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REVIEW ARTICLE

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Cossid moths (Lepidoptera: Cossidae) as pests of woody plants – A review

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Abstract

1. The Cossidae is a worldwide family of macro-moths popularly known as carpenter moths due to the larval habit of boring in the wood of living plants. This review compiles current knowledge on the characteristics, diversity and bionomy of cossid moths as well as the damage they cause on woody plants.
2. Adult cossids are nocturnal, robust and generally have a low dispersal ability. Their habitat is very diverse from desert to boreal forests and high mountains. They have a long life cycle that varies from 1 to 3 years, the majority of which is spent in the larval stage. Most cossid larvae are highly polyphagous caterpillars and can migrate both intra-host and inter-host.
3. Twenty-six species of cossid have been reported as pests of commercial woody plants in forestry and horticulture. The feeding tunnels of cossid larvae can make large branches or trunks of small trees prone to wind breakage and can lead to tree decline and mortality. Cossid larvae damage reduces growth, yield, quality of fruit and wood as well as its commercial value.
4. Current knowledge on cossid pest management is reviewed highlighting the importance of pheromone traps and the need for an integrated pest management approach for effective control. Lastly, future risks and challenges are discussed.

KEYWORDS
bionomy, damage, ecological requirements, pest management, taxonomy, wood-boring caterpillars

INTRODUCTION

Wood-boring insects in forests and wooded lands are an important functional group in native ecosystems. However, some species can cause considerable damage, particularly in commercial forests and orchards, and are considered to be pests of great importance (Demidko et al., 2021; Fierro et al., 2017; Herms & McCullough, 2014; Hlásny et al., 2021; Jiménez et al., 2012; Sallé et al., 2014; Smith et al., 2009). Thus, a great deal of research has been conducted on bark- and wood-boring pests over the past decades. These efforts have resulted in a wealth of information, particularly about damaging bark beetles (Curculionidae: Scolytinae) and some invasive species (e.g., emerald ash borer *Agrilus planipennis* Fairmaire, 1888) and longhorn beetles (*Anoplophora* spp.) (Demidko et al., 2021; Jiménez et al., 2012; Sallé et al., 2014; Smith et al., 2009). In contrast, our knowledge remains much more limited in the case of other groups of bark- and wood-boring insects, even though they also include pests of considerable importance.

Cossid moths (Cossidae) are an ecologically specific group of Lepidoptera whose larvae usually develop inside plant tissues, and many species are associated with woody plants. Most cossid species larvae are large, wood-boring and highly polyphagous caterpillars that feed on the inner bark and both the sapwood and heartwood of living trees or other woody plants (Schoorl, 1990). Hence, they are popularly known as carpenter moths or wood moths.

FIGURE 1 Cossid moth imago appearance (a–d) and various life stages of *Cossus* (e–g). (a) *Acossus terebra* (Denis & Schiffermuller, 1775); (b) *Zeuzera pyrina*; (C) *Xyleutes ceramica*; (d) *Cossus cossus*; (e) lateral side of a larva; (f) dorsal side of a larva; (g) a pupa. Photo (E) taken by O. Machač, photo (g) by M. Zúbrik, other photos taken by Z. Laštůvka.

Several species of cossid moths are reported as pests. The most well known of these are the goat moth (*Cossus cossus* (Linnaeus, 1758)) which attacks a variety of trees such as willow, poplar, elm, oak, alder, beech, birch, maple, ash, linden, apples, pears, walnuts and chestnuts in Europe, Asia and North Africa (T'Sai et al., 1974; Lapietra & Allegro, 1986; Falsafi et al., 2014; Kaplan & Turanlı, 2018; Yakovlev, Shapoval, et al., 2019); the Eucalyptus cossid moth (*Coryphodema tristis* (Drury, 1782)) which attacks *Eucalyptus nitens* and a few species of fruit trees in South Africa (Gebeyehu et al., 2005; Kumbula et al., 2019); the carpenterworm moth (*Prionoxystus robiniae* (Peck, 1818)) that affects several species of wild, ornamental, as well as commercial forest broadleaf trees in Canada and the United States (Hannon et al., 2017); the leopard moth (*Zeuzera pyrina* (Linnaeus, 1761)) which attacks ash, apple, beech, maple, oak, olive, elm, hazel, hickory, plum, walnut, etc. in Europe, Asia, North Africa, Canada and the United States (Demirel, 2018; Hegazi et al., 2010; Sarto i Monteys, 2015); and the teak bee-hole borer (*Xyleutes ceramica* (Walker, 1865)) which affects teak in several Southeast Asian countries (Gotoh et al., 2007; Wylie & Speight, 2012). The impacts of tree infestation by these species include reduced tree growth, decreased commercial value of the wood, stem and branch breakage and general dieback of the trees (Boreham, 2006; Hannon et al., 2017; Kliejunas et al., 2001; Lanfranco & Dungey, 2001; Mathew, 1990; Solomon, 1995; Thurman, 2022; Wylie & Speight, 2012). Despite the considerable economic importance of cossid moths, inadequate effort has been given to their study and the available information is scattered across many sources.

The present paper aims to compile the current knowledge on the characteristics, diversity and bionomy of cossid moths as well as their importance as pests of woody plants. Species that have been reported as pests of important commercial trees are listed, and their host trees and geographical distributions are reviewed. Their physiological and technical damage to living trees is explained in order to clarify the cause of tree decline and mortality, especially with regard to economic losses. Lastly, current knowledge on their management, future risks and challenges is discussed.

Characteristics

Cossidae is a worldwide family of macro-moths, of which the adults are large, robust moths (9–250 mm wingspan). The largest species in the family is the giant wood moth (*Endoxyla cinereus* (Tepper, 1890)), which is also considered one of the largest and heaviest moths in the world (Beccaloni, 2010). Female moths are significantly larger than male moths. The head is small with average or slightly rough scaling. The wings are typically broad and elongated, with a triangular or trapezoidal shape. The forewings are usually elongated, with the hindwings often being rather small and rounded. The coloration and pattern on the wings often feature a combination of shades of brown, grey, black or white with markings, with a subdued or mottled pattern, most likely for camouflage on their host trees (Figure 1a–d). They have rudimentary mouthparts, are nonfeeding, and can live for 2 to 16 days, depending on the species, using fats acquired during the larval stage (Heppner, 2005). They are mostly nocturnal, except for the genera *Dieida*, *Stygia* and *Stygioides*, which have been seen flying during the day (Saldaitis et al., 2007; Yakovlev, 2015), and are generally sluggish flyers (Gotoh et al., 2007; Kliejunas et al., 2001; Solomon, 1995).

The majority of known Cossidae live as larvae in branches, stems and even roots of a wide variety of woody plants, although several are known to live in succulents and in the roots of herbs. In this review, we focus only on those developing in woody plants. Cossid larvae, being xylophagous, superficially resemble other wood-boring larvae, such as those of clearwing moths (Sesiidae) and ghost moths (Hepialidae), due to their similar lifestyles. However, cossid larvae can be differentiated from the others primarily by the characteristics of their prothoracic shield and crochets (Edwards et al., 1998) (Figure 1e,f). For cossid larvae, the size of the mature instar is considered to be medium to very large (body length is 20–150 mm). The head is relatively small, broad, longer than wide, and the mandibles are enlarged. The body is almost cylindrical and usually robust (but can be flattened in the Zeuzerinae). Coloration of the body ranges from white, yellow or pink to red and is sometimes dusky dorsally. On each segment, the pinacula are heavily chitinized and the setae are relatively reduced. There are up to four extra setae present dorsocaudally above the spiracle and sometimes extra subventral setae. The prothorax is covered by a well-developed plate or shield and is often humped and/or rugose. All prolegs are also relatively reduced with crochets arranged in a complete circle (Edwards et al., 1998). Pupae are adecticous and obtect, enclosed in an oval or cylindrical silk cocoon, sometimes mixing with frass or wood particles. For some species that can pupate underground, cocoons can be made of silk mixed with soil. The pupae are often of a reddish-brown or brown tone (Gotoh et al., 2007; Hannon et al., 2017; Lapietra & Allegro, 1986; Mathew, 1990; Solomon, 1995; Thurman, 2022) (Figure 1g). Eggs are oval- or cylindrical-shaped and generally laid singly or in small clusters, with a sticky secretion. Egg size ranges from 1 to 1.7 mm long and 0.6–0.9 mm wide, depending on species. The coloration of eggs ranges from reddish-brown to pinkish-orange or yellow (Areces-Berazain, 2022; Chi, Pham Duy, & Yakovlev, 2022; Gotoh et al., 2007; Hannon et al., 2017; Lapietra & Allegro, 1986; Solomon, 1995; Thurman, 2022).

