



Invasion history and management of *Eucalyptus* snout beetles in the *Gonipterus scutellatus* species complex

Michelle L. Schröder¹ · Bernard Slippers² · Michael J. Wingfield² · Brett P. Hurley¹

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Abstract

Gonipterus scutellatus (Coleoptera: Curculionidae), once thought to be a single species, is now known to reside in a complex of at least eight cryptic species. Two of these species (*G. platensis* and *G. pulverulentus*) and an undescribed species (*Gonipterus* sp. n. 2) are invasive pests on five continents. A single population of *Anaphes nitens*, an egg parasitoid, has been used to control all three species of *Gonipterus* throughout the invaded range. Limited knowledge regarding the different cryptic species and their diversity significantly impedes efforts to manage the pest complex outside the native range. In this review, we consider the invasion and taxonomic history of the *G. scutellatus* cryptic species complex and the implications that the cryptic species diversity could have on management strategies. The ecological and biological aspects of these pests that require further research are identified. Strategies that could be used to develop an ecological approach towards managing the *G. scutellatus* species complex are also suggested.

Keywords *Gonipterus scutellatus* · Cryptic species · Invasion history · Biological control · *Anaphes nitens* · *Eucalyptus* snout beetle

Key message

- The *Eucalyptus* snout beetle (ESB) continues to spread and impact *Eucalyptus* production worldwide.
- ESB has a confused taxonomic history and is known today to contain a number of cryptic species, which should be considered in management decisions.
- An integrated management approach is discussed for the future of ESB management.

Introduction

Eucalyptus spp. and their relatives have been extensively planted outside their native range for more than a century with planted areas expanding dramatically during the past three decades (Bennett 2011; Wingfield et al. 2015). This expansion of planted forests is partly due to the over exploitation of natural forests for timber products. The separation of *Eucalyptus* from their natural enemies and favourable abiotic conditions for growth have been key drivers contributing to the global expansion of *Eucalyptus* L'Héritier planted in intensively managed stands (Colautti et al. 2004; Jeffries and Lawton 1984; Olivier 2009).

A complex of invasive pests and diseases threatens the global planted *Eucalyptus* forest resource (Paine et al. 2011; Withers 2001). This threat is increasing, and the number of insect introductions has increased exponentially since 1986 (Hurley et al. 2016). In terms of insect pests, 42 species in 16 families have been documented feeding on *Eucalyptus* outside the native range of these trees. These pests are all of economic importance in the areas where they are invasive (Hurley et al. 2016; Nahrung and Swain 2015; Withers 2001).

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✉ Michelle L. Schröder
michelle.schroder@fabi.up.ac.za

¹ Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa

² Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, South Africa

The Eucalyptus snout beetle *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae), presently recognised as representing a cryptic species complex, was one of the first invasive insect pests on *Eucalyptus* to be recorded outside its native range (Clark 1937; Tooke 1955; Withers 2001). It was first detected in New Zealand and South Africa, in 1890 and 1916, respectively. This pest has since become a global pest of *Eucalyptus* and has spread to numerous countries on five continents (Hurley et al. 2016; Mapondera et al. 2012; Tooke 1955; Withers 2001).

Significant losses in growth and wood production have been recorded due to *Gonipterus* feeding damage in *Eucalyptus* plantations. *Gonipterus* feeding damage includes defoliation of the crown, epicormic and stunted growth, and trees may take on a stag-horned or witches broom appearance with clusters of dead shoots, resulting in significant growth loss (Lanfranco and Dungey 2001; Tooke 1955). Projections of wood loss indicate that 25% and 50% crown defoliation can result in over 20% and 85% loss in wood production, respectively, over a 10-year growth period (Reis et al. 2012).

Both the adult and larval stages of *Gonipterus* species are leaf feeding, but the larvae are responsible for most of the damage (Mally 1924). The adults (Fig. 1a) feed on the edges of the mature leaves, giving them a scalloped appearance (Fig. 1b). The larvae feed on the epidermis and mesophyll of the young leaves, leaving behind the fibrous leaf tissue forming tracks the width of the larvae (Fig. 1c) (Mally 1924). Female beetles oviposit on the young foliage of the trees in clusters of four to 20, which are covered with a frass excrement (Fig. 1c) (Mally 1924; Tooke 1955). Two classic reviews by Tooke (1955) and Jeger et al. (2018) provide details of the biology of the pest and these are not repeated here.

Gonipterus populations have been successfully managed by means of biological control (Tooke 1955). *Anaphes nitens* Girault (Hymenoptera: Mymaridae), an egg parasitoid native to Australia, was first introduced into South Africa in 1926 where it established rapidly. Releases of *A. nitens* in South Africa ended in 1950 when *Gonipterus* was considered to be under economic control (Tooke 1955). The *Gonipterus* biological control programme in South Africa proved to be so successful that it provided a global solution for the management of *Gonipterus* populations in *Eucalyptus* plantations (Béêche Cisternas and Rothmann 2000; Cadahia 1980; Clark 1931; Cordero Rivera et al. 1999; EPPO 2005; Frappa 1950; Hanks et al. 2000; Lanfranco and Dungey 2001; Miller 1927; Pinet 1986; Williams et al. 1951).

Anaphes nitens is an endoparasitic egg parasitoid of *Gonipterus* species, where the larvae feed on the yolk of the host eggs (Tooke 1955). The females oviposit a single egg into a single *Gonipterus* egg within the egg capsule. Upon adult eclosion, they have an average of 46 mature eggs, but



Fig. 1 *Gonipterus* species 2, **a** adult, **b** adult feeding damage, **c** larva and larval feeding damage, **d** dorsal view of egg capsule attached to leaf with insert of ventral view

can produce an additional 20% over the first 5 days (Santolamazza-Carbone and Cordero Rivera 2003). The entire life cycle takes 17–32 days to complete, depending on the climatic conditions (Santolamazza-Carbone et al. 2006; Tooke 1955).

Very little research towards understanding the *Eucalyptus*–*Gonipterus*–*A. nitens* interactions was published between the 1950s and 1990s. However, there has been a renewed interest in the pest and its biological control due to *Gonipterus* population outbreaks during the course of the past two decades (Huber and Prinsloo 1990; Loch 2008; Loch and Floyd 2001; Reis et al. 2012; Cordero Rivera et al. 1999; Valente et al. 2017b; Valente et al. 2004). A significant outcome of this renewed interest has been the discovery that the insect known as *G. scutellatus* throughout its invasive range represents a complex of cryptic species (Mapondera et al. 2012). This complex is currently considered to include at least eight species (Mapondera et al. 2012). Three of the cryptic species have been moved from their native range to

become invasive (Mapondera et al. 2012). These include *G. platensis* (Marelli), *G. pulverulentus* Lea and an undescribed species, currently known as *Gonipterus* sp. n. 2.

