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ORIGINAL PAPER

Three new species of ambrosia beetles established in Great Britain illustrate unresolved risks from imported wood

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Abstract
Bark and ambrosia beetles (Scolytinae) are frequently introduced to new areas through international trade of wood and wood products. When novel host trees are encountered, they can be naïve and susceptible to attack, enabling previously harmless scolytine species to become damaging, or the symbiotic fungi of ambrosia beetles to become pathogenic. Invasive Scolytinae are often only recognised after they have become harmful, so the early detection of such species is important for forest protection and management. The first nationwide survey of Scolytinae in Great Britain was conducted between 2013 and 2017, to determine the presence and distribution of previously undetected alien species. Study sites included pine, spruce and oak forests and forests near ports where wood and forest products are imported. Insect traps baited with 'broad-spectrum' lures were employed to maximise the diversity of scolytine species collected. Three recently established alien species were detected, *Xylosandrus germanus*, *Gnathotrichus materiarius* and *Cyclorhipidion bodoanum*; the latter two species are new records for Britain. All three species appear to be largely restricted to south-east England at present, and strikingly, all are ambrosia beetles. Current EU plant health regulations for wood importation and movement are limited in their effectiveness against ambrosia beetles, since bark removal does not typically destroy them. In the relatively cool summer climate of Britain, southern England appears to provide the most optimal thermal conditions for the establishment of invasive wood and bark-boring beetle species.

Keywords Scolytinae · Bark beetles · Invasive pests · Biosecurity · Plant health · International trade

Key message

- The early detection of invasive bark and ambrosia beetles is an important part of integrated pest management.
- A comprehensive survey detected three species of ambrosia beetle recently established in Britain.
- Gaps exist in the plant health regulations of Britain and the EU, allowing widespread movement of ambrosia beetles in wood.
- The climate of southern England appears to be the most suitable in Britain for the establishment of alien wood and bark-boring species.

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Introduction

Invasive pests are one of the most serious threats facing forests worldwide in the twenty-first century, with international trade providing innumerable pathways for a wide range of non-native insects (Meurisse et al. 2019). Due to their small size, intimate association with host trees, and cryptic nature, bark and ambrosia beetles (Coleoptera: Scolytinae) are readily and frequently transported in wood products around the world. Wood packaging material (WPM) including pallets, crates and dunnage, as well as timber, logs and fuel wood, are a major source of scolytine interceptions and introductions (Brockerhoff et al. 2006a; Haack and Rabaglia 2013). International trade has inadvertently allowed at least 58 species of exotic Scolytinae to establish in the USA (Haack and Rabaglia 2013), and at least 20 species in continental Europe (Kirkendall and Faccoli 2010; Rassati et al. 2016a).

The Scolytinae are a diverse and species-rich subfamily, but can be considered in terms of two distinct ecological groups: bark beetles and ambrosia beetles. Bark beetles tunnel and breed in the inner bark of their host plants, primarily deriving their nutrition from phloem feeding, although they usually associate with fungi for purposes of food enrichment and overcoming host defences (Harrington 2005). The ambrosia beetles have developed even closer symbiotic relationships and have become 'fungus–farmers'. The term 'ambrosia beetle' is an ecological classification describing the larval and adult habit of feeding upon mutualistic fungi cultivated in the woody host tissue (xylomycetophagy), and as an ecological group includes species of both Scolytinae and the distantly related Platypodidae. The ambrosia fungi are transported by the adult beetles in specialised structures (mycangia) or on the body surface and inoculated onto the gallery walls as they tunnel into the host (Kirkendall et al. 2015). Fungus farming provides a nutritious diet, and is evidently a highly advantageous strategy, since it has evolved on at least ten independent occasions within the Scolytinae and is present in some 3400 described species (Jordal and Cognato 2012). Although the nature of their relationship is often unclear, most of the identified fungi associated with ambrosia beetles are ascomycetes of the order Ophiostomatales, including many species of *Ophiostoma*, as well as *Ambrosiella*, *Raffaelea* and *Ceratocystis* (Harrington 2005), the latter two genera including many important plant pathogens.