Diversity and global distribution

The Cossidae family is composed of 10 confirmed subfamilies, divided into 158 genera which encompass approximately 966 species (Figure 2). The cossid fauna can be separated into those originating from the Old World (118 genera) and those originating from the New World (40 genera) (Yakovlev, 2015). The patterns of geographical distribution of individual cossid species are governed by the broad general principles applying to most species, such as the availability of host plants, mountain ranges, large rivers and desert massifs forming barriers to distribution. However, the most important factors limiting distribution are temperature and humidity gradients. For example, species diversity of cossid moths in the Palearctic is intrinsically linked to the arid areas and mountain systems of the region where a decline in species diversity is correlated with an increase in humidity and altitude. Meanwhile, geomorphological-phytocoenotic borders in the Afrotropic, Indomalaya and Australia are represented by deserts, mountain ranges and water barriers, and the increase in cossid species diversity occurs at the expense of endemics and inclusion of tropical environments (Yakovlev, 2015).

In the Old World, the Paleotropical kingdom has the richest cossid fauna in the world regarding the number of subfamilies, genera and species (7 subfamilies, 88 genera, 471 species). The largest number of species belongs to the Zeuzerinae and Cossinae subfamilies, which are distributed across the entire zone (Yakovlev, 2015). In the Indomalayan realm, the Catoptinae subfamily is predominantly distributed in mountainous areas from northern India to southeastern China and northern Southeast Asia (Yakovlev, 2009; Yakovlev et al., 2013). In the Afrotropic realm, the Stygiinae subfamily occurs only in the Arabian Peninsula (Yakovlev, 2011b), while the Pseudocossinae subfamily is restricted to Madagascar (Yakovlev, 2015). On the main African continent, the Politzariellinae subfamily is distributed in the humid zone of central Africa (Yakovlev, 2015), whereas the Mehariinae subfamily occupies the arid zone (Yakovlev & Dubatolov, 2013).

After the Paleotropical kingdom, the Palearctic realm is the second most taxonomically diverse area, containing 5 subfamilies, 26 genera and 260 species. The greatest number of species occurs in warmer areas, especially the Eastern Palearctic for Cossinae and Zeuzerinae subfamilies. Only the subfamilies Cossinae, Zeuzerinae and Catoptinae are widespread in the boreal region (Yakovlev, 2015). Stygiinae are distributed in the Mediterranean subregion (Yakovlev, 2011a), while Catoptinae are predominantly distributed in

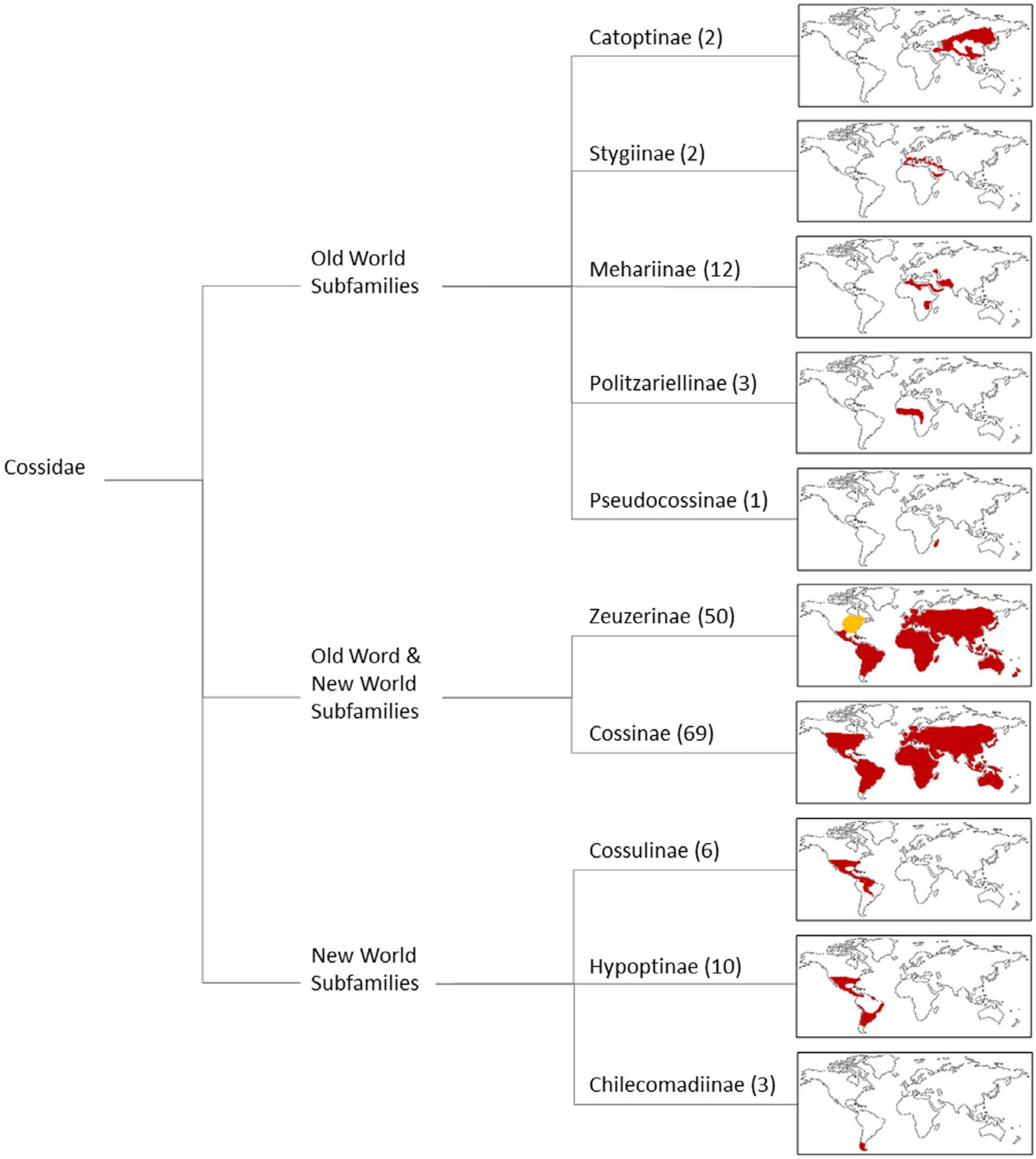

FIGURE 2 Geographical distribution of the Cossidae, with the number of genera (n) of each subfamily. The area was delineated based on published occurrence records of each subfamily (Metalmark Web and Data, 2023; Penco et al., 2022; Yakovlev, 2009; Yakovlev, 2015; Yakovlev, 2011b; Yakovlev et al., 2013; Yakovlev, Naydenov, & Penco, 2019; Yakovlev & Dubatolov, 2013; Yakovlev & László, 2021). Red coloured areas represent the native range, while yellow coloured areas represent a non-native (invasive) range.

the mountainous and cold regions of Asia (Yakovlev, 2009; Yakovlev et al., 2013), and most species of the Mehariinae subfamily occur in the drylands of Asia and Africa (Yakovlev & Dubatolov, 2013).

The cossid fauna of the New World is less diverse than that of the Old World; however, this may simply be a reflection of the less intensive study of the Cossidae in North and South America compared to Eurasia. The lowest diversity of cossid moths occurs in the Nearctic realm (3 subfamilies, 8 genera, 24 species) (Metalmark Web and Data, 2023), and while it is higher in the Neotropical realm, it is still relatively poor (5 subfamilies, 25 genera, 100 species) (Yakovlev, 2015). The endemic species, probably having a neotropical origin, are represented in Central-South America and the southern United States by the subfamilies Hypoptinae and Cossulinae, and in Chile–Patagonia by the subfamily Chilecomadinae (Penco et al., 2022; Yakovlev, 2015). The Zeuzerinae and Cossinae subfamilies are also considered native to the New World. Most species that are native to the Nearctic, particularly those distributed in the boreal region, belong to the Cossinae, whereas only three genera from the Zeuzerinae subfamily are reported from the Nearctic (one of them represented by a single invasive species from Europe, *Z. pyrina*) (Solomon, 1995). In Australia, the