The diversity of the cryptic species in the *G. scutellatus* complex in the invaded range has important implications for its management. To understand and respond to these implications, it is important to consider the taxonomy, distribution, biology and ecology of *Gonipterus* spp. It is equally relevant to consider these issues for the widely deployed biological control agent, *A. nitens*, as well as other potential natural enemies used to manage *Gonipterus* spp. Despite the long history of this insect as a global pest of *Eucalyptus*, there has not been a review of the management approaches. The focus of this review is consequently to (1) consider the invasion history of the *G. scutellatus* species complex within the context of recent taxonomic studies that have defined species boundaries and to (2) evaluate current and (3) suggest future management strategies for the *G. scutellatus* species complex in *Eucalyptus* plantations.

Discovery of the *Gonipterus scutellatus* cryptic species complex

Taxonomic history

There was considerable confusion regarding the taxonomy of the Eucalyptus snout beetle after it was detected outside its native range (Fig. 2) (Mally 1924; Tooke 1955). It was identified as *G. scutellatus* after it was detected in New Zealand in 1890. Before the name *G. scutellatus* was accepted for the beetle detected in South Africa, it was assigned to five different names (Tooke 1955). It was first identified as *G. reticulatus* Bois. shortly after it was detected in South Africa in 1916 (Mally 1924). This initial identification was questioned, and samples were sent to Australia and the UK for further identification. In 1921, the original identification, *G. reticulatus* was confirmed by the Australian taxonomist, W.W. Froggat. Later, A.K. Marshall, Director of the UK Commonwealth Institute, identified it as *G. scutellatus* (Mally 1924). Subsequently, an additional three names were assigned to the beetle including *G. exaratus* Fåraeus, *G. rufus* Blackburn and *G. gibberus* Bois (Mally 1924). In 1926, a revision of the *Gonipterus* taxonomy by A.M. Lea concluded that the insect known in various parts of the world as the Eucalyptus snout beetle should best be treated as the single species *G. scutellatus* (Tooke 1955).

Identification of *G. scutellatus* was confounded by the confusion emerging from the identification of another *Eucalyptus*-feeding snout beetle, detected in South America. Insects in that part of the world were thought to represent two species and they were initially described as *Dacnirotatus bruchi* and *D. platensis* (Fig. 2) (EPPO 2005; Marelli

1926; Oberprieler and Caldara 2012; Rosado-Neto and Marques 1996). It was, however, later determined that they were *Gonipterus* species. These were then recorded as *G. giberrus* in Argentina, Brazil and Uruguay and *G. scutellatus* in Argentina, Brazil, Uruguay and Chile (Marelli 1927; Rosado-Neto and Marques 1996).

Gonipterus outbreaks have continued to emerge during the course of the past two decades in *Eucalyptus* plantations in Western Australia (where the pest is not native) and other countries where *A. nitens* has been used as classical biological control agent (Cordero Rivera et al. 1999; Loch and Floyd 2001; Reis et al. 2012; Tooke 1955). This led to a resurgence of research and a re-evaluation of the taxonomy of *G. scutellatus* in the twenty-first century (Mapondera et al. 2012). DNA barcoding made it possible to recognise that *G. scutellatus* represented different cryptic species (Mapondera et al. 2012). In addition, Mapondera et al. (2012) examined the morphological characteristics with the focus on the morphology of the male genitalia (Mapondera et al. 2012). Their study revealed 10 distinctly different species of which eight species are part of a cryptic species complex (Fig. 2). Five of the ten species have been described, and these include *G. balteatus*, *G. scutellatus*, *G. pulverulentus*, *G. platensis* and *G. notographus*. There are also five undescribed species, presently provided with numerical identifiers (*Gonipterus* sp. 1–5) (Mapondera et al. 2012). Given the confusion regarding the taxonomy of the beetle, for the purpose of this review, we use the term Eucalyptus snout beetle (ESB) when referring to the pest in its introduced range. Where specific mention of the cryptic species is made, the most recent taxonomic nomenclature Mapondera et al. (2012) is applied.

Invasion history

The ESB, then known as *G. scutellatus*, was first detected outside its native range in 1890, in New Zealand (Clark 1937). During the twenty-first century, ESB was reported from various *Eucalyptus*-growing countries on five continents (Fig. 3a) (Hurley et al. 2016; Withers 2001). It was first detected in South Africa in 1916 (Mally 1924) and had spread throughout the country by 1929 (Mally 1924; Tooke 1955). The pest also spread to neighbouring countries, and by 1944 it was present in Lesotho, Swaziland and Zimbabwe, and eventually northwards to, Malawi, Kenya and Uganda (Cadahia 1986; EPPO 2005; Kevan 1946; Tooke 1955). Between 1940 and 1950, it was reported on islands off the coast of Africa in Mauritius and Madagascar (Cadahia 1980; EPPO 2005; Frappa 1950; Williams et al. 1951). It has also been reported in Mozambique and St Helena, although the dates of introduction are not clear (Cadahia 1986). In 1926 the ESB was reported for the first time in South America, in Argentina (Marelli 1926; Oberprieler and Caldara 2012).

Fig. 2 Timeline summarising the taxonomic history of *Gonipterus scutellatus* species complex and the introduction of *Anaphes nitens* from 1890 to 2017. Acronyms used, NZ New Zealand, SA South Africa, SAm South America. Sources: Cadahia (1980), Cadahia (1986, 1931), Clark (1937), Cowles and Downer (1995), EPPO (2005), Haines (2006), Lanfranco and Dungey (2001), Mally (1924), Mansilla Vazquez (1992), Mapondera et al. (2012), Mazza et al. (2015), Miller (1927), Tooke (1955), Pinet (1986), Rabassa and Perrin (1995), Rodas (2018), Rosado-Neto and Marques (1996) and Williams et al. (1951)