Typically, bark and ambrosia beetles attack weakened, dying or recently dead host trees in their native ranges. However, when ambrosia beetles are introduced to new areas, previously harmless beetle–fungus symbioses may become pathogenic and kill novel host species. The new hosts lack a shared evolutionary history, and may be 'naïve' and susceptible, and the beetles may be attracted to live trees rather than being confined to dead or dying hosts (Hulcr and Dunn 2011). The risk to tree health from invasive Scolytinae is significant, and the rate of new and damaging introductions worldwide continues to grow (Ploetz et al. 2013). For example, the introduction of an Asian ambrosia beetle *Xyleborus glabratus* to the USA has brought its ambrosia fungus *Raffaelea lauricola* into contact with Lauraceae species on which it is highly pathogenic, causing Laurel wilt and the widespread death of redbay and swampbay (Hughes et al. 2017). Another ambrosia beetle, *Pityophthorus juglandis* vectors the fungus *Geosmithia morbida* and causes thousand cankers disease on walnut in the USA. Illustrating the risk of international trade routes as pathways for such pests, *P. juglandis* has recently been introduced into Italy (Faccoli et al. 2016).

The early detection of new and emerging pests is critical to forest protection, whether the subsequent goal is to eradicate, contain, or manage the threat. Unfortunately, novel establishments are rarely detected until a pest has begun to cause damage. Such was the case for the last notable bark beetle to have been introduced to Britain, *Dendroctonus micans*, which arrived in the early 1970s, most likely on poorly debarked spruce timber (Bevan and King 1983). This species has caused extensive damage in continental European spruce forests (Grégoire 1988), but has been managed in Britain through the widespread release of its natural predator *Rhizophagus grandis* (Evans and Fielding 1994). Proactive and routine surveillance of ports and timber-mills handling high-risk wood products, and broader forest-based surveys have been used worldwide to identify new introductions of wood and bark-boring beetles, typically using baited insect traps. Trapping in ports tends to detect more invasive beetle species than forest-based surveys, but these may include 'interceptions' as well as incipient establishing populations. Studies by Humble (2001) around Vancouver, Canada, and by Rabaglia et al. (2008) across the USA, each detected five species of Scolytinae which had become established in those countries, but were previously unrecognised. Two other countrywide surveys in New Zealand (Brockerhoff et al. 2006b) and Italy (Rassati et al. 2015) targeted ports of entry and nearby forests; both collected many introduced Scolytinae species, although all were previously known to be established, or considered to be interceptions.

Although protected zone surveys for *Ips* and *Dendroctonus* spp. are undertaken annually in Britain alongside port surveillance (Forestry Commission 2012), a nationwide survey for invasive wood and bark-boring beetles has not previously been conducted. The present study therefore aimed to address this by surveying key forest areas throughout England, Wales and Scotland with baited insect traps to determine the presence and distribution of any previously undetected alien Scolytinae. Three ecologically and economically important forest types were targeted (oak, pine and spruce), and additional 'high-risk' forests (of assorted species) were also surveyed close to key ports importing wood and forest products. By trapping in forests close to the ports the study aimed to detect established alien species, rather than in the ports themselves where some captures may represent interceptions of recent arrivals not necessarily established.

Materials and methods

Attractant-baited insect traps were deployed at 67 forest sites across Britain as part of a nationwide survey of Scolytinae (Fig. 1). Different plantation forest sites were monitored each year between 2013 and 2015 and were selected to represent the geographical range of pine (*Pinus sylvestris*, *P. nigra* ssp. *laricio)*, spruce (*Picea sitchensis*, *P. abies*) and oak (*Quercus robur*, *Q. petraea*) forests across Britain. Additionally in 2017, 20 woodland sites were surveyed which were located close to the 25 ports which had imported the greatest tonnage of wood and other forest products between 2000 and 2015 into England, Wales and Scotland (Department of