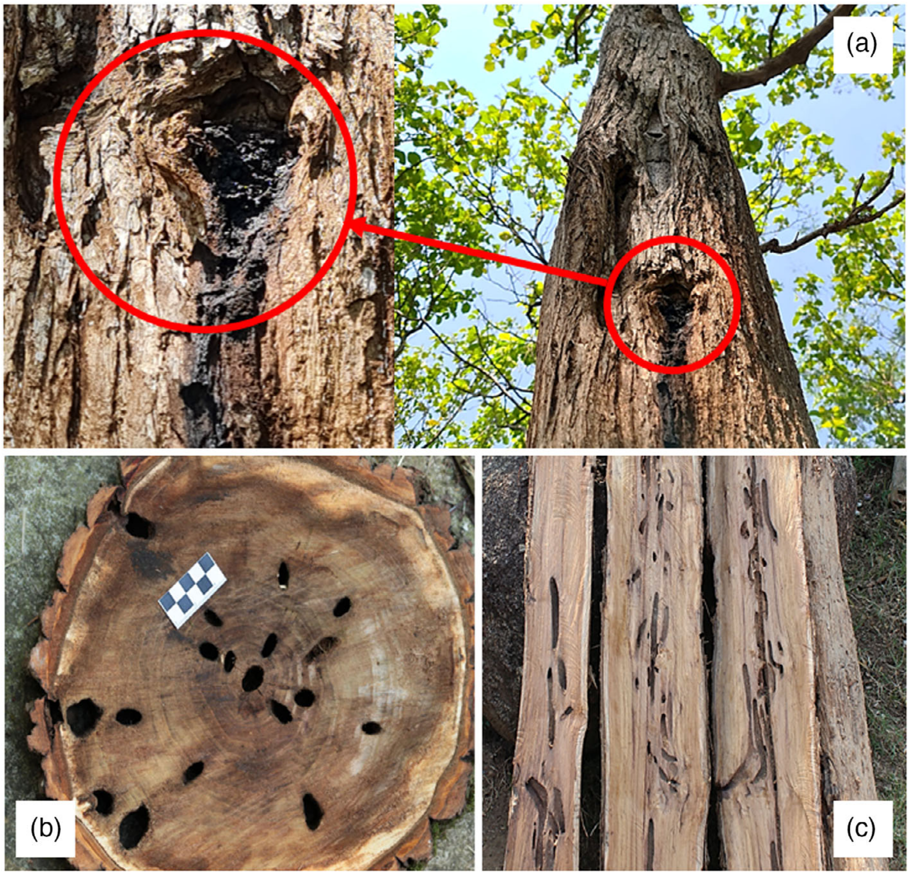

FIGURE 3 Damage caused by Cossid larvae: (a) red circles highlight a gallery, composed of an entrance hole and ejected frass; (b) cross section of an infested trunk (photo taken by M. Zúbrik); (c) vertical section of infested trunks.

taxonomic diversity is low; however, endemism is high (2 subfamilies, 9 genera, 75 species). Most species in Australia belong to the subfamily Zeuzerinae, while a few belong to Cossinae (Yakovlev, 2015).

Undoubtedly, the greatest number of cossid species belongs to the subfamilies Zeuzerinae and Cossinae. They are considered to comprise 80 percent of the endemic species in the world (over 740 species from 114 genera) and are distributed in all biogeographic realms (Figure 2) demonstrating their potential adaptation to a wide range of ecologic conditions.

Bionomy and ecological requirements

Cossids have a long life cycle that varies from 1 to 3 years, during which they spend most of their time in the larval stage. Nonetheless, the life cycle can exceed 3 years depending on the host plant species and climatic conditions, particularly for species living in arid and/or cold regions. For example, the life cycle of *P. robiniae* can extend to over 3 years in the cold climate of the northern region of the United States, while it is usually less than 2 years in the warmer climate of the southern region (Hannon et al., 2017). Research has also shown that warm temperatures can reduce development time. For example, temperatures in the optimum range of 25–30°C can shorten the life cycle of *Streltzoviella insularis* (Staudinger, 1892) from 2 years to less than 1 year (Nakanishi et al., 2016). Interestingly, rearing the larvae of *C. cossus* in captivity has revealed that they can also eat fruit, vegetables and bread, and their life cycle is reduced from 2 to 4 years to only 6–10 months due to the higher nutritional content of their food compared to the difficult to digest cellulose obtained from their usual diet of wood. However, for unknown reasons, adults reared on such a diet are much smaller than individuals found in natural environments (Coppens, 2019).

At the beginning of the life cycle, the young larvae hatch from eggs and seek a suitable site to penetrate twigs, branches or stems in order to feed gregariously on callus, inner bark and cambium tissues. There are reports that the larvae of *C. cossus*, *Dervishiya cadambae* (Moore, 1865) and *Chilecomadia valdiviana* (Philippi, 1860) are also attracted by aggregation pheromones contained in the musky odour released from other larvae (Capizzi et al., 1983; Mathew, 1990; Reyes-Garcia et al., 2011). The earliest signs of an infestation are sap spots and exuded frass on twigs, branches and trunks of trees. After the initial phases, later instar larvae penetrate deep into sapwood and heartwood (prior to this, larvae feeding on twigs or small branches can move down to larger branches or the main stem). Two exceptions to this behaviour are *Culama australis* (Walker, 1856) and *Roepkiella chloratus* (Swinhoe, 1892), species known to feed only on inner bark

FIGURE 4 Pupal case of an emerged adult of *Acossus terebra* on an infested trunk (photo taken by Z. Laštůvka).

and cambium tissues and therefore do not move into the wood in later instars (Carnegie et al., 2008; Ong et al., 2014). An initial horizontal tunnel is bored, which then curves upwards, becoming vertical, resulting in a J-shape (Figure 3). There is no clear explanation for this vertically upward feeding habit. However, it can be expected that it is probably to avoid flooding of the tunnel. An exception to the J-shape tunnelling pattern has been found in *D. cadambae*, which feeds in a horizontal zigzag pattern (Mathew, 1990). The tunnels of cossid larvae are steadily enlarged as the larvae develop. Larvae do not feed only on the wood but also on the callus tissue developing on the wound around the entrance of the tunnel.

Towards the end of larval development, a large chamber is excavated in the bark and outer sapwood to prepare for pupation. One or more small holes are drilled to the outside of this chamber for ejecting frass and a large hole to prepare for the emergence of the moth. Signs of an infestation are most easily distinguishable at this time due to the more visible frass or sawdust that the larvae expel out of the tunnels. The larvae go through stationary moults until suitable environmental conditions trigger pupation. The number of larval instars can range between 5 and 8, depending on the particular species (Areces-Berazain, 2022; Gotoh et al., 2007; Hannon et al., 2017; Hernandez-Livera et al., 2005; Solomon, 1995; Tavares et al., 2020; Thurman, 2022). When the larvae reach the final instar, they close the emergence hole with a circular disc of silk and debris and begin pupation in the chamber near the bark or, in some cases, return to the upper end of the tunnel to pupate behind a loose wad of silk. The emergence of adults usually occurs in the summer for species living in both temperate and tropical climates. Just prior to adult emergence, the pupae cut themselves out of the cocoons using a cutting spine on their head and wriggle towards the tunnel openings using dense rows of fine cuticular hooks across each abdominal segment of the pupal exoskeleton, which allow them to grip the sides of the chamber and inch forward or twist (McInnes & Carne, 1978). The pupae cut through the disc covering the emergence holes and stick their bodies halfway out of the hole. In this position, the moths emerge from the pupal cases, resulting in the shed pupal cases protruding halfway out of the tree or falling to the ground (Thurman, 2022) (Figure 4). The larvae of cossids living in cold regions (e.g., *Z. pyrina* and *C. cossus*) sometimes move down to the lower part of the tree to create a new tunnel for overwintering and resume active feeding the following summer, pass a second winter in dormancy within their tunnel, and begin pupation in the second spring (Lapietra & Allegro, 1986; Nasonova, 1960). Moreover, the pupation of some Cossinae species can occur both in the tree trunk and in loose soil on the ground (e.g., *C. cossus* and *D. cadambae*) (Mathew, 1990).

