colours and textures (Froggatt 1923; Hollis 2004) which are generally characteristic for each genus and, to a lesser extent, species. Examples include the conical, fluffy lerps of *Glycaspis* (Moore 1975), the lace-shaped lerps of *Cardiaspina* (Taylor 1962), the circular or horn-shaped lerps of *Creiis* (Froggatt 1923) or the clam-shaped lerps of *Spondyliaspis* (Bush et al. 2016). The lerps provide protection from harsh, semi-arid climatic conditions and predators (Collet 2001; Hollis 2004).

Gall induction occurs among 13% of eucalypt psyllids, only slightly less common than in psyllids in general (15%) (Hodkinson 1984). All members of *Schedotrioza* induce closed galls on the upper side of the leaves ranging from globular to elongate elliptical shapes. The first instar induces the gall by feeding, usually near the place where it hatched from the egg

(Taylor 1990). Within Spondyliaspidinae, gall induction occurs in three genera (Table 1) which have also free-living or lerp-building species. *Platyobria maddeni* Taylor, induces shallow pit galls in young leaves (Taylor 1987). The immatures of *Australopsylla carinata* Froggatt and *Blepharocosta marmorata* (Froggatt) induce a curling of the leaf tip (Hollis 2004). Within *Glycaspis*, gall induction is restricted to species of the subgenus *Synglycaspis*, which also secrete sugary material that plugs the gall ostiole. The galls are usually globular (Sharma et al. 2015). As with lerps, galls help to protect the immature against desiccation and the attack of predators, but in addition constitute a source of high-quality diet (Hodkinson 1984; Burckhardt 2005).

Within Australia, only a small number of eucalypt psyllids are reported as pests (Burckhardt 1994), as the psyllid populations are usually controlled by natural enemies such as parasitoids and predators (Hodkinson 1974; Hollis 2004). Psyllids reach injurious population densities in Australian eucalypt plantations when parasitoids and other natural enemies are suppressed or eliminated by their own natural enemies such as hyperparasitoids and generalist predators (Clark 1962; Nylin 2001; Steinbauer et al. 2015). Nylin (2001) also reported that low temperature can reduce parasitism.

Cardiaspina spp. are the most devastating psyllid pests of eucalypts in Australia and are reported to cause considerable loss in eucalypt plantations (Steinbauer et al. 2014). Periodic outbreaks of several species were reported since the early 1900s (Taylor 1962; Clark 1962; Morgan and Bungey 1981; Campbell 1992; Collet 2001). Most of these outbreaks concern *E. camaldulensis* Dehnh., a dominant *Eucalyptus* species in the whole of continental Australia (Hirsch et al. 2019). Other eucalypt species severely affected by *Cardiaspina* spp. are *E. grandis* W.Hill and *E. tereticornis* Sm. (Stone et al. 1998; Hall et al. 2015; Gherlenda et al.

2016). Another lerp-building psyllid, *Creiis lituratus* (Froggatt) constitutes a severely damaging pest of commercial eucalypt plantations, notably of young *E. dunnii* Maiden (Carnegie and Angel 2005; Stone et al. 2010). *Glycaspis* spp. are reported to cause serious defoliation of *E. saligna* Sm. and *E. delegatensis* F.Muell. ex R.T.Baker in native forests. Documented outbreaks of eucalypt psyllids in Australia are strongly correlated to drought-induced stress (White 1969; Queiroz et al. 2012), but stress from waterlogged conditions were also found to exacerbate *C. lituratus* attack on *E. dunnii* (Stone et al. 2010). Lack of proper management coupled with recurrent psyllid attacks can result in death of *E. dunnii* trees.

Eucalypts in their native environments have evolved physical and chemical traits making them resistant or less vulnerable to psyllid attack (Henery 2011). These include the presence of non-structural waxes (e.g., epicuticular wax) on some eucalypts (Brennan et al. 2001). Some resistant eucalypts are characterized by thick epicuticular wax that hampers the adherence and stylet probing by psyllids. *Ctenarytaina spatulata* Taylor and *Glycaspis brimblecombei* Moore avoid the waxy leaves of *E. globulus* Labill. which are nearly impossible to probe (Brennan and Weinbaum 2001; Queiroz et al. 2012). There are also chemical defences that may act on psyllids. *Eucalyptus camaldulensis* produces high amounts of phenolic compounds that negatively affect the population of *Cardiaspina albitextura* Taylor (Taylor 1997).