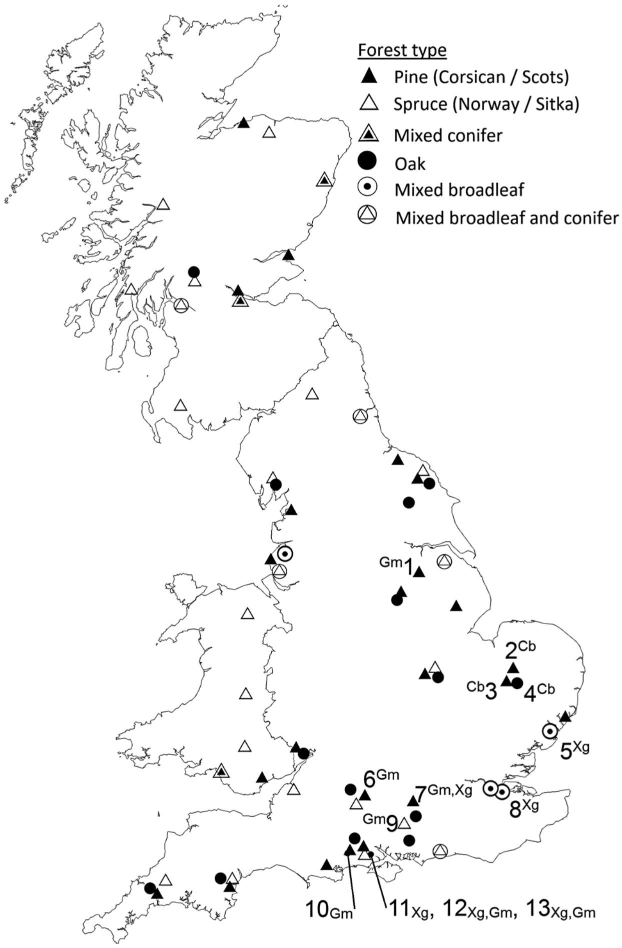

Fig. 1 Location of British forest sites surveyed for Scolytinae, 2013–17. Number codes indicate sites where non-native species were detected (detailed in Table 1); Cb = *Cyclorhipidion bodoanum*, Gm = *Gnathotrichus materiarius*, Xg = *Xylosandrus germanus*

Transport 2016). Forest sites surveyed therefore represent a selection of single species forestry plantations and species mixtures (Fig. 1). All forests were deemed ‘mature’ (planting date range of 1750–1983) and had undergone typical forest management.

A standardised trapping method was employed using either Lindgren multi-funnel traps or cross-vane panel traps (Contech Enterprises Ltd) interchangeably, after studies demonstrated that both types were equally effective for collecting bark beetles (D. Inward unpublished, Dodds et al. 2010). Lures were hung from each trap to attract Scolytinae, mimicking volatile chemicals emitted by damaged and stressed trees. 100% ethanol was used in all cases, released from 50-ml polypropylene screw-top containers with four 3-mm drilled holes in the lid, at a rate of approximately 200 mg/day at 15 °C. In all coniferous and mixed forests, an additional lure (-)-alpha-pinene was also employed, released from a polypropylene tube with a 1 cm wick of viscose tape, at a rate of approximately 300 mg/day. Ethanol and alpha-pinene are well known to be synergistically attractive to many species of wood and bark-boring beetles and are widely used ‘broad-spectrum’ lures (e.g. Brockerhoff et al. 2006b; Miller and Rabaglia 2009; Dodds et al. 2010), although they are not equally attractive to all Scolytinae species. They are therefore appropriate for determining the overall Scolytinae community composition in a forest, rather than using pheromones which are more taxon-specific. Propylene glycol (65% concentration) was used in all traps to preserve collected specimens. Traps were suspended from a rope tied between two trees, with the base approximately 50 cm above the ground. At each field site, five traps were placed along a straight-line transect, at least 50 m apart, from the end of March until the end of July, a period covering the peak flight season of the forest Scolytinae in Britain (D. Inward unpublished). Traps were emptied every 2 weeks, and the lures and preservative fluid changed. Collected insects were transferred to 100% ethanol and stored in a domestic freezer for optimal DNA preservation. Scolytinae were identified using the keys and descriptions in Duffy (1953), Grüne (1979), Wood (1982), Vandenberg et al. (2000) and Duff (2016), and confirmed using the collections of Forest Research and the Natural History Museum, London.