<i>Gonipterus</i> detected in NZ	1890	The Eucalyptus snout beetle, detected in NZ, identified as <i>G. scutellatus</i>
<i>Gonipterus</i> detected in Africa (SA)	1916	SA population identified as <i>G. reticulatus</i>
	1924	NZ population identified as <i>G. exaratus</i> ; SA population identified as <i>G. rufus</i> .
<i>Gonipterus</i> detected in S-America (Argentina)	1926 – 1928	SA population identified as <i>G. gibberus</i> , thought to be a synonym of <i>G. scutellatus</i> . SA population confirmed to be <i>G. scutallatus</i> and <i>G. gibberus</i> a separate species. Two species identified in Argentina, first described as <i>Dacnirotatus bruchi</i> & <i>D. platensis</i> . Determined to be <i>Gonipterus</i> . Synonymised with <i>G. gibberus</i> . Later distinguished between <i>G. gibberus</i> and <i>G. scutallatus</i> .
<i>A. nitens</i> introduced in Africa (SA) and NZ;		
<i>A. nitens</i> established in SA not in NZ		
Second introduction of <i>A. nitens</i> in NZ	1929 – 1931	
<i>A. nitens</i> introduced in Kenya	1945	
<i>A. nitens</i> introduced in Mauritius	1946	
<i>A. nitens</i> introduced in Madagascar	1950	
<i>Gonipterus</i> in Europe	1978	
<i>A. nitens</i> introduced in Italy and France	1980's	<i>G. gibberus</i> synonymised with <i>G. scutellatus</i>
<i>Gonipterus</i> & <i>A. nitens</i> introduced in USA	1994	
<i>A. nitens</i> introduced in Spain		
<i>A. nitens</i> introduced in Portugal	1996	Two species present in SAm; <i>G. gibberus</i> in Argentina, Brazil, Uruguay and <i>G. scutellatus</i> in Argentina, Brazil, Uruguay & Chile
<i>Gonipterus</i> introduced in Hawaii	2004	
	2012	<i>G. scutellatus</i> was identified as a cryptic species complex consisting of 8 closely related species

It subsequently spread to Uruguay (EPPO 2005) and Brazil, (Rosado-Neto 1993; Rosado-Neto and Marques 1996; Wilcken et al. 2008) but was not reported from Chile until 1998 (Lanfranco and Dungey 2001). In Europe, ESB was first detected in Italy in 1975, after which it was detected in France (1978), Spain (1991) and Portugal (1995) (Cadahia 1980; Mansilla Vazquez 1992; Mazza et al. 2015; Rabasse and Perrin 1979; Pérez Otero et al. 2003). In the USA, ESB was first reported in California in 1994 (Cowles and Downer 1995; Hanks et al. 2000). In the twenty-first century, the ESB continued to spread and there were reports of the pest in China in 2003, (EPPO 2005) although its presence in that country has not been confirmed (Jeger et al. 2018). The ESB was found in Hawaii in 2004 (Haines 2006) and in Colombia

in 2016 (Rodas 2018). It has also been reported in Rwanda (Brett P. Hurley, unpublished) and is assumed to be widely spread in southern and eastern Africa.

Clarity regarding taxonomy has dramatically changed the global understanding of the distribution of the ESB (Fig. 3). Prior to 2012, it was thought that two ESB species, *Gonipterus scutellatus* and *G. gibberus*, were invasive (Fig. 3a). After the study of Mapondera et al. (2012), it became clear that three species, *G. platensis*, *G. pulverulentus* and an undescribed species *Gonipterus* sp. n. 2 were invasive (Fig. 3b). In the invasive range, *G. platensis* is known from New Zealand, South America, the USA, the Iberian Peninsula in Europe and Western Australia. *G. pulverulentus* was identified from Uruguay in South America

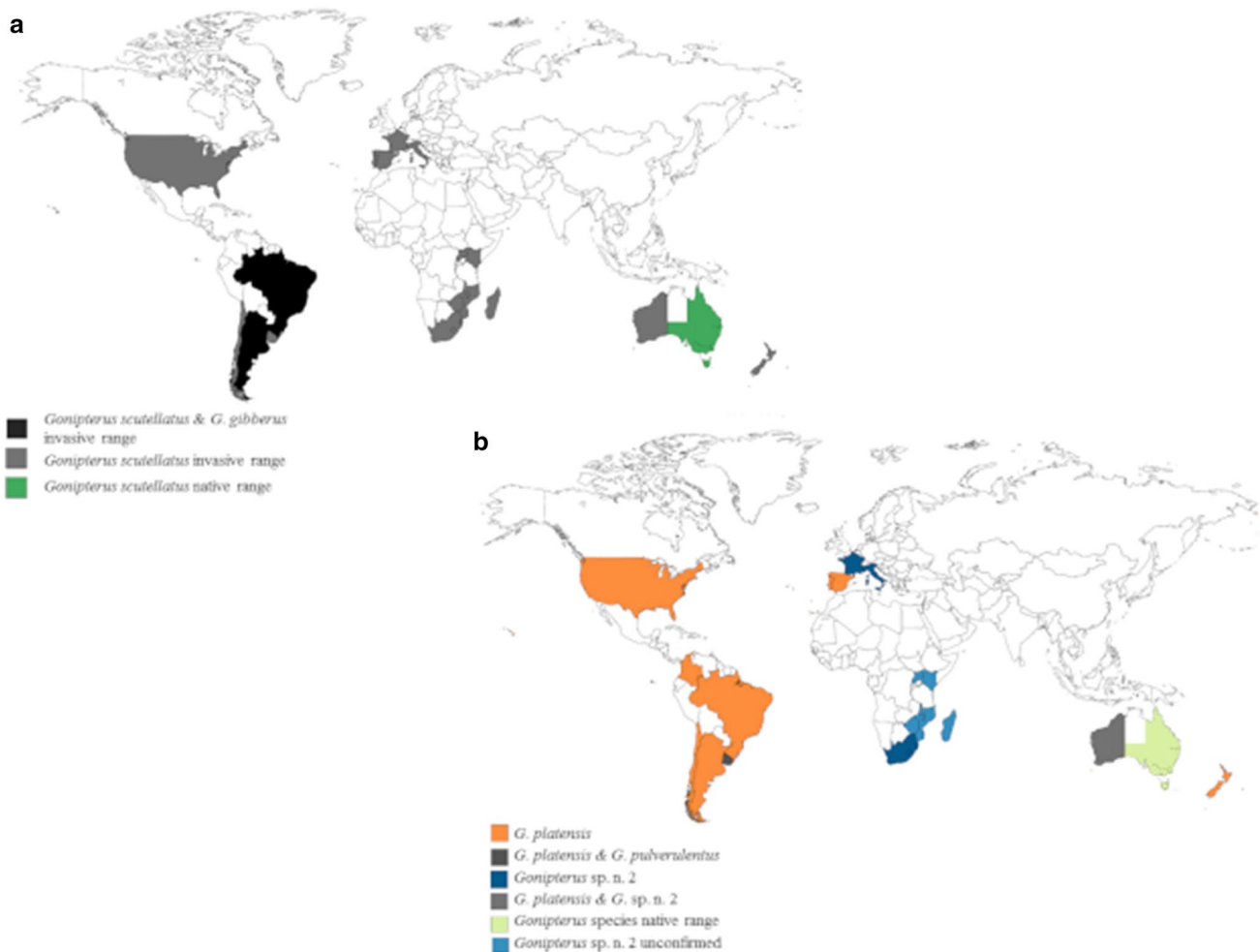


Fig. 3 Distribution and spread of *Gonipterus scutellatus* species complex, **a** before 2012 and **b** after 2012, including the description of the cryptic species complex. Distribution in native range shown per state. Sources: Cadahia (1980), Clark (1931, 1937), Cowles and Downer (1995), EPPO (2005), Frappa (1950), Haines (2006), Hanks et al.

