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Open Access Review Article

Territorial expansion of the European *Ips* species in the 20th century – a review

Jean-Claude Grégoire[1,*], Jochem Bonte[2], Andy Bourke[3], Dragos Cocos[4], Nick Fielding[5], Jostein Gohli[6], Daegan Inward[5], Maartje Klapwijk[4], Christo Nikolov[7], Bjørn Økland[6], Martin Schroeder[4], Florentine Spaans[8], Jozef Vakula[7], Max Blake[5], Rafael De Andrade Moral[9], Maria Destefanis[10], Christine Griffin[11], Andrej Kunca[7], Archie Murchie[8], Cathal Ryan[10], Aoife Smith[12], Hugh F. Evans[5]

[1] Jean-Claude Grégoire. Spatial Epidemiology lab (SpELL), Université libre de Bruxelles, Belgium
[2] Jochem Bonte. Plant Sciences, Institute for Agricultural, Fisheries and Food Research (ILVO), Belgium
[3] Andy Bourke. Department of Agriculture, Food and the Marine, Ireland
[4] Dragos Cocos. Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07, Uppsala, Sweden
[5] Nick Fielding. Forest Research, Alice Holt Lodge, Farnham, GU10 4LH
[6] Jostein Gohli. Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, Ås, Norway
[5] Daegan Inward. Forest Research, Alice Holt Lodge, Farnham, GU10 4LH
[4] Maartje Klapwijk. Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07, Uppsala, Sweden
[7] Christo Nikolov. National Forest Centre, Forest Research Institute, T.G. Masaryka 22, 960 01 Zvolen, Slovakia
[6] Bjørn Økland. Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, Ås, Norway
[4] Martin Schroeder. Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07, Uppsala, Sweden
[8] Florentine Spaans. Agri-Food and Biosciences Institute, Belfast, Northern Ireland
[7] Jozef Vakula. National Forest Centre, Forest Research Institute, T.G. Masaryka 22, 960 01 Zvolen, Slovakia
[5] Max Blake. Forest Research, Alice Holt Lodge, Farnham, GU10 4LH
[9] Rafael De Andrade Moral. Department of Mathematics and Statistics, Maynooth University, Ireland
[10] Maria Destefanis. Department of Agriculture, Food and the Marine, Ireland
[11] Christine Griffin. Department of Biology, Maynooth University, Ireland
[7] Andrej Kunca. National Forest Centre, Forest Research Institute, T.G. Masaryka 22, 960 01 Zvolen, Slovakia
[8] Archie Murchie. Agri-Food and Biosciences Institute, Belfast, Northern Ireland
[10] Cathal Ryan. Department of Agriculture, Food and the Marine, Ireland
[12] Aoife Smith. Forest Service, Department of Agriculture Environment and Rural Affairs
[5] Hugh F. Evans. Forest Research, Alice Holt Lodge, Farnham, GU10 4LH
[*] Corresponding author: jean-claude.gregoire@ulb.be

With 4 figures

Abstract: Six species of *Ips* de Geer (Coleoptera: Curculionidae; Scolytinae) occur in Europe. They attack weakened or dead conifers but may become aggressive and mass-attack living trees. All species have expanded their ranges in Europe since the late 19th century. Here, we analyse the patterns of this spread and discuss the factors at play. Starting with an assessment of distribution changes of the insects and of their host trees since the nineteenth century, we describe how and, when known, why territorial changes occurred in Fennoscandia (Norway, Sweden, Denmark, and Finland), Central Europe (Czechia, Slovakia, Hungary, Poland, Austria, Germany), the Netherlands, Belgium and Great Britain. Based on these country narratives, we discuss the conditions for, and causes of, territorial expansion. A necessary condition is the presence of host trees of vulnerable ages and sizes, resulting from the post-glaciation expansion of host range. Population changes and territorial expansion are influenced by environmental or anthropic drivers: climatic events (droughts and storms), silvicultural practices and trade. Three main factors favour or hamper the response of the different species to these drivers: active and passive flight capacity, dispersal upon emergence and response to pheromones after take-off, and pre-dispersal

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E. Schweizerbart'sche Verlagsbuchhandlung, 70176 Stuttgart, Germany, www.schweizerbart.de

mating. These criteria enable identification of differences in the invasive capacities of the six species. In particular, *Ips typographus* appears to be a poor invader worldwide because of its wide dispersal upon emergence and its delayed response to pheromones. Finally, we discuss the risks to the Irish forests so far uncolonised by *Ips* species.