Results

During the GB-wide survey, over 61,000 individual bark and ambrosia beetles were collected and identified, representing 39 Scolytinae species in total (29 phloem-feeding bark beetles and ten ambrosia beetles). Amongst these, three recently established alien species were detected: *Xylosandrus germanus* (Blandford), *Gnathotrichus materiarius* (Fitch) and *Cyclorhipidion bodoanum* (Reitter). These three invasive species are all ambrosia beetles of two different subtribes. Only *X. germanus* has been previously recorded in Britain (Allen et al. 2015), *G. materiarius* and *C. bodoanum* are new UK records. Thirteen forest sites (of 67 investigated) were found to contain one or more of these invasive species; these were nearly all restricted to south-east England (Fig. 1, Table 1). A brief description of the ecology and distribution of the species is provided below, and photographs presented in Fig. 2.

Xylosandrus germanus

Xylosandrus germanus was collected from six sites, and with the records from Allen et al. (2015), and it is apparent that the species is well distributed in an arc across south-east England, from Harwich in Suffolk to the New Forest in Hampshire (Fig. 1, Table 1). This suggests establishment

Table 1 Forest site details where invasive ambrosia beetles were detected, 2013–2017

Figure 1 code	Field site	Total number of individuals			Site details					
		Gnathotrichus materiarius	*Xylosandrus germanus*	*Cyclorhipidion bodoanum*	Main tree species	Secondary tree species	Latitude, longitude	Altitude (m)	Planting date	Collection year
1	Laughton Forest, Lincolnshire	2			CP	BI (29%)	53.47N, 0.74 W	5	1978	2017
2	Cold Harbour, Thetford Forest, Norfolk			3	CP	SP (21%)	52.47 N, 0.65E	25	1969	2013
3	Rougham Corner, Thetford Forest, Norfolk			2	CP	–	52.50 N, 0.63E	25	1975	2014
4	Emily's Wood, Thetford Forest, Norfolk			2	OK	BE/AH (30%)	52.47 N, 0.64E	20	1850	2014
5	Stour Wood Nature Reserve, Wrabness, Essex		1467		MB	(SC,OK,BI)	51.94 N, 1.19E	25	Ancient*	2017
6	Chisbury Wood, Savernake Forest, Wiltshire	1			CP	DF (20%)	51.39 N, 1.61 W	155	1977	2014
7	Bramshill Plantation, Hampshire	1	25		CP	SP (5%)	51.33 N, 0.89 W	90	1975	2013
8	Cobham Wood, Rochester, Kent		48		MB	(OK,AH, SC,HBM,HAW)	51.39 N, 0.44E	110	Ancient	2017
9	Chawton Park Wood, Hampshire	1			NS	–	51.13 N, 1.03 W	185	1951	2015
10	Ringwood Forest, Hampshire	4			CP	SP (25%)	50.88 N, 1.83 W	55	1970	2013
11	Islands Thorns Inclosure, New Forest, Hampshire		267		OK	BE (33%)	50.93 N, 1.69 W	80	1852	2014
12	King's Garn Gutter Inclosure, New Forest, Hampshire	389	291		SP	BE/OK (22%)	50.92 N, 1.63 W	65	1945	2014
13	Coppice of Linwood, New Forest, Hampshire	247	704		NS	(OK, BE, CP adjacent)	50.93 N, 1.65 W	100	1947	2015

* Primarily sweet chestnut coppice c. 1975

Tree species: *AH* ash, *BE* beech, *BI* birch, *CP* Corsican pine, *DF* Douglas fir, *HBM* hornbeam, *HAW* hawthorn, *NS* Norway spruce, *MB* mixed broadleaves, *OK* oak, *SC* sweet chestnut, *SP* Scots pine