2.2 Introduced eucalypt psyllids

To-date, 14 Australian eucalypt psyllids have been introduced into other continents (Paine et al. 2011; Queiroz et al. 2012; Burckhardt et al. 2014; Bush et al. 2016) (Table 2). New Zealand has the highest number (10) of introduced species namely *Anoeconeossa communis*

Taylor, *Blastopsylla occidentalis* Taylor, *Cardiaspina fiscella* Taylor, *Cryptoneossa triangula* Taylor, *Creiis lituratus, Ctenarytaina eucalypti* (Maskell), *C. spatulata, Eucalyptolyma maideni* Froggatt, *Glycaspis granulata* (Froggatt) and *Phellopsylla formicosa* (Froggatt) (Withers and Bain 2009; Hurley et al. 2016; Martoni et al. 2016, 2018). This may be expected due to its geographic proximity, suitable climatic conditions, large trade volumes with Australia and that eucalypts are widely planted trees in the landscape. The United States of America (USA) is second, with seven species (*Blastopsylla occidentalis, Cardiaspina fiscella, Cryptoneossa triangula* Taylor, *Ctenarytaina eucalypti, C. spatulata, Eucalyptolyma maideni* and *Glycaspis brimblecombei*) (Paine et al. 2011). Brazil with the largest area of eucalypt plantations has four species (*Blastopsylla occidentalis, Ctenarytaina eucalypti, C. spatulata* and *Glycaspis brimblecombei*) (Queiroz and Burckhardt 2007; Queiroz et al. 2018). The same four species are now present in most of the eucalypt growing regions of the world, while the distribution of the others is more limited to not more than two countries or continents (Table 2).

The pest status of the introduced eucalypt psyllids varies between species and regions. *Blastopsylla occidentalis* and *Ctenarytaina spatulata* colonize a variety of eucalypt species, but rarely cause significant damage (Brennan et al. 2001), though they may be very destructive in nurseries (Burckhardt et al. 1999; Queiroz et al. 2012). In the USA (California), *Ctenarytaina eucalypti* caused a significant production loss (30%) in commercial plantations of *E. pulverulenta* Sims (Dahlsten et al. 1998). Though it was observed on several eucalypt species in Brazil, economic impact was only realised on *E. dunnii* in the southern part of Brazil (Santana et al. 1999; Queiroz and Burckhardt 2007). In Europe, *Ctenarytaina eucalypti* inflicted severe damage to plantations of *E. globulus* (Azevedo and Figo 1979; Valente et al. 2004). In the USA (California) *G. brimblecombei* caused substantial damage on *E.*

Table 2. Introduced eucalypt psyllids established as pests outside their native range (Hollis 2004; Burckhardt et al. 1999; Neser & Millar 2007; Percy et al. 2012; Queiroz et al. 2012; Bush et al. 2016; Queiroz et al. 2018; Ouvrard 2020 and publications cited therein).

Psyllid name	Native distribution	Introduced distribution	Host species in introduced regions
Anoeconeossa communis Taylor, 1987	Australia (New South Wales, Northern Territory, Queensland, South Australia, Western Australia)	New Zealand	*E. botryoides*, *E. dunnii*
Blastopsylla occidentalis Taylor, 1985	Australia (New South Wales, Queensland, South Australia, Western Australia)	Argentina (Entre Ríos, Santiago del Estero), Brazil (Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Paraná, São Paulo), Burundi, Cameroon, Chile, China (Guangdong, Guangxi, Hong Kong), Egypt, Israel, Italy, Kenya, Mexico, New Zealand, Nicaragua, Spain, South Africa, Turkey, USA (California, Florida, Hawaii), Yemen	*E. blakelyi*, *E. brassiana*, *E. camaldulensis*, *E. forrestiana*, *E. globulus*, *E. gomphocephala*, *E. grandis*, *E. microneura*, *E. microtheca*, *E. nicholii*, *E. oleosa*, *E. rudis*, *E. saligna*, *E. spathulata*, *E. tereticornis*, *E. urophylla*, *E. viminalis*
Cardiaspina fiscella Taylor, 1961	Australia (Australian Capital Territory, New South Wales, Victoria)	New Zealand	*E. botryoides*, *E. grandis*, *E. saligna*