After adult emergence, the flight orientation of many cossid moths is governed by semiochemicals, that is, chemicals used to associate with other individuals, consisting of sex-aggregation pheromones for mating and seeking a suitable host for brood development (Capizzi et al., 1983; Chen et al., 2006; Eungwijarnpanya et al., 1990). Males respond to sex pheromones released from females and approach them for mating. Female adults of many species are considered weak fliers and have a low dispersal ability due to the massive, heavy body carrying a large number of eggs. Therefore, eggs are frequently laid near emergence sites (Gotoh et al., 2007; Kliejunas et al., 2001; Solomon, 1995). Selection of host plants is influenced by odorant binding proteins (OBPs, i.e., proteins facilitating the transport of odorant molecules to the receptors), at least in some species (e.g., *Eogystia hippophaecolus* (Hua, Chou, Fang & Chen, 1990) and *S. insularis*) (Hu et al., 2016; Yang et al., 2019). OBPs respond to plant-emitted volatile organic compounds (VOCs), such as 2-ethylhexanol, hexanol, α-terpineol, (Z)-3-Hexenyl-3-methylbutanoate and methyl salicylate (Hu et al., 2016; Shixiang et al., 2017; Wang et al., 2014; Yang et al., 2019). Most OBPs are found in the olfactory organs of the moth's antennae, assisting in finding the direction of host plants, while fewer OBPs are found in the gustatory organs on the moth's legs, assisting in recognizing the taste of host plants (Hu et al., 2016; Shixiang et al., 2017; Wang et al., 2014; Yang et al., 2019). Once a suitable host plant has been selected, eggs are laid singly or in small clusters in wounds, cracks and crevices in the bark of the branches and main stems of trees. Roughed bark is preferred as it may increase the grip of the female while laying eggs as well as adhesion of the eggs onto the surface. However, this is not true for all species, as certain species (e.g., *C. tristis*, *C. valdiviana* and *E. cinereus*) prefer smoothed bark *Eucalyptus* (Kumbula et al., 2019; Lanfranco & Dungey, 2001; Thurman, 2022). Damaged trees are also preferred as wounded trees offer a suitable site for penetration and favourable developmental conditions for the larvae (Ferrenberg & Mitton, 2014; Hannon et al., 2017; Yamamoto et al., 2022). Given these habits and preferences of both larvae and adult females it is unsurprising that some cossid species target already infested areas of trees, leading to the characteristic honey-combed appearance of the infested trees (Chen et al., 2006; Kliejunas et al., 2001; Mathew, 1990; Reyes-Garcia et al., 2011) (Figure 5).

Most larvae of cossid species are highly polyphagous caterpillars that feed primarily on broad-leaved (angiosperm) woody plants. A typical example is *Polyphagozerra coffeae* (Nietner, 1861), which can live on approximately 62 genera from 30 families of plants, including various broadleaf species and one coniferous species (*Cryptomeria*

FIGURE 5 Honey-combed damage pattern on trunks infested by *Cossus cossus* (left and right photos taken by V. Holec and P. Martinek, respectively).

japonica) (Roychoudhury & Mishra, 2022; Tavares et al., 2020; Yakovlev, 2011a). Larvae of cossids associated with woody plants feed predominantly on the inner bark and both sapwood and heartwood in the trunk. An exception to this is *Endoxyla leucomochla* (Turner, 1915), the only species known to feed externally on roots (of *Acacia kempeana* and *A. ligurata*) (Schoorl, 1990). Cossid larvae can migrate intra-host, which differs from other bark and wood-boring insects, and some species can even migrate inter-host (i.e., shift to a new host) in later larval instars when the original host can no longer offer sufficient nutrients (e.g., *E. hippophaecolus*, *Deserticossus artemisiae* (Chou et Hua, 1986), *Deserticossus arenicola* (Staudinger, 1879) and *S. insularis*) (Xu et al., 2017). Additionally, young larvae of *P. coffeae*, *X. ceramica* and *Z. pyrina* are capable of producing silk strands on which they are carried and dispersed by wind to a new position or host, a phenomenon known as ballooning (Bell et al., 2005; Gotoh et al., 2003). Generally, according to observational reports, several larvae of cossid species seem to prefer fast-growing tree species rather than slow-growing ones. For example, *C. cossus* and *Z. pyrina* are usually found infesting moderate to fast-growing forest trees, fruit trees and/or ornamental trees such as willow, poplar, apple, pear and aspen rather than slow-growing species such as oaks (Abdel-Moaty et al., 2019; Faccioli et al., 1993; Solomon, 1995; Turundaevskaya, 1992). *Coryphodema tristis* and *C. valdiviana* are also found infesting the aforementioned tree species, but heavier damage usually occurs on *Eucalyptus* spp., which grow even faster (Degefu et al., 2013; Gebeyehu et al., 2005). Moreover, severe damage in teak plantations caused by *X. ceramica* usually occurs in rapidly growing teak trees/stands rather than slow-growing trees/stands (Choochuen et al., 2024; Gotoh et al., 2007; Tasen & Wiwatwitaya, 2022). In addition to the fact that fast-growing trees offer better nutrition and more abundant food resources, the preference shown by the aforementioned cossid species for fast-growing trees might be explained by the growth-differentiation balance hypothesis. This hypothesis posits that fast-growing trees are less resistant to insect attacks because more resources are allocated to growth rather than physical and chemical defences (Boege & Marquis, 2005; de la Mata et al., 2017).

Cossid larvae damage to woody plants

The ecological role of bark and wood-boring insects in forests and wooded lands ranges from being primary tree killers to acting as decomposers of deadwood. While these insects play a crucial role in native ecosystems, they can cause significant damage to commercial timber operations (Demidko et al., 2021; Hannon et al., 2017; Jiménez et al., 2012; Sallé et al., 2014; Smith et al., 2009; Vansteenkiste et al., 2004). Tree-killing phloeophagous species such as bark beetles (*Dendroctonus ponderosae* Hopkins, 1902, *Dendroctonus frontalis* Zimmermann, 1868 or *Ips typographus* (Linnaeus, 1758)) and the emerald ash borer feed on inner bark tissues, usually resulting in extensive damage to the phloem and cambium (girdling of the tree), interrupting sap and water conduction of trees and rapid dieback (Clark et al., 2012; Demidko et al., 2021; Jiménez et al., 2012; Sallé et al., 2014; Vansteenkiste et al., 2004). On the other hand, other tree-damaging bark and wood-boring insects, such as cerambycids (e.g., *Anoplophora glabripennis* (Motschulsky, 1853), *Anoplophora chinensis* (Forster, 1771), *Aromia bungii* Faldermann, 1835, *Aromia moschata* (Linnaeus, 1758) or *Saperda carcharias* (Linnaeus, 1758)) as well as cossid moths, feed on both phloem and xylem tissues of living trees, resulting in more localized and dispersed damage within these host tissues. Consequently, the conduction of nutrients and water between the canopy and roots of infested trees is compromised to varying degrees, leading to tree weakening, slower decline or eventually gradual dieback (Čakšs et al., 2022; Demidko et al., 2021; Hannon et al., 2017; Horrocks et al., 2024; Sallé et al., 2014; Smith et al., 2009). Cossid larvae generally feed voraciously on inner bark tissue only during the early instar stages; for the remainder of their life cycle, they feed principally on callus and xylem tissues in the sapwood and heartwood, which primarily disrupts the transportation of water and dissolved minerals. In contrast, the aforementioned bark beetles and emerald ash borer feed mainly on cambium and phloem tissues, interrupting secondary growth of plants directly. Therefore, host trees infested by cossid larvae may exhibit a comparatively slower decline than those infested by phloeophagous insects and frequently tolerate the infestation. On the other hand, it has been reported that tunnels bored by cossid larvae can make large branches or even trunks of small trees prone to wind breakage. For this reason, some researchers suggest that damage caused by cossid larvae poses a higher risk of killing small or young trees but is generally less severe for large or old trees (Kliejunas et al., 2001; Solomon, 1995; Wylie & Speight, 2012).

Furthermore, the direct damage caused by the insects can be exacerbated by birds searching for and feeding on the larvae; and this indirect damage increases the likelihood of a tree snapping (Thurman, 2022). For example, yellow-tailed black cockatoos (*Calyptorhynchus funereus* (Shaw, 1794)) excavate the larvae of *E. cinereus* from trees by ripping away bark and wood, exposing the larval tunnel up to the centre of the tree. Similar damage to bark and sapwood can be caused by woodpeckers preying on various cossid larvae, e.g., *P. robiniae* (Hannon & Beers, 2007).

In addition to their direct damage and that caused by birds, many bark and wood-boring insects are considered potential vectors of tree pathogens. The interactions among themselves and with microorganisms are diverse and varied and can lead to tree weakness and mortality. For example, some cossids, such as *P. robiniae*, *C. tristis*, *C. valdiviana* and *D. cadambae*, have been reported to induce pathogenic or saprophytic fungi within their feeding tunnels on host trees (Hoppner & Ferreira, 1990; Lanfranco & Dungey, 2001; Mathew, 1990; Solomon & Toole, 1971). However, it remains unclear whether the fungi are transmitted by the insects or were already present on the trees.

Pest impacts

Although many bark and wood-boring insects play a crucial role in decomposition and succession in forest ecosystems, many species are considered significant pests when their populations exceed optimum levels. In natural forest ecosystems, cossids have never been reported as pests, even though most species have a polyphagous habit. Apart from the presence of natural enemies, their low dispersal ability and the connectivity of available hosts are likely to be the main factors limiting their distribution to clustered aggregations (Gotoh et al., 2007; Kliejunas et al., 2001; Solomon, 1995). However, they can become destructive pests when introduced to a monoculture, especially where pest control is weak due to the homogeneity of the host and lack of predators. Thus, some species of cossid moths are of economic importance. They are considered to be both major and minor pests of forestry and horticulture that cause serious damage to many broadleaf shrubs and trees in forest plantations, orchards, gardens and urban greenery. The damage from cossid larvae does not only reduce growth and yield but also dramatically degrades the quality of fruits and spices, the technical properties of wood, as well as its commercial value.