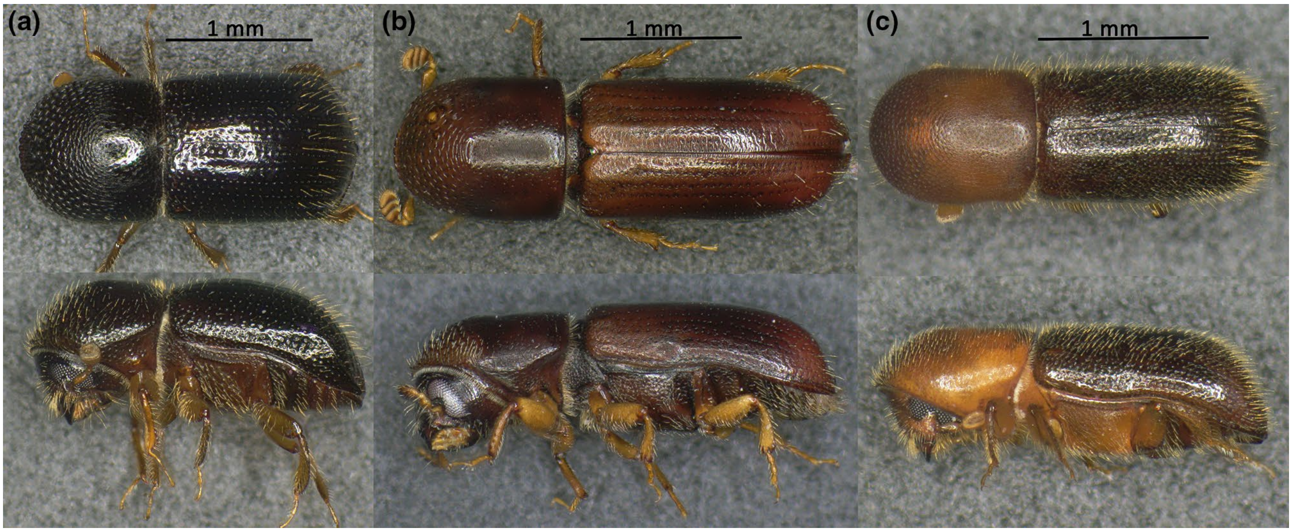

Fig. 2 Dorsal and lateral photographs of exotic Scolytinae species newly established in Britain; **a** *Xylosandrus germanus*, **b** *Gnathotrichus materiarius* and **c** *Cyclorhipidion bodoanum*

some years ago with subsequent spread across this area. The ecology, distribution and impact of *X. germanus* have been reviewed recently by Inward (2015) and CABI (2018) and are only summarised here. Descriptions and keys to *X. germanus* may be found in Wood (1982), Faccoli (2008) and Gomez et al. (2018). This xylomycetophagous beetle of the subtribe Xyleborini is originally native to Japan, Korea and eastern China, but is now widely established in central and western Europe, southern Russia and Turkey, and in the eastern and Pacific Northwest regions of North America. A small species, the females only 2–2.3 mm long (Fig. 2a), it typically has one or two generations per year depending on climate. It is thought to readily disperse up to 2 km, though several tens of km/year are possible with human assistance. The females inbreed with flightless male siblings, and disperse carrying a symbiotic fungus *Ambrosiella hartigii*, a species also carried by the native European *Xyleborus dispar* (French and Roeper 1972). *Xylosandrus germanus* is highly polyphagous, typically as a secondary agent upon stressed, unhealthy or recently dead hosts. Over 200 host species from 51 plant families have been identified, and it has been collected from a range of coniferous and broadleaf tree species in this and other studies (Table 1). The ecological traits of polyphagy and inbreeding have undoubtedly contributed to its wide scale establishment and relatively rapid spread. Impacts to date include damage to stored timber, including *Quercus*, *Fagus*, *Tilia*, *Picea* and *Pinus*, to nursery and orchard trees including *Juglans*, *Castanea* and *Corylus*, and collective attacks with other ambrosia beetles on mature beech trees and even grapevine. Environmental stresses such as flood stress, drought or frost damage appear to have been primary factors in the attacks on live hosts, however.