Creiis lituratus (Froggatt, 1900)	Australia (New South Wales)	New Zealand	*E. botryoides*, *E. dunnii*
Cryptoneossa triangula Taylor, 1990	Australia (Australian Capital Territory, New South Wales, South Australia)	New Zealand, USA (California, Oregon)	*E. citriodora*
Ctenarytaina eucalypti (Maskell, 1890)	Australia (Australian Capital Territory, New South Wales, South Australia, Tasmania, Victoria, Western Australia)	Bolivia, Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), Bolivia, Chile, Colombia, France, Germany, Great Britain, Hungary, Ireland, Italy, New Zealand, Papua New Guinea, Portugal (Azores, Madeira, mainland), South Africa, Spain, Sri Lanka, Switzerland, USA (California, Oregon)	*E. benthamii*, *E. bicostata*, *E. camaldulensis*, *E. cinerea*, *E. dunnii*, *E. globulus*, *E. maidenii*, *E. nitens*, *E. pulverulenta*
Ctenarytaina peregrina Hodkinson, 2007	unknown	France, Germany, Great Britain, Hungary, Ireland, Italy	*E. aggregata*, *E. dunnii*, *E. parvula*
Ctenarytaina spatulata Taylor, 1997	Australia (Australian Capital Territory, New South Wales, South Australia, Tasmania, Victoria)	Argentina (Entre Ríos), Brazil (Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), France, Great Britain, Ireland, Italy, New	*E. alba*, *E. amplifolia*, *E. camaldulensis*, *E. dalrympleana*, *E. deanei*, *E. globulus*, *E. grandis*, *E. microcorys*, *E. nitens*, *E. maidenii*, *E. parvifolia*, *E.*

		Zealand, Portugal, Spain, Uruguay, USA (California)	*pellita*, *E. resinifera*, *E. robusta*, *E. rostrata*, *E. saligna*, *E. tereticornis*, *E. urophylla*, *E. viminalis*
Eucalyptolyma maideni Froggatt, 1901	Australia (Australian Capital Territory, New South Wales, South Australia)	New Zealand, USA (California)	*E. botryoides*, *E. citriodora*, *E. maculata*, *E. saligna*
Glycaspis brimblecombei Moore, 1964	Australia (Australian Capital Territory, New South Wales, Queensland, South Australia, Victoria)	Algeria, Argentina (Entre Ríos), Brazil (Bahia, Distrito Federal, Espírito Santo, Goiás, Mato Grosso do Sul, Minas Gerais, Paraná, Pernambuco, Rio Grande do Sul, Santa Catarina, São Paulo, Tocantins), Chile, Ecuador, France (Corsica, mainland), Greece, Israel, Italy, Madagascar, Mauritius, Mexico, Montenegro, Morocco, Peru, Portugal, South Africa, Spain, Syria, Tunisia, Turkey, USA (California, Florida, Hawaii, Oregon), Venezuela, Zambia, Zimbabwe	*E. bridgesiana*, *E. camaldulensis*, *E. camphora*, *E. dealbata*, *E. diversicolor*, *E. globulus*, *E. mannifera*, *E. mannifera maculosa*, *E. nitens*, *E. sideroxylon*, *E. tereticornis* and several hybrids of *E. camaldulensis* with *E. grandis* or *E. urophylla*

Glycaspis granulata (Froggatt, 1901)	Australia (New South Wales)	New Zealand	*E. saligna*
Phellopsylla formicosa (Froggatt, 1900)	Australia (New South Wales)	New Zealand	*E. saligna*
Platyobria biemani Burckhardt, Queiroz & Malenovský, 2014	unknown	Greece, Israel	*E. camaldulensis*
Spondyliaspis cf. *plicatuloides* (Froggatt, 1900)	Australia (New South Wales, South Australia, Victoria)	Eswatini, Mozambique, South Africa	*E. dunii, E. grandis, E. microcorys, E. sideroxylon* and hybrids with *E. grandis* and *E. urophylla*

camaldulensis (Brennan et al. 1999). *Glycaspis brimblecombei* is also responsible for serious damage in many other countries, such as Brazil and Colombia (Queiroz and Burckhardt 2007; EPPO 2013; Rodas et al. 2014). Withers (2001) reported infestations of *E. saligna* and *E. botryoides* Sm. in New Zealand caused by *Cardiaspina fiscella.* Additionally, *Eucalyptolyma maideni* and *Cryptoneossa triangula* can cause harm to their hosts in producing large quantities of honeydew, but no tree death has been reported (Paine 2016).