In this review, we list the cossid species that have been reported as pests of commercial woody plants and provide details of their hosts and distributions (Table 1). Subsequently, we briefly review the main cossid pest species from each biogeographic region. Despite our extensive review, the published list is likely to be incomplete, if only because the harmful effects of some species may not yet have been documented.

In the Palearctic realm, *Z. pyrina* and *C. cossus* are widespread and serious pests of several economically important fruit plants and roadside trees. They can cause mortality of many orchard tree species and also of vineyards, resulting in severe losses in fruit yields (Demirel, 2018; Faccioli & Baronio, 1993; Fekrat & Farashi, 2022; Hegazi et al., 2015; Kaplan & Turanlı, 2018; Kutinkova et al., 2006; Lapietra & Allegro, 1986; Turundaevskaya, 1992). Where ornamental trees are concerned, several literature sources suggest they prefer to attack softwood species such as willow and poplar (Doom, 1979; Pasqualini, 1993; Przepiora et al., 2022). Both cossid species often infest weak or damaged trees that are already affected by pathogens. In some areas, *C. cossus* can be considered a secondary pest, as it has been observed attacking pear, apple, olive and walnut trees already infested by *Z. pyrina* (Kaplan & Turanlı, 2018; Sengalewitsch, 1971; Solomon, 1995; Turundaevskaya, 1992). *Zeuzera pyrina* has been accidentally introduced to the United States and Canada, most likely by plant transportation, and has become a major invasive pest there (Solomon, 1995). The other major destructive pests in this region are *E. hippophaecolus*, a primary pest of sea buckthorn planted in Mongolia and China (Youqing et al., 2007; Zong et al., 2008), and *S. insularis*, naturally occurring on willow and poplar trees but primarily causing damage to apple and Asian pear orchards, especially in Japan (Hoshi et al., 2016; Nakanishi, 2005). Finally, *Paropta paradoxus* (Herrich-Schäffer, 1851) has been recognized as a pest of grapevines in Israel and Turkey (Atay et al., 2019; Plaut, 1973).

In the Nearctic realm, *P. robiniae* inflicts significant damage on many trees in urban areas across the United States and southern Canada and also attacks fruit orchards in certain areas. It is considered one of the most damaging species to oak timber production in the southern United States (Solomon, 1995; USDA Forest Service Protection Report, 1989). Additionally, two cossid species have been identified as minor pests: *Acossus centerensis* (Lintner, 1877) infesting poplar and quaking aspen trees in urban areas and plantations across the United States and southern Canada (Doolittle et al., 1976; Solomon, 1995) and *Cossula magnifica* (Strecker, 1876) infesting plantations of pecan and some oak species in the southeastern United States (Solomon & Payne, 1986; Van Driesche et al., 2013).

TABLE 1 Cossid species that have been reported as pests of woody plants with the details of their hosts and distribution. The number of references from published sources illustrates the importance of the pest; specific references are listed in Table S1.

Species	Host plants	Impacts	Distribution	Number of references
Acossus centerensis (Lintner, 1877)	*Populus*	Timber	Canada and United States	2
Azygophleps scalaris (Fabricius, 1775)	*Sesbania*	Crop	West Africa, East Africa, Central Africa, South Asia, Southeast Asia	4
Chilecomadia valdiviana (Philippi, 1860)	*Acer, Alnus glutinosa, Cydonia oblonga, Eriobotrya japonica, Eucalyptus, Malus domestica, Maytenus boaria, Nothofagus, Olea europaea, Persea americana, Prunus avium, Pyrus communis, Retanilla trinervia, Salix chilensis, Quercus robur* and *Weinmannia trichosperma*	Crop, Timber, Landscape	Chile and Argentina	10
Coryphodema tristis (Drury, 1782)	*Cliffortia, Combretum apiculatum, Crataegus, Cydonia vulgaris, Eucalyptus nitens, Lagunaria patersonia, Malus domestica, Myoporum, Olea europaea, Paulownia fortune, Pyrus communis, Quercus robur, Ulmus parvifolia, Vitis vinifera* and *Ziziphus mucronata*	Crop, Timber	South Africa	10
Cossula duplex (Dyar & Schaus, 1937)	*Caryocar brasiliense*	Crop	Costa Rica, Panama and Brazil	1
Cossula magnifica (Strecker, 1876)	*Carya illinoinensis, Diospyros* and *Quercus*	Crop, Timber	United States	2
Cossus cossus (Linnaeus, 1758)	*Acer, Alnus, Armeniaca, Betula, Castanea sativa, Cerasus, Citrus limon, Cydonia oblonga, Diospyros, Eleagnus, Fagus sylvatica, Fraxinus, Hippophae, Juglans regia, Malus domestica, Morus, Olea europaea, Populus, Prunus, Pyrus communis, Salix, Sambucus, Sorbus, Tilia, Quercus, Ulmus* and *Vitis vinifera*	Crop, Timber, Landscape	China, Mongolia, Russia, Europe, North Africa, West Asia and Central Asia	17
Culama australis (Walker, 1856)	*Eucalyptus*	Timber	Australia	4
Dervishiya cadambae (Moore, 1865) (synonyms = *Alcterogystia cadambae* and *Cossus cadambae*)	*Butea monosperma, Diospyros melanoxylon, Grewia tiliifolia, Mangifera indica, Nauclea cadamba, Tectona grandis, Terminalia bellirica* and *Vitis vinifera*	Crop, Timber	India and Sri Lanka	8
Endoxyla cinereus (Tepper, 1890)	*Eucalyptus*	Timber	Australia	6
Eogystia hippophaecolus (Hua, Chou, Fang & Chen, 1990) (synonym = *Holcocerus hippophaecolus*)	*Hippophae rhamnoides*	Crop, Landscape	China and Mongolia	13
Eulophonotus myrmeleon (Felder, 1874)	*Acalypha, Carya illinoinensis, Coffea, Cola acuminate, Cola nitida, Combretum, Populus, Theobroma cacao* and *Triplochiton scleroxylon*	Crop	Cameroon, Ivory coast, Congo, Ghana, Nigeria, Sierra Leone, South Africa and Togo	7
Givira ethela (Neumoegen & Dyar, 1893)	*Purshia tridentata* and *Vitis vinifera*	Crop	California	1
Magulacra nigripennata (Dognin, 1924)	*Theobroma cacao* and *Theobroma grandiflorum*	Crop	Brazil and French Guiana	1
Neurozerra conferta (Walker, 1856)	*Aegiceras corniculatum, Aquilaria malaccensis, Avicennia, Coffea, Elettaria cardamomum, Erythroxylum, Eucalyptus deglupta, Melaleuca, Ochroma lagopus, Rhizophora, Sonneratia, Tamarix indica* and *Theobroma cacao*	Crop, Timber	Sri Lanka, India, Bangladesh, Malaysia, Vietnam, Thailand and Taiwan	5
Orientozeuzera rhabdota (Jordan, 1932) (synonym = *Zeuzera rhabdota*)	*Manglietia conifera* and *Michelia mediocris*	Crop, Timber	Indonesia, Thailand, Vietnam, Myanmar and the Philippines	1

TABLE 1 (Continued)