Gnathotrichus materiarius

Gnathotrichus materiarius was detected in seven sites, primarily grouped in the far south of England, with an additional finding in north Lincolnshire (Fig. 1, Table 1). This presumably represents two separate introductions or human-mediated spread from the southern to the northern site. Native to eastern North America, *G. materiarius* was first detected in France in 1933 (Balachowsky 1949) and is now widespread across much of Europe (Valkama et al. 1998; López et al. 2007; Kirkendall and Faccoli 2010; Mazur et al. 2018). Descriptions and a key may be found in Balachowsky (1949), Wood (1982) and Mazur et al. (2018), but it remains little studied. A member of the subtribe Corthylini, *G. materiarius* is a monogynous, outbreeding species with a balanced sex ratio (Flechtmann and Berisford 2003). The males initiate gallery construction and release a pheromone to attract a female and introduce the symbiotic ambrosia fungus *Ambrosiozyma monospora* (syn. *Endomycopsis fasciculata)* into the host (Batra 1963), which is then used as a food source for adults and larvae. Females are 1.7–3.1 mm long. Recorded breeding resources include *Pinus, Picea, Larix, Tsuga, Pseudotsuga* and *Abies* (Balachowsky 1949); accordingly it was detected in Scots pine, Corsican pine and Norway spruce forests in this study (Table 1). *Gnathotrichus materiarius* attacks only dead and dying hosts, and damage to date has been limited to the excavation of galleries in timber and staining by the fungus (Valkama et al. 1998; Mazur et al.

2018). It has been recorded attacking debarked timber, however (Bussler and Immler 2007), an important consideration regarding spread.

Cyclorhipidion bodoanum

Cyclorhipidion bodoanum was only detected at Thetford forest in Norfolk (Fig. 1, Table 1), and may be the most recently established species, have had less opportunity to spread, or be climatically restricted. Another inbreeding species of the subtribe Xyleborini, *C. bodoanum* is native to northern Asia (Siberia, China) (Vandenberg et al. 2000), but has been introduced to North America, where it was described as *Xyleborus californicus* (Wood 1975), before being synonymised and moved into the genus *Cyclorhipidion* by Knížek (2011). It is also now widespread in western Europe (Kirkendall and Faccoli 2010). Another small species of only 2–2.2 mm long, descriptions and keys are available in Wood (1982) and Vandenberg et al. (2000) as *X. californicus* and Gomez et al. (2018). Very little studied, it is typically associated with Fagaceae, particularly *Quercus* (Wood 1982; McPherson et al. 2008; Blaschke and Bussler 2012), but has also been recorded attacking declining walnut trees (Seybold et al. 2016). It has been most often collected in small numbers (Table 1, Blaschke and Bussler 2012; Seybold et al. 2016) and is not generally considered to be economically important. In Bavaria, however, larger populations have been collected in oak forest, where the species was seen to prefer larger branches in the crowns of oak and occasionally sweet chestnut (Bussler and Immler 2007). Although detected in two pine stands in addition to an oak stand in Thetford (Table 1), it seems likely that the species was attracted to the ethanol lure from nearby Fagaceae hosts.

Discussion

Ecological and economic significance

Only seven species of ambrosia beetle have been previously recorded as native or established in the UK (Duff 2016), compared to 57 species of phloem-feeding bark beetles. It is notable then that three new species of ambrosia beetle were detected in the study, but no new phloem feeders. Of course, the use of 'broad-spectrum' trapping lures such as ethanol and alpha-pinene will not be equally attractive to all species; taxa which use aggregation pheromones to coordinate mass attacks on their hosts, such as *Ips* and *Dendroctonus,* typically respond better to pheromone lures (e.g. Wermelinger 2004) and may not have been detected. However, ambrosia beetles are known to be highly successful invaders, making up 25 of the 58 invasive scolytines established in the USA (Haack and Rabaglia 2013), and two-thirds of the exotic species established in continental Europe (Kirkendall and Faccoli 2010). Fungus farming is a successful strategy not only because it provides a nutrient-rich diet, but because most of the mutualistic ambrosia fungi are polyphagous (Beaver 1989), enabling exotic ambrosia beetles to utilise a range of novel hosts in an invaded area. *Xylosandrus germanus* is a good example, breeding in a wide range of both broadleaf and coniferous hosts, whilst *G. materiarius and C. bodoanum* are also polyphagous within the *Pinaceae* and *Fagaceae*, respectively. Invasive ambrosia beetles are also often assisted by the widespread strategy of reproduction by sibling mating (inbreeding) before dispersal. This means that the initial spread of such species is not limited by difficulties of mate location, and small populations are less vulnerable to extinctions (Kirkendall et al. 2015). The successful establishment and spread of these exotic scolytines in Britain are therefore likely to have been facilitated by fungus farming, polyphagy and (in the Xyleborini species) inbreeding.