(2000), Kevan (1946), Lanfranco and Dungey (2001), Mally (1924), Mansilla Vazquez (1992), Mapondera et al. (2012), Marelli (1926, 1927), Mazza et al. (2015), Pinet (1986), Rabasse and Perrin (1979), Rodas (2018), Rosado-Neto and Marques (1996), Tooke (1955) and Williams et al. (1951)

and *Gonipterus* sp. n. 2 occurs in Africa, France and Italy in Europe, and Western Australia (Mapondera et al. 2012). Prior to the recognition of the cryptic species complex, *G. scutellatus* was thought to be native in South-East Australia (Mapondera et al. 2012; Tooke 1955). It is now known that there are differences in species composition in the different Australian states where *Gonipterus* species are found (Fig. 4) (Mapondera et al. 2012).

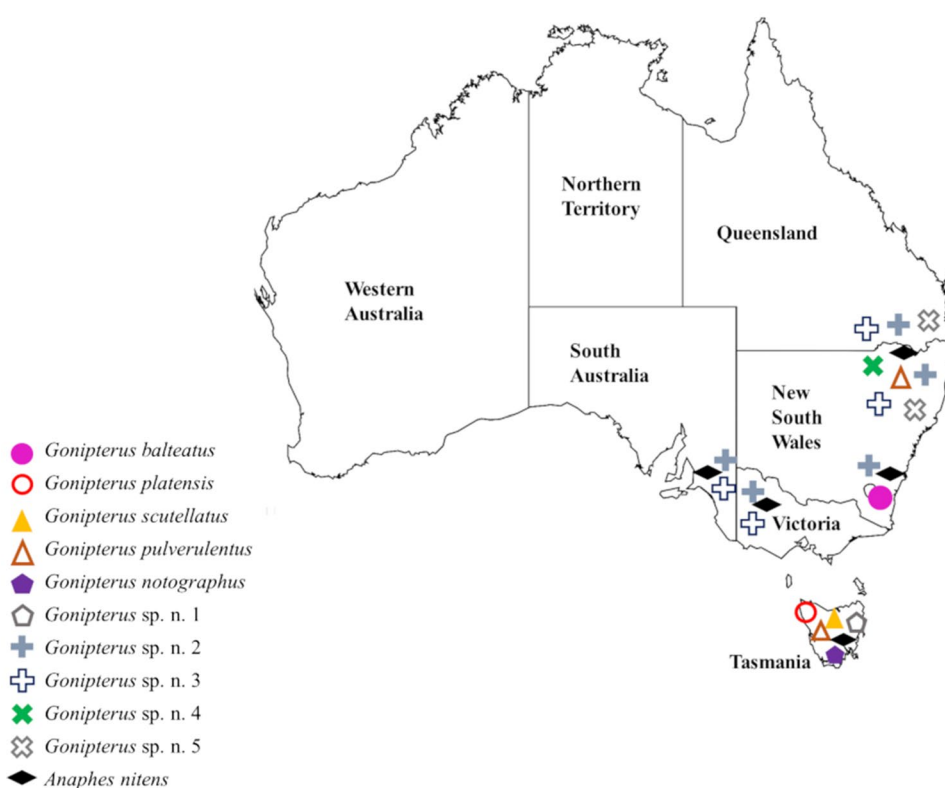
The results of the Mapondera et al. (2012) study have necessitated a revision of our understanding of the distribution of species in the *G. scutellatus* complex. For example, in Africa, only specimens from South Africa have been critically evaluated and they are known to represent *Gonipterus* sp. n. 2. It is not known whether records from other countries in Africa are those for this or some other species. It is clear from the recent appearance of *G. platenis* in Colombia

(Rodas 2018) that *Gonipterus* species continue to spread globally. There is consequently a need to accurately identify known and new populations of these insects.

The *Gonipterus scutellatus* species complex: implications for management

Confusion regarding the taxonomy of ESB, and the recognition that most early reports referring to a single species actually represented numerous different taxa, has been one of the most important obstacles to research and management of these pests in *Eucalyptus* plantations. A comprehensive understanding of the morphological as well as the ecological differences between cryptic species and the environment in which they occur is key to developing successful

Fig. 4 *Gonipterus scutellatus* cryptic species complex and *Anaphes nitens* distribution in Australia. Only the native range is indicated, thus excluding the occurrence in Western Australia where *Gonipterus* was introduced. Figure based on collections from previous studies. Clark (1931), Mapondera et al. (2012), Miller (1927), Tooke (1955) and Valente et al. (2017a, b)



management strategies (Debach 1960; Rosen 1986; Thomas 1999; Thomas and Blanford 2003; Wharton and Kriticos 2004). Even though the cryptic species in the *G. scutellatus* complex are closely related, differences have commonly been found in the colouration and markings of different life stages, as well as in host and seasonal preferences (Berkov 2002; Burns et al. 2008; Hebert et al. 2004). These differences between the cryptic species could also provide important cues for parasitoid oviposition and development. And this could significantly influence the species and ecology of natural enemies used in management strategies such as classical biological control (McCormick et al. 2012; Mumm et al. 2005). Comparative studies on the ecology of the different species in the *G. scutellatus* complex are lacking at present, but they could aid in developing region-specific management approaches.

Implications for biological control

Taxonomic confusion and uncertainty regarding parasitoid–host associations of potential biological control agents in their native range often result in problems regarding the development, establishment and successful implementation of biological control programmes (Clarke 1990; Hoelmer and Kirk 2005). There are many examples where such confusion has led to the failure of natural enemy establishment or insufficient suppression of the pest population (Beard 1999;

Clarke 1990; Stiling 1993; Williams 2001). One example where insufficient parasitism rates were observed was with the introduction of *Pauesia juniperorum* Starý (Hymenoptera: Braconidae: Aphidinae) in Africa to control *Cinara cupressivora* Watson & Voegtlin (Hemiptera: Aphididae), which forms part of the *C. cupressi* Buckton species complex (Ciesla 1991; Day et al. 2003; Orondo and Day 1994). At the time of introduction, the pest was incorrectly identified as *C. cupressi* and it was later established that *P. juniperorum* preferentially parasitised *C. fresai* Blanchard (Hemiptera: Aphididae) rather than *C. cupressivora* Watson & Voegtlin, within the *C. cupressi* species complex (Day et al. 2003). In a similar manner, incorrect species identification for the ESB may have contributed to variation in classical biological control of this pest (Howarth 1983; Loch 2008; Mapondera et al. 2012; Stiling 1993).