Species	Host plants	Impacts	Distribution	Number of references
Paropta paradoxus (Herrich-Schäffer, 1851)	*Acacia arabica*, *Cercis siliquastrum*, *Crataegus*, *Ficus carica*, *Ficus pseudo-sycomorus* and *Vitis vinifera*	Crop	Lebanon, Syria, Egypt, Saudi Arabia, Israel, Iran, Jordan and Turkey	2
Polyphagozerra coffeae (Nietner, 1861) (synonym = *Zeuzera coffeae*)	*Acacia*, *Acalypha*, *Albizia falcata*, *Amherstia nobilis*, *Anisoptera costata*, *Annona*, *Artocarpus heterophyllus*, *Bauhinia*, *Camellia*, *Capsicum annum*, *Cassia*, *Casuarina equisetifolia*, *Cedrela*, *Ceiba pentanara*, *Ceslapinia pulcherrima*, *Cestrum nocturnum*, *Chukrasia tabularis*, *Cinnamomum*, *Citrus*, *Clerodendrum*, *Coffea*, *Crataegus*, *Cryptomeria japonica*, *Cymbopogon citralis*, *Delonix regia*, *Dimocarpus longan*, *Dovyalis*, *Durio zibethinus*, *Elatteria cardamonum*, *Eriobotrya japonica*, *Erythroxylum*, *Eucalyptus*, *Filicium decipiens*, *Flindersia bravlevana*, *Gmelina arborea*, *Gossypium*, *Graptophyllum pictum*, *Grevillea robusta*, *Hibiscus*, *Hydnocarpus*, *Juglans regia*, *Melia*, *Michelia champaca*, *Lantana camara*, *Nephelium lappaceum*, *Ochroma lagopus*, *Pericopsis mooniana*, *Persea*, *Phoebe*, *Phyllanthus*, *Psidium guajava*, *Punica granatum*, *Rhizophora mucronata*, *Rosa*, *Santalum album*, *Schleichera oleosa*, *Shorea*, *Spathodea*, *Swietenia macrophylla*, *Tectona grandis*, *Terminalia*, *Theobroma cacao*, *Turnera subulate*, *Vitex pinnata* and *Xylia xylocarpa*	Crop, Timber	China, Taiwan, Japan, Papua New Guinea, South Asia and Southeast Asia	16
Prionoxystus robiniae (Peck, 1818)	*Acer negundo*, *Betula papyrifera*, *Carya illinoinensis*, *Castanea dentata*, *Fraxinus*, *Populus*, *Prunus*, *Pyrus*, *Robinia pseudoacacia*, *Salix*, *Quercus* and *Ulmus americana*	Crop, Timber, Landscape	Canada and United States	15
Roepkiella chloratus (Swinhoe, 1892) (synonym = *Cossus chloratus*)	*Intsia palembanica*, *Khaya ivorensis*, *Lansium parasiticum*, *Litchi chinensis*, *Nephelium lappaceum*, *Parkia* and *Phyllanthus officinalis*	Crop, Timber	Thailand, Malaysia, Indonesia	3
Simplicivalva ampliophilobia (Davis, Gentili-Poole & Mitter, 2008)	*Myrtus communis* and *Psidium guajava*	Crop	Costa Rica and Colombia	2
Streltzoviella insularis (Staudinger, 1892) (synonyms = *Holcocerus insularis* and *Cossus insularis*)	*Fraxinus*, *Ginkgo biloba*, *Malus domestica*, *Populus*, *Pyrus pyrifolia*, *Salix*, *Sophora japonica* and *Ulmus*.	Crop, Landscape	North Asia and East Asia	8
Xyleutes ceramica (Walker, 1865) (synonym = *Duomitus ceramicus*)	*Callicarpa arborea*, *Camellia sinensis*, *Clerodendron infortunatum*, *Dubanga sonneratoides*, *D. grandiflora*, *Erythrina*, *Gmelina arborea*, *Sesbania grandiflora*, *Spathodea campanulate*, *Tectona grandis* and *Vitex parviflora*	Timber	Southeast Asia, China, India and Papua New Guinea	9
Xyleutes persona (Le Guillou, 1841) (synonym = *Zeuzera leuconotus*)	*Cassia*, *Casuarina equisitifolia*, *Durio zibethinus*, *Fraxinus chinensis*, *Premna*, *Robinia pseudoacacia*, *Salix babylonica*, *Sesbania grandiflora*, *Tamarix chinensis* and *Vitis vinifera*	Crop	China, India, Sri Lanka, Papua New Guinea, Queensland, Southeast Asia	4
Zeuzera multistrigata (Moore, 1881)	*Buxus*, *Camellia sinensis*, *Casuarina equisitifolia*, *Coffea arabica*, *Cryptomeria japonica*, *Eucalyptus*, *Glyptostrobus pensilis*, *Ilex*, *Litsaea polyantha*, *Mahonia nepalensis*, *Malus domestica*, *Mussaenda frondose*, *Passiflora edulis*, *Persea bombycine*, *Prunus*, *Santalum album*, *Streblus*, *Quercus glauca* and *Q. lineatum*	Crop, Timber	China, South Asia and Southeast Asia	8

(Continues)

TABLE 1 (Continued)

Species	Host plants	Impacts	Distribution	Number of references
Zeuzera pyrina (Linnaeus, 1761)	*Acer*, *Aesculus*, *Albizia julibrissin*, *Alnus*, *Azalea*, *Betula*, *Castanea sativa*, *Carpinus betulus*, *Casuarina*, *Ceratonia siliqua*, *Citrus limon*, *Cornus*, *Corylus*, *Crataegus*, *Cydonia oblonga*, *Diospyros virginiana*, *Euonymus*, *Fagus sylvatica*, *Ficus carica*, *Frangula alnus*, *Fraxinus*, *Hippopae rhamnoides*, *Ilex*, *Juglans*, *Ligustrum*, *Lonicera*, *Mahonia*, *Malus domestica*, *Morus*, *Olea europaea*, *Platanus*, *Populus*, *Prunus*, *Pyrus communis*, *Punica granatum*, *Ribes*, *Rhododendron*, *Rubus*, *Salix*, *Sambucus*, *Sorbus*, *Spiraea*, *Syringa vulgaris*, *Tamarix ramosissima*, *Tilia*, *Quercus*, *Ulmus*, *Viburnum*, *Viscum album* and *Vitis vinifera*	Crop, Timber, Landscape	Canada (introduced) and United States (introduced), Russia, Europe, North Africa and West Asia	27

More recently, *Givira ethela* (Neumoegen & Dyar, 1893) has been found boring into grapevine trunks and is emerging as a newly recognized wood-boring pest of vineyards in California (Scaccini et al., 2021).

In the Neotropic realm, *C. valdiviana* is the most important native insect in the cold-tolerant areas of Chile and Argentina infesting commercial *Eucalyptus* plantations, particularly *E. nitens* (Estay, 2020). It attacks both saplings and mature trees, with mortality often higher in young stands due to infested trunks snapping in the wind. It has been reported as a pest of ornamental and economically important fruit trees. However, it does not appear to cause extensive economic losses in these crops (Kliejunas et al., 2001; Lanfranco & Dungey, 2001). Recently, three cossid species have been considered to be newly emerging potential pests: *Simplicivalva ampliophilobia* (Davis, Gentili-Poole & Mitter, 2008) attacking many trees in guava orchards in Colombia and Costa Rica (Pulido Blanco et al., 2019; Pulido-Blanco et al., 2021); *Cossula duplex* (Dyar & Schaus, 1937) attacking some trees in orchards of pequi, an edible fruit popular in some areas of Brazil (Carneiro et al., 2024); and *Magulacra nigripennata* (Dognin, 1924) infesting plantations of cocoa and cupuassu in Brazil (Santos et al., 2020).

In the Afrotropical realm, *C. tristis* is a native moth of South Africa and is considered the most serious pest of *E. nitens* plantations in the region. It is also a minor pest of ornamental and commercial fruit trees. However, it has never been found to feed on the other *Eucalyptus* species planted nearby (Gebeyehu et al., 2005). The other serious pest in this region is *Eulophonotus myrmeleon* (Felder, 1874), a major pest of cacao in many countries in the region and a minor pest of pecan in South Africa (Kingsley-Umana et al., 2022; N'Guessan et al., 2010).

In Australia, *E. cinereus* and *C. australis* attack many native *Eucalyptus* species, with the most severe damage found in *Eucalyptus grandis* and *E. dunii* stands. Infestations of *C. australis* are often associated with primary attacks from longhorn beetles and *E. cinereus*. Tree mortality rates are often higher in young stands due to wind snapping the main stem, a phenomenon also found in plantations infested by *C. tristis* and *C. valdiviana* in Africa and the Neotropics, respectively. Additionally, damage to medium and old stands has been reported from yellow-tailed black cockatoos excavating the trees to hunt *E. cinereus* larvae (Carnegie et al., 2008; Thurman, 2022).