The three newly established beetles in Britain are all secondary pests, and damage in their introduced ranges has been typically associated with weakened or stressed hosts. Due to the effects of a changing climate, we may, however, expect to see increasing levels of damage from such pests, due to more frequent drought stress of host trees, increased frequency of windblows and increased voltinism (Wainhouse and Inward 2016). To date, *X. germanus* has demonstrated considerable potential for economic and environmental damage in both Europe and North America (Inward 2015). The present study also demonstrates its capacity for numerical dominance: around 90% of individuals collected at a sweet chestnut-dominated forest in Essex were *X. germanus* (Table 1). Chestnut-dominated forests in Italy and the USA have also been shown to be particularly attractive to *X. germanus* and favourable for large populations (Oliver and Mannion 2001; Rassati et al. 2016b). Focusing trapping efforts in such forests may therefore provide an effective means of detecting the further spread of *X. germanus*.

Pathways for the movement of ambrosia beetles

The detection of three exotic species of ambrosia beetles raises the question of how they were introduced, and what plant health regulations are in place to prevent further introductions. The source of these newly recorded species cannot be accurately determined since all are now globally distributed; however, movement of such beetles into the British Isles is very unlikely to be by natural spread. The initial introduction and subsequent onward spread of *X. germanus* in Europe and North America was via movement of infested wood (Bruge 1995; LaBonte et al. 2005; López et al. 2007). However, the importation of wood commodities into Britain and Europe is only regulated for those tree species known to host harmful pests and diseases; this includes all conifers and a limited number of broadleaf genera. In these cases, import requirements are quite detailed and vary according to tree species, country of origin and the precise commodity (Forestry Commission 2018a, b). In brief, however, coniferous wood which is bark free may be imported into the UK from any other country. If originating from within the EU, it may alternatively be transported (with bark attached) when accompanied by a plant passport stating it to be from a pest-free area or to have been kiln-dried. Coniferous wood from outside the EU must be bark free and be free from 'grub holes' over 3 mm diameter, or to have been kiln-dried or heat-treated. Due to common plant health regulations, movement of broadleaf wood between EU countries is not subject to any form of regulation (except for plane and sweet chestnut), and importing wood of broadleaf species from outside the EU is only regulated for a few genera where specific pest or disease threats have been identified. These include for example, *Betula* and *Fraxinus* species from North America, due to the risks from Bronze Birch Borer *Agrilus anxius* and Emerald Ash Borer *A. planipennis*, respectively.

There are some notable gaps within these regulations which may have facilitated the spread of *X. germanus*, *G. materiarius* and *C. bodoanum* across Europe and into Britain, and which offer open pathways for the introduction of other, unidentified wood and bark-boring beetles from around the world. Bark removal from timber prior to export serves an important role in limiting the spread of damaging phloem-feeding beetles, but it is not effective against ambrosia beetles. Their strategy of boring into the xylem of their hosts means that mechanical bark removal does not physically remove them from the wood. This means that wood of any coniferous or broadleaf tree being imported into the UK or EU countries, which has not been thoroughly heat-treated, irradiated, or fumigated, remains a potential pathway for the movement of invasive ambrosia beetles. Even squared wood and wood with the sapwood removed may harbour insects if not treated. Most broadleaf wood does not even require its bark to be removed and may additionally carry phloem-feeding beetles. Additionally, by allowing coniferous wood with grub holes up to 3 mm in diameter to enter the EU, the regulations disregard the galleries of the great majority of ambrosia beetle species, as they are typically very small.