The high populations and resulting damage of these introduced psyllid species are mostly due to insufficient or absent host resistance in the planted eucalypts and the absence of natural enemies (Lodge 1993; Wingfield et al., 2008; Branco et al. 2014; Hurley et al. 2016), a phenomenon commonly referred to as the enemy-release hypothesis (ERH) (Jeffries and Lawton 1984). Other bottom-up factors such as the effect of monoculture in eucalypt production can also favour high populations of invasive pests. Exotic eucalypts are grown in plantations of large monocultures with low genetic diversity, which can result in the trees being more vulnerable to invasive pests than they would be in a natural system (van Driesche 2006; Henery 2011). In other cases, outbreaks of psyllid pests are influenced by large scale abiotic factors such as drought or weather mediated changes in the degree of insect-plant synchrony (van Driesche 2006).

The rate at which eucalypt psyllids have been introduced to new ranges and become pests has risen exponentially since the late 1980s (Figure 1). This represents a serious threat to eucalypt plantations worldwide. Burckhardt et al. (1999) recorded three eucalypt psyllid species more or less simultaneously introduced into Brazil and Uruguay. Hurley et al. (2016) reported a five-fold increase in the rate of new introduced *Eucalyptus* pests since the 1980s. First reports of invasive eucalypt psyllids outside their native ranges have thus far been recorded from

New Zealand, USA, Greece, South Africa and Ireland (Figure 1). Indications are that the increased rate of introduction of invasive species, including eucalypt psyllids, will likely continue unless comprehensive global measures are implemented (Paine et al. 2011; Garnas et al. 2012).

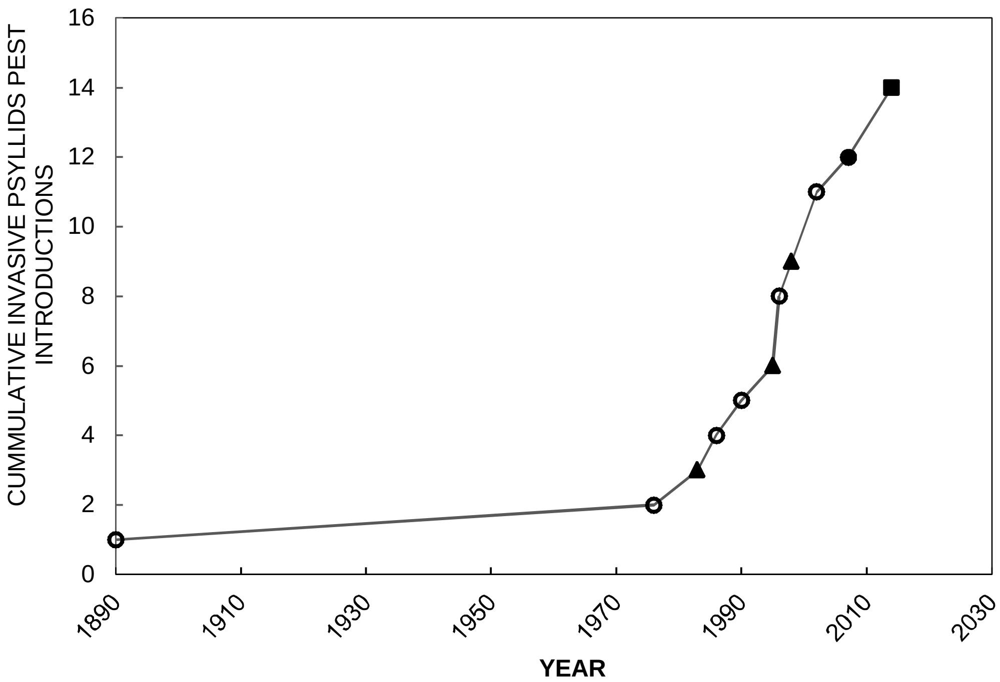

Figure 1. Cumulative introduction of eucalypt psyllids outside their native range of Australia. Symbols indicate the country of first detection: New Zealand (open circle): *Ctenarytaina eucalyptii* (1890), *Blastopsylla occidentalis* (1976), *Glycaspis granulata* (1986), *Ctenarytaina spatulata* (1990), *Cardiaspina fiscella, Eucalyptolyma maideni* (1996), *Anoeconeossa communis* and *Creiis lituratus* (2002); USA (filled triangle): *Ctenarytaina longicauda* (1983), *Cryptoneossa triangula* (1995), *Glycaspis brimblecombei* (1998); Ireland (filled circle): *Ctenarytaina peregrina* (2007); South Africa and Greece (filled square*): *Spondyliaspis* cf. *plicatuloides* (2014, South Africa) and *Platyobria biemani* (2014, Greece). Adapted from Hurley et al. (2016). *Eucalypt psyllids reported in different countries in the same year.