Lastly, in the Indomalayan realm, *P. coffeae* is one of the most destructive pest species affecting a wide variety of crop and timber species. It causes severe damage to vineyards in Taiwan (Chang, 1984), *Eucalyptus urophylla* plantations in Vietnam (Thu et al., 2010), *E. pellita* plantations in Indonesia and walnut orchards in Pakistan and India (Ahmad, 2017; Tavares et al., 2020). Its larvae are very small and primarily damage branches or small trunks of various commercial fruit and forest trees. Tree mortality in orchards and forest plantations is typically high in young stands due to canopy dieback and branch and trunk snapping. Occasionally, it is also found infesting seedlings in nurseries (Tavares et al., 2020; Thu et al., 2010). *Zeuzera multistrigata* (Moore, 1881) is considered a significant pest in plantations of *E. urophylla* in Vietnam and *Casuarina equisetifolia* in China, particularly in young stands, and can cause damage to some fruit tree species (Chi, Pham Duy, & Yakovlev, 2022; Huang et al., 2012). Lately, it has also been reported to cause damage to coffee and passion fruit crops in Vietnam (Thanh et al., 2024), as well as apple crops in northern India (Chandel et al., 2024). *Neurozerra conferta* (Walker, 1856) has caused significant damage to plantations of *Melaleuca leucadendra* and *M. cajuputi* that are extensively grown for cajuput oil and wood in Vietnam (Chi, Vu, et al., 2022). It has been recorded as a minor pest in young stands of planted *Aquilaria malaccensis*, a species used for agarwood production, in India and Malaysia, but interestingly, infestation in medium to old stands can result in higher quality agarwood (Khakhlari & Sen, 2023; Syazwan et al., 2019). *Azygophleps scalaris* (Fabricius, 1775) has a wide distribution, ranging from Africa to Southeast Asia. Still, it has only been recorded as a pest of *Sesbania grandiflora*, an important agroforestry species used for food and various purposes, in home gardens in some regions of India (Agrawal & Agrawal, 1960). Another significant pest in India is *D. cadambae*, one of the most damaging species to teak timber production, predominantly infesting medium to old stands of teak and grape production (Mathew, 1990; Yadav et al., 2020). *X. ceramica* is another major pest of teak plantations in Southeast Asia, particularly in Myanmar and Thailand, where it bores into the trunks of both saplings and mature trees, reducing growth rates and quality of wood but rarely causing tree mortality (Myint & Htwe, 2013; Wylie & Speight, 2012). *R. chloratus* has been reported as a serious pest of longkong orchards in Thailand and plantations of African mahogany, an economically important timber species in Malaysia (Ong et al., 2014; Thaochan et al., 2020). Recently, two cossid species have been identified as new pests: *Xyleutes persona* (Le Guillou, 1841) infesting grapevines in India (Sunitha et al., 2022) and *Orientozeuzera rhabdota* (Jordan, 1932) infesting plantations of *Manglietia conifera*, a high-value timber species, and *Michelia mediocris*, used for spice production, in Vietnam (Chi et al., 2023).

PEST MANAGEMENT

Economic loss is not only measured by estimating the negative impacts on yield of a pest, but also includes the pest control costs, which can be substantial. The cost of pest control must be equal to, or less than, the profit loss resulting from uncontrolled pest populations. Since cossids are recognized wood-boring pests, various approaches have been employed to prevent and control their infestations. These include the use of chemical insecticides (e.g., Solomon, 1985), pheromone traps (e.g., Pasqualini et al., 1985), mechanical methods such as sanitation cutting and light trapping (Jonason et al., 2014), cultural practices such as mixed species planting and biological control methods that utilize the pests' natural enemies (Forschler & Nordin, 1988; Suheri et al., 2020).

Spraying of chemical pesticides is often ineffective against cossid pests, especially in large or old trees, because the larvae spend most of their lifetimes within the trunk, branches and shoots (Kaplan & Turanlı, 2018; Mokhtaryan et al., 2021; Solomon, 1995; Solomon, 1985). Additionally, chemical pesticides can have negative effects on the environment, such as killing non-target insects, which can potentially result in an outbreak of secondary pests (Chagnon et al., 2015; Goulson, 2013). On the other hand, injection of pesticides into the tree trunk or the larvae's gallery has been reported to reduce damage more effectively and safely than spraying. For example, trunk injection can reduce damage caused by larvae of *Z. pyrina* by an average of 40–85% after 2 years, depending on the pesticides and concentrations used (Mokhtaryan et al., 2021). Meanwhile, gallery injection can cause up to 100% larval mortality of *Z. multistrigata* after 3 years (Chandel et al., 2024). However, this control method would need to be applied to individual trees; thus, it is unlikely to be economically feasible for large plantations and orchards covering thousands of hectares (Goulson, 2013; Liebhold et al., 2016).

Utilizing the pests' natural enemies can possibly provide economic, social and ecological gains while effectively controlling the pests. Generally, cossids have various natural enemies. Several hymenopteran and dipteran parasitoids, especially in the families Ichneumonidae and Tachninidae, are common parasites of cossids. Spiders, ants and birds, especially woodpeckers, are also recognized as predators of many cossid pest species (Estay, 2020; Hannon & Beers, 2007; Hegazi et al., 2015; Mathew, 1990; Sengalewitsch, 1971; Solomon, 1995; Tasen & Wiwatwitaya, 2022; Tavares et al., 2020; Thurman, 2022). Most of these natural enemies play an important role in regulating cossid populations predominantly during the early stages of their life cycle, that is, eggs, newly hatched larvae and/or early instar larvae that have not penetrated deep into wood. Among natural enemies, birds seem to be the most potential predators that can destroy many cossid adults and even feed on well-protected life stages hidden in the wood (woodpeckers, cockatoos, etc.). These natural enemies can control cossid populations in diverse forest ecosystems. However, in monoculture plantations, where host plants are abundant and closely connected, cossid populations can increase rapidly and natural enemies are often insufficient to reduce damage to acceptable levels (Solomon, 1995). Furthermore, various studies conducted under field conditions have revealed that injection of pathogens into larval galleries has a high potential to suppress cossid populations. For instance, entomopathogenic nematodes such as *Steinernema feltiae* (Filipjev, 1934) and *Steinernema bibionis* (Bovien, 1937) used against the larvae of *P. robiniae* on infested oak trees, resulted in 70–100% mortality after 2 years (Forschler & Nordin, 1988). Similarly, *Steinernema carpocapsae* (Weiser, 1955) has been used against larvae of *Z. pyrina*, where it resulted in up to 80% mortality after 2 years (Salari et al., 2021). In addition, *S. carpocapsae* and *Heterorhabditis bacteriophora* (Poinar, 1976) can cause up to 93% and 90% larval mortality of *Z. multistrigata* and *S. insularis*, respectively, after 3 years (Chandel et al., 2024; Yang et al., 1993). On the other hand, entomopathogenic fungi like *Beauveria bassiana* (Bals.-Criv.) Vuill. (1912) and *Metarhizium* spp. have often been reported to be less effective than nematodes (Chandel et al., 2024; Chi, Vu, et al., 2022; Ibrahim et al., 2019; Suheri et al., 2020; Veeranna & Remadevi, 2022). Importantly, the ability of the nematodes to disperse and infect the larvae inside their tunnels can be influenced by several factors such as depth, structure, temperature and moisture levels within tunnels (Forschler & Nordin, 1988). Moreover, as an individual tree protection approach, using nematodes suffers similar practical and economic limitations as pesticide injection when applied to large plantations, etc.

For large-scale farming, artificial sex pheromones are widely used for preventing the reproduction of moths and are the most successful approach to overcome cossid pests with the least environmental impact. For example, applying pheromone traps can reduce infestation of *Z. pyrina* in olive orchards by 58.8 and 87.5% after 1 and 2 years, respectively (Hegazi et al., 2015). As flight orientation of cossids and many other lepidopterans depends on species-specific sex pheromones, mass trapping of male moths can be conducted in large areas of plantations and orchards (Barros-Parada et al., 2021; Hegazi et al., 2015; Noeth et al., 2020; Pasqualini et al., 1985). Moreover, pheromone trapping is used to monitor pest population levels and accurately time insecticide applications for more effective control and can also be used for mating disruption (Cardé & Minks, 2003; Hegazi et al., 2010; Hoshi et al., 2016). The efficiency of pheromone traps is highly dependent on climatic conditions as well as various species-specific features such as the attractiveness of pheromone blend combinations, trap types, height of trap installation and number of traps per area (Barros-Parada et al., 2021; Faccioli et al., 1993; Maini et al., 2000). Thus, for cost-effectiveness, optimum trap types and numbers should be applied for the particular species at the right time and locations. However, the cost of pheromone identification, synthesis and production can be a significant barrier to expanding their use against additional cossid pest species. For the most part, pheromone lures have, to date, been synthesized for and applied to cossid species in temperate regions including *C. cossus* (Capizzi et al., 1983), *C. tristis* (Bouwer et al., 2015), *C. valdiviana* (Herrera et al., 2016), *E. hippophaecolus* (Fang et al., 2005), *P. robiniae* (Doolittle & Solomon, 1986), *S. insularis* (Chen et al., 2006) and *Z. pyrina* (Tonini et al., 1986). No sex pheromones have yet been identified for cossid pests in tropical regions.