One commodity which is now well regulated is wood packaging material (WPM), reflecting the significant role that this commodity has played in spreading invasive pests around the world (Haack et al. 2014). Importation of WPM into Britain and the EU is based on the 'International Standard for Phytosanitary Measures 15' (ISPM15), requiring the wood to be debarked *and* either heat-treated or fumigated (Forestry Commission 2018a; IPPC 2016a, b). Critically, these treatments should be effective against ambrosia beetles as well as other wood and bark-boring pests. However, WPM movement between EU countries requires less stringent treatment; coniferous WPM may be either bark free, kiln-dried with bark present, or declared to be from an area free of certain bark beetles (except from Portugal due to pinewood nematode), whilst WPM made from broadleaf timber is again largely unregulated.

Conclusions

The great diversity of ambrosia beetles around the world comprises a large pool of potentially invasive species, and the international movement of wood provides a ready pathway for their distribution. Although most accidental introductions fail to establish, or are of limited impact, the increasing frequency of Scolytinae and other forest pest and disease introductions worldwide (Brasier 2008; Roy et al. 2014) demonstrates that the risks are significant, and that stricter phytosanitary measures are called for. Current international guidelines for the movement of wood suggest that '*Phytosanitary measures should not be required without appropriate technical justification based on PRA*' (IPPC 2017). This means that all 'unlisted' organisms remain unregulated (Brasier 2008). The retrospective approach of regulation by PRA, based on damage inflicted *after* a pest has already established on a new host or in a new area, may help limit the onward spread of such an organism, but cannot prevent the initial impact, nor the unexpectedly destructive 'black swan' disease interactions when Scolytinae encounter new pathogens or naïve hosts (Ploetz et al. 2013). Because of the cryptic nature of bark and ambrosia beetles, by the time such damage is recognised, the insect has usually spread so widely that eradication is impossible.

Several ambrosia beetle species have been placed on the EPPO Alert, A1 or A2 lists, highlighting the potential risk they pose to the member countries, yet the great majority of potentially damaging species remain unlisted due to limited evidence of impact in their current range. Wood currently being imported into Britain and the EU therefore remains an open pathway for unidentified ambrosia beetles and associated fungi from all over the world. Responding to this threat, a recent EPPO expert working group study of exotic bark and ambrosia beetles of broadleaf trees determined that the risk posed was too broad to address by pest-specific PRAs or regulation of particular host species. Instead it recommended the adoption of horizontal measures for all non-coniferous wood from all origins (EPPO, to be published 2019). This would ideally mean that the same phytosanitary measures currently applied to wood packaging material would be applied to all broadleaf wood being imported into the member countries.

The detection of three new species of ambrosia beetle in Britain should be seen as a warning of where gaps in current phytosanitary measures exist. The British Scolytinae fauna is relatively low in diversity with just 64 previously recorded species compared to continental Europe; in Germany for example, Bussler et al. (2011) recorded 109 species. This may indicate a greater susceptibility of British forests to colonisation by invasive species, due to fewer competitors and more available niche space (Mack et al. 2000). Conversely, the maritime climate of the British Isles may provide some protection against establishment. In particular, the damp and relatively cool summer climate appears to be limiting for thermophilic forest pest beetles (Straw et al. 2015; Reed et al. 2018). This may also explain the currently limited distributions of *X. germanus*, *G. materiarius* and particularly *C. bodoanum* to the warmer and drier climate of south-eastern England. Data on their thermal requirements for development would be needed to confirm this, but there is no other factor to limit their wider spread throughout Britain, as none will be host limited. Marini et al. (2011) found that a warmer, wetter climate was a good predictor of the establishment of exotic ambrosia beetles in the USA, probably because such conditions favour the growth of their symbiotic fungi.

In December 2018, another invasive scolytine species was also found to have established in southern England, the phloem-feeding European spruce bark beetle *Ips typographus*. This highly damaging pest species has been frequently intercepted at UK ports (Winter 1985), but until now has not established. A breeding population has now been detected in Kent, strikingly close to the only site of establishment of Asian longhorn beetle *Anoplophora glabripennis* to date in Britain (Straw et al. 2015). Southern England's geographical proximity to continental Europe may be a factor in the transportation or natural spread of these alien wood and bark-boring beetles, but it also appears to provide the most optimal thermal conditions for their establishment.

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Compliance with ethical standards

Conflict of interest The author declares that he has no competing interests.

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