Keywords: Biological invasions; forest health; pathways; pest risk assessment; Scolytinae; trade

1 Introduction

Six species of *Ips* de Geer (Coleoptera: Curculionidae; Scolytinae) are considered native to Europe: *I. typographus* (L.), *I. amitinus* (Eichhoff), *I. duplicatus* (Sahlberg), *I. cembrae* (Heer), *I. sexdentatus* (Börner), *I. acuminatus* (Gyllenhal). All six species are specialists on conifers, show diverse levels of polygyny, develop through three larval instars, are associated with fungi, and respond to aggregation pheromones. At variable levels, all species can attack living trees and develop outbreaks. Specific features are summarised in Supplementary Table 1. These species would be expected to have contracted and expanded their range in synchrony with the ranges of their hosts after the last ice age, approximately 10,000 years ago. Huntley (1990) shows that by 8,000 years ago, most of central and north-western Europe was covered predominantly by broadleaf forest, whereas spruce (*Picea* spp.) and pine (*Pinus* spp.) were expanding north and west from their refugia in eastern Europe. The natural spread of spruce and pine eventually extended across much of Fennoscandia, but north-western Europe remained dominated by broadleaf forest. As humans settled across the land, much of the broadleaf forest was cleared, and forests were often utilised intensively (Kaplan et al. 2009).

Occurrence data for the six *Ips* species were downloaded from GBIF (GBIF 2023) and plotted along with the species' primary host distributions (Caudullo et al. 2017): Figs. 1 and 2. To visualise temporal developments in species distribution, occurrence data were plotted on a grid, where each cell was colour-coded by the date of first occurrence. While it can be assumed that the data shown in Fig. 1- and 2 do not accurately represent the maximum distribution ranges, they are comparable across species, cover a long time span, and thus provide a helpful representation of temporal development of geographical distributions. Depending on the species, historical expansion was documented from the published and grey literature, museum collections and/or direct field surveys.

Generally, occurrence data sourced from GBIF are considered reliable, but cannot be compared to observational data that has been validated by taxonomists. Surely, there are several identification errors in the data shown in Figs. 1 and 2; however, given the large geographical scope of the data such errors do probably not significantly change the general patterns. GBIF data can also not be compared to data collected in a standardized manner and will contain considerable spatial biases due to uneven sampling effort (Beck et al. 2014). Such biases will influence the accuracy of the species occurrences shown in Figs. 1 and 2; however, occurrence data collected in a standardized manner was not available for these species on this geographical scale. Furthermore, Figs. 1 and 2 are meant to illustrate changes in distributions over time and should not be considered accurate representations of species distributions.

In this review we analyse the expansion of these six *Ips* species since 1900 and try to identify and discuss the biotic, climatic and anthropogenic expansion drivers. First, we present a descriptive approach of forest expansion and *Ips* spp. range shifts, based on country narratives describing range shifts in Fennoscandia (Denmark, Sweden, Norway and Finland), Central Europe (Czechia, Slovakia, Hungary, Poland, Austria, Germany), the Netherlands, Belgium, and Great Britain. Secondly, we compare and discuss the factors affecting the six species' spread. Finally, drawing on this discussion, we outline the risks associated with *Ips* species gaining more ground in Europe, with an emphasis on Northern Ireland and Ireland, still uncolonized so far by any *Ips* species.

2 Country narratives

2.1 Fennoscandia (Norway, Sweden, Denmark, Finland)

Ips typographus

Records dating from 1025–1075 in Oslo (Kenward 1988) indicate that the spruce specialist *I. typographus* arrived after Fennoscandia was recolonized by spruce expanding from glacial refugia in Russia, 1–2 thousand years ago (Tollefsrud et al. 2008). Today, *I. typographus* is distributed in most areas where spruce is found and has occasionally caused extensive forest damage (Kausrud et al. 2012; Marini et al. 2013; Kärvemo & Schroeder 2010; Schroeder & Kärvemo 2022). *Ips typographus* and other *Ips* species can disperse long distances. In northern Fennoscandia, beyond the continuous distribution of *P. abies*, in northern Finland, around the Russian–Norwegian border and towards the mountainous areas within Fennoscandia, there are scattered records of *I. typographus* (Fig. 3A). They do not represent established populations in these areas solely dominated by *Betula pubescens* or a mixture of birch and *P. sylvestris*.