Accordingly, selecting the most appropriate method to prevent or control cossid infestations might depend on budget, infestation severity and size of crop production area. However, since the majority of the cossid life cycle is spent in the larval stage inside trees, relying on a single control method, including pheromone trapping, is unlikely to fully mitigate the damage caused by these pests. An integrated pest management approach is essential for effectively preventing or controlling cossid infestations. This technique involves combining multiple methods tailored to the insect's behaviour at different life stages to achieve more comprehensive and sustainable control. For instance, as female adults of many species prefer to oviposit on weak or damaged trees, avoiding mechanical injury to the trees is a necessary first step. Subsequently, if any signs of infestation are detected on twigs or branches, sanitation pruning should be immediately implemented. Spraying of pesticides and insect pathogens is most effective when applied to early instar larvae that live in small or young trees; the height of larger trees can limit thorough application, particularly if the infestation extends high into the crown (Chi, Vu, et al., 2022; Forschler & Nordin, 1988; Ibrahim et al., 2019; Thaochan et al., 2020). Thus, injection of pesticide and insect pathogens into the tree is a more effective alternative to control larvae in large or older trees; however, its effectiveness diminishes when applied to later instar larvae that have penetrated deep into the heartwood, which consists of non-living xylem tissues (Forschler & Nordin, 1988; Mokhtaryan et al., 2021). In such cases, injection directly into the larvae's gallery is necessary. For heavily infested trees, sanitation cutting is likely to be necessary to prevent further expansion of the infestation. In addition, mixed species plantings and the promotion of understorey vegetation have been suggested as strategies to prevent and reduce the spread of cossid species with a less polyphagous habit, such as *X. ceramica* in teak plantations (Choochuen et al., 2024). During the season of adult moth emergence, pheromone traps can be used to monitor insect population density, helping assess the severity of infestation across forests or orchards. This information can then inform decisions on the number of additional traps required for mass trapping and determine the most effective locations for their deployment (Barros-Parada et al., 2021; Hegazi et al., 2015; Noeth et al., 2020; Pasqualini et al., 1985).

More importantly, studying the habitat requirements of particular cossid species, including tree characteristics, stand conditions and other environmental factors, could provide valuable insights for infestation-risk assessment. This knowledge can help predict when and where the likelihood of infestation is high, enabling more targeted and effective management strategies (Choochuen et al., 2024; Fekrat & Farashi, 2022; Kumbula et al., 2019). Furthermore, understanding the seasonal emergence pattern of cossid moths under different environmental conditions, such as climate and topography, is crucial (Solomon & Neel, 1972). When combined with mass trapping, this information can enhance the precision of pest monitoring and contribute to more cost-effective pest management strategies.

FUTURE RISKS AND CHALLENGES

Considering the wide distribution of cossid moths and their considerable impacts, it is worth investigating whether global climate change is increasing the risk of exposure to these pests. A number of studies have aimed to identify and understand how climatic and environmental variables influence the spatial distribution of pests (Fekrat & Farashi, 2022; Horrocks et al., 2024; Schneider et al., 2021; Tang et al., 2019; Yan et al., 2017). Researchers have noted that rising summer temperatures and shorter winter periods have resulted in accelerated reproduction and faster growth of insect pests (Ma et al., 2021). In temperate climates, such conditions allow them to expand their attacks to new areas or host plant species, as drought stress increases the susceptibility of the hosts. Tropical climates are also likely to face an increase in insect pest attacks, though the effect is generally expected to be less pronounced compared to temperate regions (Schneider et al., 2022). For cossids, the interaction between drought-stressed susceptible hosts and the drought-tolerant nature of insects has been observed in *Z. pyrina* and *C. tristis*, which are linked to warmer temperature and low moisture content or precipitation (Adam et al., 2013; Fekrat & Farashi, 2022; Kumbula et al., 2019; Mokhtaryan et al., 2021). Global species distribution models, incorporating future climate projections, have been conducted for *Z. pyrina* and show a northward expansion trend in the Northern Hemisphere and a southward expansion trend in the Southern Hemisphere as a result of global warming (Fekrat & Farashi, 2022). These expansion trends are unlikely to be restricted to *Z. pyrina*. In addition to range expansion, another climate change driven effect on pests to consider is host plant shifts. Many cossid species can live on various plant species, that is, they are generalist insect herbivores; therefore, it is foreseeable that they may adapt to their secondary or even entirely new host plants, especially if their primary hosts become scarce due to climate change or other environmental pressures. This could lead to an increase in the severity of infestation of secondary host plant species or an incidence of pest infestation on previously unaffected plant species (Berg et al., 2010; Bovay et al., 2024; Gilman et al., 2010). This issue is of particular concern for *C. tristis* in South Africa, where it may shift from its primary host, *E. nitens*, into plantations of other *Eucalyptus* spp. (Kumbula et al., 2019). As some cossid species target the same plant species, genera or families, climate change could enable a single plant species to be affected by multiple cossid species, particularly those inhabiting the same biogeographical regions or similar environmental conditions.

As most cossid moths are known to be weak flyers, the transportation of plants, logs or wood material infested with eggs or early instar larvae is expected to be the most likely pathway for the spread of a species outside its natural range. This has been the case with *Z. pyrina*, which was introduced into the United States. However, *Z. pyrina* is the only cossid species reported to have spread to a new biogeographical region, which might be due to the low ability of cossid moths to develop or complete their life cycle in cut trees, packaging material, etc. Alternatively, exotic, susceptible plant species may be introduced into the native range or suitable habitats of particular cossid species. This has been the case for *C. tristis* and *C. valdiviana* that damage *Eucalyptus* planted in South Africa and South America, respectively.

In conclusion, on a large scale, early detection and control of infested plants and materials is considered an efficient way to prevent the introduction of cossid pests to new habitats through transportation. Modelling the potential distribution of insects in relation to climatic conditions is essential for assessing potential expansion and understanding the ecological requirements of key cossid pests, especially those that share the same host plant species or families. In addition to potential distribution, studying the temporal and long-term effects of climate change on the life cycle and population dynamics of insects is crucial for effective pest management. Such research helps develop strategies that align with the behaviours of insects at different life stages under varying climatic conditions. Importantly, knowledge of the characteristics of hosts that are susceptible or resistant to insect attack is also needed in order to prevent and minimize damage from pest infestations. Such studies investigating the response of insects to changing climatic parameters, and host density and susceptibility have been conducted on other lepidopteran pests to gain knowledge of their ecological requirements and adaptive behaviours, demonstrating that it can be done with cossids as well (Robinet et al., 2014; Robinet & Roques, 2010; Roques et al., 2015; Tamura et al., 2022). Finally, further studies on sex pheromone identification and synthesis and optimal mass trapping strategies are needed to support monitoring efforts, particularly for tropical species that have not been thoroughly studied. These recommendations are expected to allow us to understand the complexity of host plant-pest interactions and the adaptation of pests to a changing climate and contribute to the effective management of cossid pests.

CONCLUSIONS

1. The Cossidae is a worldwide family of macro-moths. It is composed of 10 confirmed subfamilies, with the greatest number of species represented in the subfamilies Zeuzerinae and Cossinae. Their habitat is very diverse, ranging from deserts to boreal regions and high mountains. Most cossid species' larvae are highly polyphagous caterpillars that feed on inner bark tissues and/or sapwood and heartwood on the main stems of woody plants. However, several species are known to live in succulents, and one species feeds on the roots of plants.
2. Cossids have a long life cycle that varies from 1 to 3 years, with the majority of this time spent in the larval stage. The adults of many species have a low dispersal ability, which results in aggregated distributions. Cossid larvae can migrate intra-host, and some species can even shift to a new host (inter-host migration) in later larval instars when the host can no longer offer sufficient nutrients.
3. The feeding tunnels of cossid larvae can compartmentalize the host tissues and further make large branches or even the trunks of small trees prone to wind breakage, interrupting the nutrients and water conduction between the canopy and roots of infested trees, leading to tree decline and eventually death. However, the rate of decline in trees damaged by cossid larvae is slower compared to those damaged by phloeophagous insects.
4. There are 26 species of cossid moth that have been reported as pests of woody plants in forestry and horticulture. Cossid larvae damage not only reduces growth and yield but also dramatically degrades the quality of fruit products and technical properties of the wood, as well as its commercial value.
5. Pheromone trapping is considered an effective approach to control cossid infestations. Species-specific sex pheromones have been identified for many temperate species, whereas none have been identified for tropical species. Nonetheless, as these insects spend the majority of their life cycle as larvae inside host tissue, an integrated pest management approach tailored to the insects' behaviour at different life stages is essential.
6. Global warming is linked to possible range expansion of some cossid species. Future research should focus on host shifts and the introduction of pests into new habitats and new host species into existing pest ranges. Further study on the characteristics of host plants that are susceptible or resistant to pest attacks, the effects of climate change on the susceptibility of host plants and pest life cycles, population dynamics and potential distribution are required to understand the ecological requirements and adaptive behaviours of key cossid species.

AUTHOR CONTRIBUTIONS

Thanapol Choochuen: Conceptualization; project administration; writing – original draft; writing – review and editing. **Jiří Foit:** Conceptualization; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Cossid species that have been reported as pests of commercial woody plants with references from published sources.

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