The speed of the invasion events has also increased, and this is likely due to fast transport systems, global trade and expansion of eucalypt plantations (Wingfield et al. 2008). A study by Queiroz et al. (2013) using Environmental Distance modelling predicted that *G.*

brimblecombei will expand into new territories, colonising suitable areas in Africa, Europe and South America. *Spondyliaspis* cf. *plicatuloides* (Froggatt) was first reported outside Australia in South Africa in 2014 (Bush et al. 2016) and there are subsequent unpublished reports of its presence in neighbouring countries (e.g., Eswatini and Mozambique). Its biology and ecology, as well as the threat to commercial *Eucalyptus* plantations, are currently not known. Of concern is the large number of other eucalypt psyllids in Australia that could potentially be introduced and whose biology and potential impact is not known. In addition to the described species, there are probably just as many undescribed eucalypt psyllid species in Australia (Burckhardt, pers. obs.).

3 Pathways of introduction

Despite the countermeasures to prevent the introduction of insect pests through traded agricultural products, biological invasions continue to occur worldwide, even in countries with robust biosecurity and quarantine regimes (Biosecurity Australia 2009). Consequently, a better understanding of the pathways and patterns for the spread of invasive insect pests is needed to prevent new invasions more efficiently (Lombaert et al. 2010; Liebhold et al. 2012; Essl et al. 2015; Bertelsmeier at al. 2018; Javal et al. 2019). When major entry routes of invasive pests are known, measures can be put in place to manage these pathways through quarantine and phytosanitary regulations (Essl et al. 2015). Specific studies to investigate common or likely pathways for invasive eucalypt psyllids are lacking. Given the expected increase in the introduction of psyllids around the world, this is clearly an important knowledge gap that needs to be addressed.

Human assisted movement, including inert dispersal with plants for planting, has been recognized as a common pathway for forest insects (Liebhold et al. 2012; Meurisse et al.

2019). Traded plants for planting can potentially carry diverse invasive psyllid pests in different life stages. Invasive insects, including forestry and agricultural psyllids, can also be spread through the illegal movement of their host plants. The introduction of *Bactericera cockerelli* into New Zealand is a possible example, as all legal imports pass through prescribed mitigation measures verified by the Ministry of Primary Industries to avoid introduction of new insect pests (Thomas et al. 2011). Smuggling of planting material with intention of propagation is also a potential pathway for insect pest introduction.

Among human-assisted pathways that may help eucalypt psyllids to reach new areas is the in adverted transport by airplanes. This pathway concerns the mobile adults which upon landing may find their eucalypt hosts nearby. *Heteropsylla cubana* Crawford, a pest of the multipurpose crop *Leucaena leucocephala* (Lam.) de Wit (Fabaceae), is the best-known example of a psyllid rapidly dispersing around the globe. Before 1979, *H. cubana* was restricted to Central America and the Caribbean. In 1979 the species was collected in the Philippines in wind propelled insect nets installed in cargo airplanes (Muddiman et al. 1992). From there the species dispersed quickly to suitable areas in the tropics around the world (Ouvrard 2020). Another way of passive dispersal is by winds. New Zealand is downwind of prevailing winds coming from Australia and displays a large number of Australian psyllid species, including some on eucalypts (Withers and Bain 2009; Paine et al. 2011; Martoni et al. 2018).

Though not yet widely used to study eucalypt psyllid invasions, the use of population genetics data has proven to be a valuable approach in illuminating pathways of insect pest invasion and has shown the complexity of invasion dynamics (Lombaert et al. 2010; Cristescu 2015; Luo and Agnarsson 2017). For example, global routes of invasion by *G.*

brimblecombei were deciphered using COI sequences and revealed that its first introduction was into the USA, from where it appears to have spread to South America and eventually to Africa. A second independent introduction appears to have occurred on the islands of Mauritius and Reunion (Dittrich-Schröder, University of Pretoria, pers. comm.).