The egg parasitoid, *A. nitens* was released globally for the biological control of the invasive *G. scutellatus* when it was assumed that the pest represented a single species. The assumption here was that F.G.C. Tooke had collected the parasitoid from *G. scutellatus* in Australia (Clark 1931; Hanks et al. 2000; Mansilla Vazquez 1992; Richardson and Meakins 1986; Tooke 1955; Williams et al. 1951). However, the contemporary knowledge that *G. scutellatus* represents a complex of cryptic species in their native range calls to question the efficacy of the single biological control agent that has been applied globally.

The distribution of *A. nitens* within its native range, overlapping in distribution with *Gonipterus* species, suggests that it may have a wider host range than previously thought (Mapondera et al. 2012; Tooke 1955). *Anaphes nitens* has been documented from South Australia, Victoria and New South Wales, where six of the cryptic species have been found (Fig. 4). In a recent study, *A. nitens* was also found in Tasmania (Valente et al. 2017b). At present, it is not clear whether it was recently introduced to the island or whether Tasmania includes part of its native range. Direct evidence linking parasitoid species with *Gonipterus* species and thus knowledge of the exact host range of *A. nitens* is currently lacking. Future studies should specifically aim to enhance an understanding of the interactions between *A. nitens* and the different *G. scutellatus* cryptic species. It is only in this way that it will be possible to fully understand possible mismatches between the herbivore host and parasitoid.

Implications for host plant susceptibility

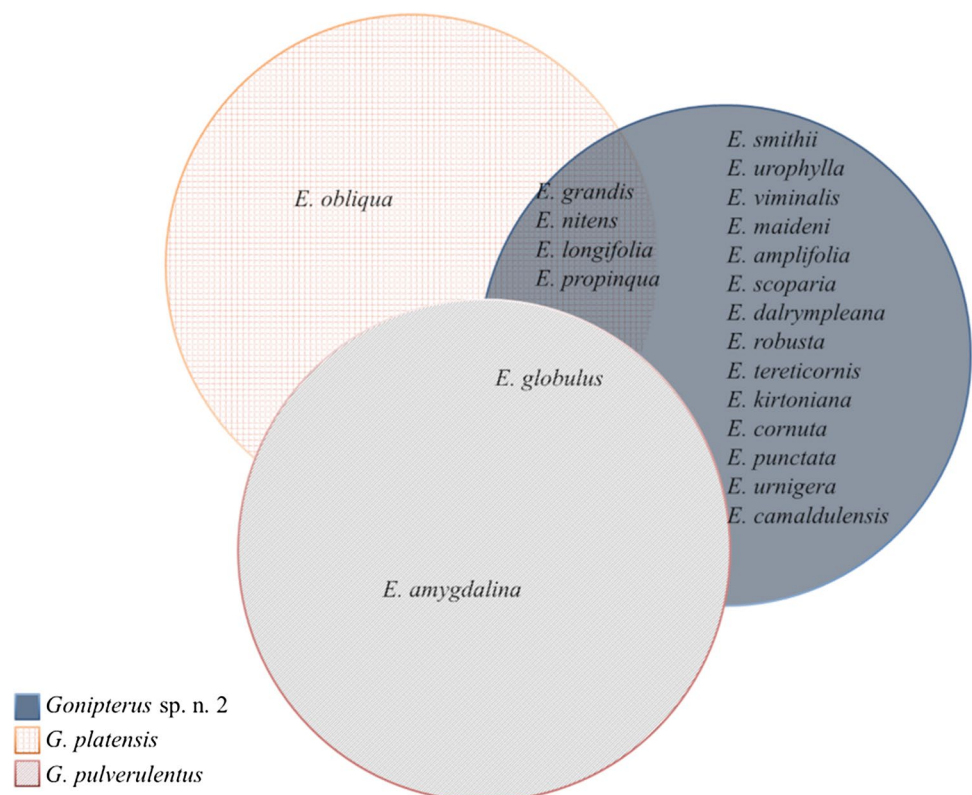
Results of host susceptibility studies need to be re-examined now that we recognise the presence of many species in the *G. scutellatus* complex. Prior to 2012, knowledge of host susceptibility varied between studies. This was most likely due to different host species tested in each of the studies and the presence of different species in the complex (Clarke et al. 1998; Mapondera et al. 2012). We reinterpreted these

data in the light of the current knowledge of the distribution of the species (Fig. 5). *Eucalyptus globulus* was reported to be a very susceptible host of all three species. *Eucalyptus grandis*, *E. nitens*, *E. longifolia* and *E. propinqua* were reported to be highly susceptible for two of the three species, *G. platensis* and *G. sp. n. 2*. However, interpretation of these studies is confounded by differences in experimental design and host species tested. Attention should consequently be given to gain a better understanding of the host plants susceptible to the various *Gonipterus* species, both in the native and invaded range.

Considerations for the future management of the *G. scutellatus* species complex

Prior to the release of *A. nitens*, other management tactics were used in an attempt to control ESB populations. A number of different insecticides have been tested, but efficacy was low and application methods costly (Mally 1924; Tooke 1955). A number of silvicultural control methods have been considered including tilling of the soil to expose the pupae and planting more resistant *Eucalyptus* species where possible (Tooke 1955). However, most of these approaches had low impact. It was not until the release of *A. nitens* for biological control that effective control of the ESB was achieved (Tooke 1955). However,

Fig. 5 Susceptible host plants recorded for the three invasive species of the *Gonipterus scutellatus* species complex, indicating overlap between species. The majority of the studies used to make the diagram tested host plant susceptibility for *Gonipterus scutellatus* prior to 2012, Clarke et al. (1998), EPPO (2005), Kevan (1946), Lanfranco and Dungey (2001), Newete et al. (2011), Richardson and Meakins (1986), Cordero Rivera and Santolamazza Carbone (2000) and Tooke (1955)



the recent occurrence of *Gonipterus* sp. population outbreaks clearly illustrates the need for a detailed understanding of the tri-trophic interactions involved and the influence of the environment. Such information is necessary to develop an effective integrated pest management programme and can be developed using a combination of top-down (e.g. natural enemies) and bottom-up (e.g. resistant species) management tactics.

Climate

Climate is amongst the most frequently cited reasons for the failure of biological control (Stiling 1993). Temperature and precipitation have an impact on the ability of insects (herbivores and parasitoids alike) to establish and reproduce in a particular environment where seasonal population fluctuations are relevant (Hawllitschek et al. 2011; Lozier and Mills 2009; Rissler and Apodaca 2007). Differences in the climatic niche of cryptic species, as well as different parasitoid populations, have been determined using ecological niche modelling (Lozier and Mills 2009). Understanding how climate influences the distribution of different species and populations of these insects is therefore important in the development of successful biological control agents. This will be especially important in the case of the ESB, where differences between species have almost certainly been overlooked.