4 Characteristics of invasive psyllids

Comparative studies to identify functional traits promoting invasiveness are few but informative. Trait-based comparisons of eucalypt pests native to Australia and those that have established overseas (alien invasives) suggest that native and alien invasive eucalypt pests differ significantly in pathway functional traits that influence long distance movement (e.g., small body size, low diapause incidence, longer flight season, multivoltine and close association with host plant) rather than traits associated with establishment and spread (Nahrung and Swain 2015). However, functional traits (e.g. clutch size, fecundity, immature lifestyle and geographic range) that support rapid population build-up are shared between native and alien invasive pests (Nahrung and Swain 2015). This is opposed to other studies that have shown clutch size and fecundity as important reproductive qualities for invasive species in achieving high intrinsic growth rates and high population densities (Jeschke and Strayer 2008).

Interesting to note is that all eucalypt psyllids (Spondyliaspidinae) have multiple generations, a potential trait for invasives as it gives a high probability of colonising eucalypts in introduced areas. Examples include *Ctenarytaina eucalypti* and *C. spatulata* in Brazil (Queiroz and Burckhardt 2007), *C. peregrina* in the United Kingdom (Hodkinson 2007, 2009) and *Glycaspis brimblecombei* in Italy (Naples and Rome) (Laudonia et al. 2014).

Blastopsylla occidentalis has 5–6 generations per year in Cameroon (Soufo and Tamesse 2015). This trait is important in invasive species achieving high numbers.

Tolerance or resistance to insecticides, and resistance to pathogens/parasitoids, are other key traits linked to invasiveness (Wang et al. 2010; Yang et al. 2013; Wan and Yang 2016). Resistance to insecticides has been reported in some psyllids, such as the citrus psyllid, *D. citri* (Wan and Yang 2016), but there are no reports of this trait for eucalypt psyllids, although this is likely influenced by the lack of studies in this area and the lack of exposure to frequent application of insecticides (i.e. low selection pressure). Hansen et al. (2007) reported that the endosymbionts in psyllids can possibly induce resistance against parasitoids, thus improving psyllid fitness.

Specific studies on traits of eucalypt psyllids associated with invasiveness are scarce and nearly lacking. It is important that this knowledge gap is addressed, as understanding the combination of generalist and specialist life history traits of eucalypt psyllids can play a role in predicting which endemic species have the potential of becoming invasive alien pests. Such studies should include investigating mechanisms of resistance to insecticides and potential natural enemies.

5 Conclusions

There is a high diversity of psyllid species associated with eucalypts in their native range. A small number of these psyllids have been introduced into other continents where they became serious pests in eucalypt plantations with great economic impact. Of further concern is the large number of eucalypt psyllid species in Australia that could potentially become invasive pests in the future. In fact, considering the general increase in the rate at which eucalypt insects are becoming established as invasive pests worldwide, the introduction of more invasive psyllid species is highly likely.

The current challenge in mitigating insect pests, including psyllids, is that the current policies for the prevention of insect pest introductions are not sufficient, or not sufficiently implemented, to reduce insect pest movements through trade and movement of people (Lovett et al. 2016). In addition, global collaboration to develop effective preventive and management strategies is needed (Wingfield et al. 2015). Policies should aim to reduce invasive pest introductions by enforcing strict inspections starting from the origin of the product, at point of entry and even post entry (Lovett et al. 2016). For this purpose, the pathways that facilitate the invasion of eucalypt psyllid pests require further investigation to inform such policies. Furthermore, post-entry quarantine, surveillance and eradication should be enforced when the pest is still localised to prevent its spread.

Most literature on eucalypt psyllids concerns studies from outside Australia, with those from the native range being rare. As a consequence, psyllids that are reported as alien invasive pests for the first time are generally not well studied. This includes basic information on biology, host preference and natural enemies. For the sustainability of eucalypt plantation forestry worldwide, it would be highly advantageous to investigate the biological characteristics of native Australian psyllids. This includes studies that investigate the invasive characteristics of these psyllids and the use of this information to predict which species pose a higher risk to be introduced and become established as pests in new regions. These studies should also include investigating the natural enemies of these psyllids that could potentially be used in biological control programmes should these psyllid species become alien invasive pests. Importantly, the diversity of the Australian eucalypt psyllids should be further explored which could likely result in substantially increasing the number of currently described species; species that should be considered in the above-mentioned studies.

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