Population outbreaks of the ESB have at times been ascribed to a climate driven phenological mismatch between ESB and its parasitoid, *A. nitens*, due to seasonal climatic fluctuations and climatic differences over an altitudinal gradient (Reis et al. 2012; Tooke 1955). At high altitudes, where winters are cold and dry, the activity of ESB adults decreases (Tooke 1955). This results in insufficient host material for the parasitoid population to overwinter (Loch 2008; Tooke 1955). In spring, host activity increases ahead of the parasitoid population increase, resulting in outbreak populations of the pest (Reis et al. 2012; Tooke 1955). Reis et al. (2012) found that parasitism rates of *A. nitens* increased when average minimum temperatures were above 10 °C. At low altitudes where the winter temperatures are more mild and in winter rainfall regions, both the ESB and *A. nitens* activities have been observed to be sufficient to sustain an *A. nitens* population over winter (Tooke 1955; Tribe 2005). Despite these observations, ESB population outbreaks have also been observed at low altitude in South Africa in recent years (Nadel et al. 2012; Verleur 2012). Further investigation into the potential effects of the climatic and phenological mismatch is required to understand how climate influences population fluctuations of ESB and *A. nitens*.

Host plant susceptibility and defence

A much improved understanding of host plant preference and susceptibility is required to inform management efforts aimed at selecting and/or developing *Eucalyptus* genotypes with tolerance to ESB infestation. With the exception of the study by Clarke et al. (1998), previous investigations have been undertaken outside the native range of *Eucalyptus* and the ESB. Host preference is a context-specific behaviour (Singer 2000). Thus, studies conducted during the invasion process outside the native range of the host could result in insect herbivores not having access to the same suite of host species than in their native range (Singer 2000). Different selection pressures may also be involved in different countries and these could influence the realised host range (plant species on which the insect population can show a positive growth rate given other abiotic and biotic constraints) within that particular environment (Hutchinson 1953; Schaffner 2001).

Understanding both the realised and fundamental host range of the *G. scutellatus* cryptic species will be important for management and risk assessment. The realised and fundamental host ranges (all host species on which the insect can complete its life cycle, regardless of abiotic and biotic interactions) within the *G. scutellatus* species complex have hardly been considered. An exception is *Gonipterus* sp. n. 2 in South Africa (Newete et al. 2011). Here, differences observed in field and laboratory trials indicated a difference in fundamental and realised host range and identified *E. urophylla* as part of the fundamental host range of *Gonipterus* sp. n. 2 (Newete et al. 2011). This species is not frequently infested in South Africa and does not occur in the native range of *Gonipterus* sp. n. 2 (Newete et al. 2011). It is used to develop hybrids in South Africa, where it is combined with *E. grandis*. These hybrids vary in susceptibility to *Gonipterus* sp. n. 2 and will therefore impact the development and implementation of *E. grandis* × *urophylla* clones (Verleur 2012). In addition, if *Gonipterus* sp. n. 2 were to spread to Indonesia where *E. urophylla* is native, this could have very serious consequences (Payn et al. 2007).

Host plant defence mechanisms and the ability of a herbivore to overcome these defences are also important considerations when seeking to understand host plant range as part of an integrated pest management strategy. *Eucalyptus* defence mechanisms have been studied for a number of other insects, but not for *Gonipterus* species. These defence mechanisms include both physical and chemical defence strategies (Malishev and Sanson 2015; Mohamed 2016). Understanding which of these strategies are involved in *Eucalyptus* defence against the ESB will be important in future tree breeding and selection programmes.

Physical defences could be important in the feeding biology of the ESB. These can include feeding barriers such as

tough leaves that require greater levels of energy or force to be consumed (Clissold et al. 2009; Malishev and Sanson 2015). For example, the physical properties of *E. ovata* and *E. viminalis* leaves differed within leaf tissues such as the midribs and veins. Younger larvae of *Exstatosoma tiaratum* (Phasmida) did not feed on the tougher leaf tissue unless starved (Malishev and Sanson 2015). However, as the larvae grew and the head capsule size increased, they were able to feed on tougher leaves and tissue than the first instar larvae. A similar change in feeding behaviour is observed in ESB larvae (Tooke 1955). The first instar larvae feed on the epidermis of the leaf lamina (Tooke 1955). The older larvae feed on the edges of the leaves and consume the entire leaf. It is likely that this could be mediated by the physical properties of the *Eucalyptus* leaves and should therefore be investigated.

Chemical defence includes both constitutive and induced defences (Hanley et al. 2007; Mohamed 2016). It is unknown how this complex suite of chemical compounds mediates ESB feeding behaviour. *Eucalyptus* leaves contain high levels of secondary plant metabolites such as tannins and formulated phloroglucinol compounds which include sideroxydonal, and phenolic compounds. These are genetically variable chemical traits within the genus, and they are important constitutive defence compounds against herbivores (Andrew et al. 2005, 2007; Eschler et al. 2000; Henery et al. 2008). For example, *Anaplognathos* (Coleoptera: Scarabidae) showed a preference for *E. tricarpa* trees with a lower concentration of sideroxydonal (type of FPG) than genetically similar trees (Andrew et al. 2007). However, FPGs or terpenoids were not shown to have any effect on the feeding of *Paropsis atomaria* (Coleoptera: Chrysomelidae) larvae despite damage to the midgut consistent with toxins (Henery et al. 2008). Identifying which groups of compounds deter feeding and have toxic effects on *Gonipterus* larvae will be important for developing tree breeding programmes aimed at developing trees that are resistant to ESB.

Biopesticides

In recent decades, attention has been paid to the development of biopesticides to control the ESB (Santolamazza-Carbone and de Ana-Magan 2004; Pérez Otero et al. 2003). These include formulations of the fungi *Beauveria bassiana* and *Metarhizium anisopliae* and the bacterium *Bacillus thuringiensis*. Some studies have indicated that *B. bassiana* and *M. anisopliae* could be promising pesticides against *Gonipterus* (Echeverri-Molina and Santolamazza-Carbone 2010; Santolamazza-Carbone and de Ana-Magan 2004), although Pérez Otero et al. (2003) did not find *B. bassiana* to be effective in controlling ESB. The efficacy of biopesticides can be influenced by a number of factors (Escribano et al. 1999; Liu et al. 2013), and the variation in *B. bassiana*

to control ESB could have been due to different strains of *B. bassiana* used in the studies or that different *Gonipterus* cryptic species were tested. The aforementioned study was conducted in Spain, where *G. platensis* is invasive (Mapondera et al. 2012; Pérez Otero et al. 2003), whereas the study by Echeverri-Molina and Santolamazza-Carbone (2010) was conducted with *Gonipterus* collected in South Africa where *Gonipterus* sp. n. 2 occurs (Mapondera et al. 2012).

An important consideration in using biopesticides in combination with biological control is the impact it has on the biological control agent. *Bacillus thuringiensis* has been found to cause mortality in *A. nitens* (Santolamazza-Carbone and de Ana-Magan 2004). *Beauveria bassiana* has been shown to be effective against *Gonipterus* populations, but its impact on *A. nitens* has not been evaluated (Echeverri-Molina and Santolamazza-Carbone 2010). It is possible that their use can have negative consequences for the long term benefits of biological control agents. It is thus important to understand the potential non-target effects of biopesticides before it can be implemented as part of an integrated pest management system for the ESB.

Much work is needed before the use of biopesticides to manage the ESB is realised. The optimal use and application of the biopesticides need further investigation, including considering economic feasibility and conservation of biological control agents. More aggressive strains of the relevant entomopathogens need to be identified and tested. In addition, the impact of host and environment on the efficacy of the biopesticides needs to be evaluated.

Augmentative biological control

Augmentative biological control can have an additive effect in suppressing pest populations below economic injury level when implemented correctly (van Lenteren 2000; van Lenteren 2012). Successful mass release programmes of *A. nitens* have been implemented in Chile, Portugal and Spain and is being developed and implemented by other countries where ESB population outbreaks are observed (CPF 2013; Galego 2016; Reis et al. 2012). Despite the success of these augmentative programmes, very little research has been published on the impact of augmentative releases of *A. nitens* on *Gonipterus* populations.

The correct timing of augmentative releases is a critical factor in determining the success of suppressing the pest population. It is also important to understand pest and parasitoid life history and phenology to ensure the correct timing of the mass releases (Messing et al. 1993; van Lenteren 2000, 2012). The ESB has one and a half generations per year in temperate climatic regions and two generations in subtropical climates (Loch 2006; Santolamazza-Carbone et al. 2008; Tooke 1955). In temperate regions, such as the Highveld of South Africa, cold and dry winters are believed

to result in a lack of sufficient egg capsules to sustain *A. nitens* populations during the winter months (Tooke 1955). Therefore, a carefully timed mass release in spring could result in a significant reduction in the pest numbers at the beginning of the season. However, if the release is conducted inordinately early, the parasitoids would likely die before a sufficient number of host egg capsules are available to sustain them. Future work in this regard should focus on evaluating the impact of mass releases on ESB populations over time.

Biological control can be a density-dependant interaction between host and parasitoid and this has been observed for *A. nitens* at a small spatial scale (Cordero Rivera et al. 1999). Therefore, the number of parasitoids released to obtain effective suppression of the host population is an important consideration in augmentative biological control (Cronin and Strong 1993; Gurr and You 2016). Inordinately low numbers may result in insufficient parasitism rate (Cronin and Strong 1993). The release of more than sufficient numbers of parasitoids can also have a negative impact on the parasitoid population due to adaptive superparasitism, which has been observed in *A. nitens* (Santolamazza-Carbone and Cordero Rivera 2003; van Alphen and Visser 1990).

Increasing diversity of biological control agents

Introducing additional parasitoid species could provide opportunities to strengthen ESB biological control programmes (Altieri 1999; Turnbull and Chant 1961). At present a single species, *A. nitens*, is used to control three different pest species, including *G. platensis*, *G. pulverulentus* and *Gonipterus* sp. n. 2 (Malausa 2000; Pinet 1986; SAG 2005; Tooke 1955; Valente et al. 2004). To date, a number of additional parasitoids known to parasitise *Gonipterus* species have been identified from Australia and Tasmania. Egg parasitoids include *Euderus* sp. Haliday (Hymenoptera: Eulophidae), *Centrodora damoni* (Girault) (Hymenoptera: Aphelinidae), *Cirrospilus* sp. Westwood (Hymenoptera: Eulophidae), *A. tasmaniae* Huber & Prinsloo (Hymenoptera: Mymaridae), *A. inexpectatus* Huber & Prinsloo (Hymenoptera: Mymaridae) and larval parasitoids are *Entedon magnificus* (Girault & Dodd) (Hymenoptera: Eulophidae) and members of the Tachinidae (Huber and Prinsloo 1990; Tooke 1955; Valente et al. 2017b). Comprehensive surveys are required to understand the species interactions and host specificity of these parasitoid species.

An additive effect in releasing multiple species for biological control programmes can be achieved by selecting species that specialise on different stages of the life cycle. For example, introducing a larval parasitoid, such as *E. magnificus*, would increase overall suppression of an ESB population by infesting the larvae that escaped parasitism during the egg stage (Gumovsky et al. 2015). *Entedon*

magnificus is a gregarious larval parasitoid and has been recorded only in Tasmania (Gumovsky et al. 2015; Valente et al. 2017b). Limited information is available regarding the host range of this species or its efficacy as a biological control agent. It was imported into a quarantine facility in Chile, but a culture was not established (Gumovsky et al. 2015).

Climatic niche differentiation can also be used to enhance the overall impact of biological control on a pest species where parasitoids infest the same life stage of the pest. *Anaphes tasmaniae* and *A. inexpectatus* have been released as biological control agents in Chile (2009) and Portugal (2012) for the control of *G. platensis* (Mayorga 2013; SAG 2014; Valente et al. 2017a, b). Little information is available regarding the efficacy of these parasitoids in combination with *A. nitens*, but experimental data on the thermal requirements of *A. nitens* and *A. inexpectatus* showed some differences between these two species (Santolamazza-Carbone et al. 2006; Valente et al. 2017b). *Anaphes nitens* and *A. inexpectatus* requires a minimum of 5 °C and 6 °C, respectively, to complete their development. Temperatures ranging between 10 and 20 °C were adequate for the development of both species but at 25 °C deleterious effects were observed for *A. inexpectatus*.

Introducing multiple species of biological control agents can also lead to intrinsic competition due to multiparasitism (Feng et al. 2015). The effect of intrinsic competition at the community level is not clear, but it could have negative impacts at the population level. This could reduce the overall suppression of the pest population. The three parasitoid species that have been developed as biological control agents are egg parasitoids and it is possible that there is competition amongst these different species (Santolamazza-Carbone et al. 2006; Valente et al. 2017b). It will consequently be important to evaluate the species interactions when considering the introduction of multiple species of parasitoids for biological control of ESB.

The impact of within-species diversity on the success of biological control is not clear. Loss of genetic variation during the invasion process does not necessarily result in a lack of fitness within the invasive range (Garnas et al. 2016; Zepeda-Paulo et al. 2016). It is, however, possible that some genetic traits related to parasitoid fitness, such as dispersal capability, could be lost during the establishment and rearing phase of laboratory cultures (Freitas et al. 2017; Mackauer 1976). Huber and Prinsloo (1990) noted a size variation between *A. nitens* individuals collected from Australia and South Africa populations. However, they did not have sufficient material to determine whether this size variation was significant. Therefore, further examination of the morphological and genetic differences between the different populations of *A. nitens* is required in order to develop this aspect of biological control.

Historical records show that a single population of *A. nitens* was collected and subsequently used for biological control of three species of *Gonipterus* in the invaded range (Beéche Cisternas and Rothmann 2000; Hanks et al. 2000; Mapondera et al. 2012; SAG 2005; Tooke 1955) (not including New Zealand and Western Australia). The original material collected for introduction of *A. nitens* into South Africa was from a single population collected in Penola, South Australia. There are no records of additional introductions of *A. nitens* into South Africa. The subsequent introductions of *A. nitens* into other countries were made from the South African population (Beéche Cisternas and Rothmann 2000; Hanks et al. 2000; Kevan 1946; Malausa 2000; SAG 2005; Tooke 1955; Valente et al. 2004; Williams et al. 1951). In New Zealand, two shipments of *A. nitens* from different localities were made. The first was from Penola (South Australia) in 1927 and the second from Canberra (Australian Capital Territory) in 1929 and 1930 (Clark 1931; Miller 1927). The situation in Western Australia is unclear and molecular studies will be required to understand the origin of *A. nitens* in that region. There is thus substantial potential to increase within-species diversity of *A. nitens* to improve biological control of the ESB, either through increased fitness, climate adaptation or host specificity. Future studies should focus on understanding how increasing genetic diversity and admixture might impact the parasitoid–host relationships at both the individual and the population level.

Achieving an integrated pest management system

A general trend in insect pest management is that different management strategies are used in isolation rather than in an integrated manner (Barzman et al. 2015; Thomas 1999). The net result is that each strategy is only partially effective and sustainable control is difficult to achieve. For example, pesticides are used in combination with classical biological control to manage ESB populations (Atkinson 1999). The effect of pesticides used against ESB on *A. nitens* has not been evaluated and pesticides typically have a negative impact on the biological control agent and can therefore negate their impact on reducing the pest population (Cloyd and Bethke 2011; Tillman and Mulrooney 2000). Selecting a pesticide with minimal or no negative effect on *A. nitens* could, however, be implemented with biological control and have an additive effect (Barzman et al. 2015; Gentz et al. 2010; Tillman and Mulrooney 2000).

Tri-trophic interactions can have a super- or a sub-additive effect on the pest population growth rate (Agrawal et al. 2000; Thomas 1999). Typical resistance screening applied by plant breeders does not always consider population dynamics of the natural enemies involved. Plant resistance traits can have either a positive or negative effect on herbivore natural enemies (Stenberg et al. 2015; Thomas

and Waage 1996). These interactions can be either direct through plant semiochemicals providing host location cues to parasitoids or indirect by altering the life history of the herbivore which may in turn impact the development time or fecundity of the natural enemies. These tri-trophic interactions have been reviewed extensively (Chen et al. 2015; Cortesero et al. 2000; Perović et al. 2018; Stenberg et al. 2015; Thomas and Waage 1996) and are not discussed further here. There is consequently a risk that a resistant clone or hybrid may be selected based upon low levels of herbivore damage observed but where it might also have a negative effect on natural enemy populations. In turn a moderately resistant clone might also be rejected even though it has a positive effect on the natural enemy population. Clearly, the interaction of the two strategies in combination could result in greater effect on the reduction of pest population growth rate than each strategy alone (Cortesero et al. 2000; Thomas and Waage 1996). To improve management strategies of ESB, the focus should not only be on improving top-down processes, such as increasing diversity of natural enemies, or bottom-up process such as selective breeding for improved resistance traits, but also the interactions between the different strategies to identify synergistic and or additive effects (Barzman et al. 2015; Thomas 1999).

Conclusions

Improved management strategies are urgently needed to enhance the control of *G. scutellatus* cryptic species in planted *Eucalyptus* forests. Releasing additional biological control agents and augmentative releases of existing parasitoid species appear to be promising options. A clear knowledge of the cryptic species of *Gonipterus* needs to become an essential component dictating decisions as to the appropriate natural enemies to introduce for biological control. An understanding of the fundamental and realised climatic niche of each of these species as well as their respective natural enemies should then be used to predict possible outbreaks and develop improved management tactics.

It must be recognised that when using biological control as a management tactic, a tri-trophic approach should be followed including an understanding that rapid evolution could alter the pest–parasitoid dynamics over time (Tomasetto et al. 2017). The ability of herbivore pests to overcome plant resistance has been well studied (Despres et al. 2007; O’Neal et al. 2018; Simon and Peccoud 2018), but little is known about the ability of herbivore pests to develop resistance to their arthropod biological control agents (Mills 2017). Rapid evolution of herbivore resistance against a biological control agent has recently been demonstrated by the Argentine pasture weevil in New Zealand. A significant decline in parasitism rate was detected 7 years after the introduction

of the parasitoid and was made possible due to 24 years of monitoring (Tomasetto et al. 2017). Consequently, it should not be assumed that a successful biological control programme will remain effective indefinitely. Furthermore, effective monitoring systems need to be established to determine whether silvicultural changes and abiotic or biotic factors have an impact on the efficacy of the biological control agents over time.

Biological control programmes have too often in the past taken a simplistic approach, where a single biological control agent, from a limited collection, with limited adaptive ability and with a lack of understanding of its complex interactions with the host and environment. This has often been necessary for practical reasons; lack of resources to do more in depth studies on diversity and interactions, the complexity and cost of collecting natural enemies in the native range of the pest or difficulties in rearing, quarantine or mass production of the pest. The use of *A. nitens* to control *Gonipterus* spp. across the world is a good example. The information described in this review, and the technologies that underpin it, now offers a foundation to add more in depth studies on these interactions and develop more locally adapted and resilient biological control programmes. This includes the introduction of multiple species and biotypes of natural enemies, using multiple organism types that target different life stages and integrating these with other control methods (breeding, chemical control, amongst others). Future options to use genetic engineering for pest management, as is already being tested for economically important insects (Sun et al. 2017), will add further options in future.

Author contributions

All authors contributed to the conception of the document. MS wrote the manuscript. All authors reviewed, edited and approved the manuscript.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval This article does not contain experiments with human participants or animals performed by any of the authors.

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