The volume of spruce in Fennoscandia has doubled (Sweden) or even tripled (Norway) during the last 90–100 years (Skogsdata 2022; Svensson & Dalen 2021), favouring beetle population growth and expansion. Furthermore, the common practice of clear-cutting creates edges especially favourable for *I. typographus*, where spruces are often wind-felled after clearcutting, and which are also more sun-exposed and attractive to *I. typographus* than inside the

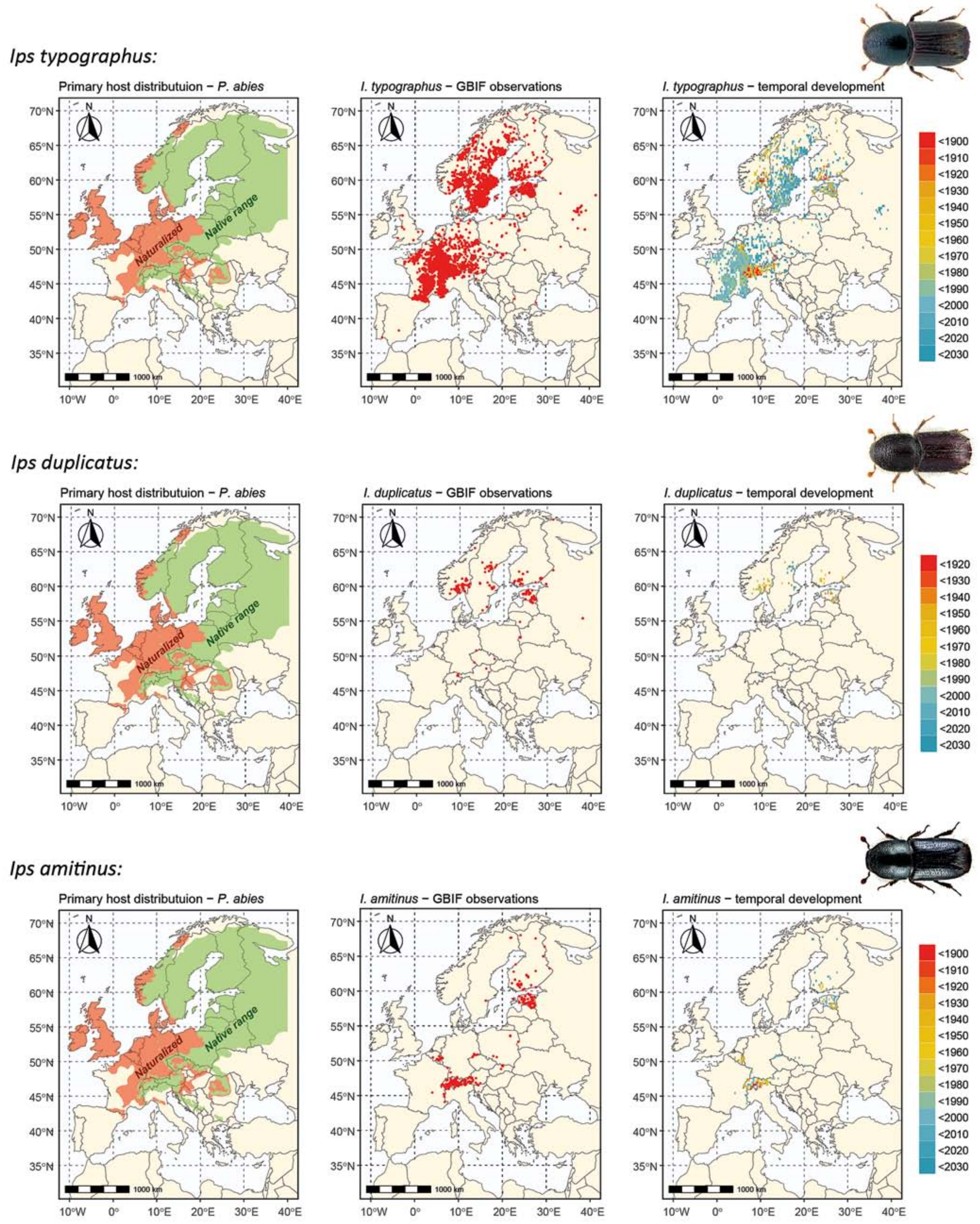

Fig. 1. Present status of *Ips typographus, Ips duplicatus* and *Ips amitinus* in Europe.
Left column: distribution of the main host tree (green: postglacial range; orange: present range); middle column: present distribution; right column: range expansion (<1900 to 2023). Photos: Udo Schmidt (*I. typographus, I. amitinus*), Lech Borowiec (*I. duplicatus*).

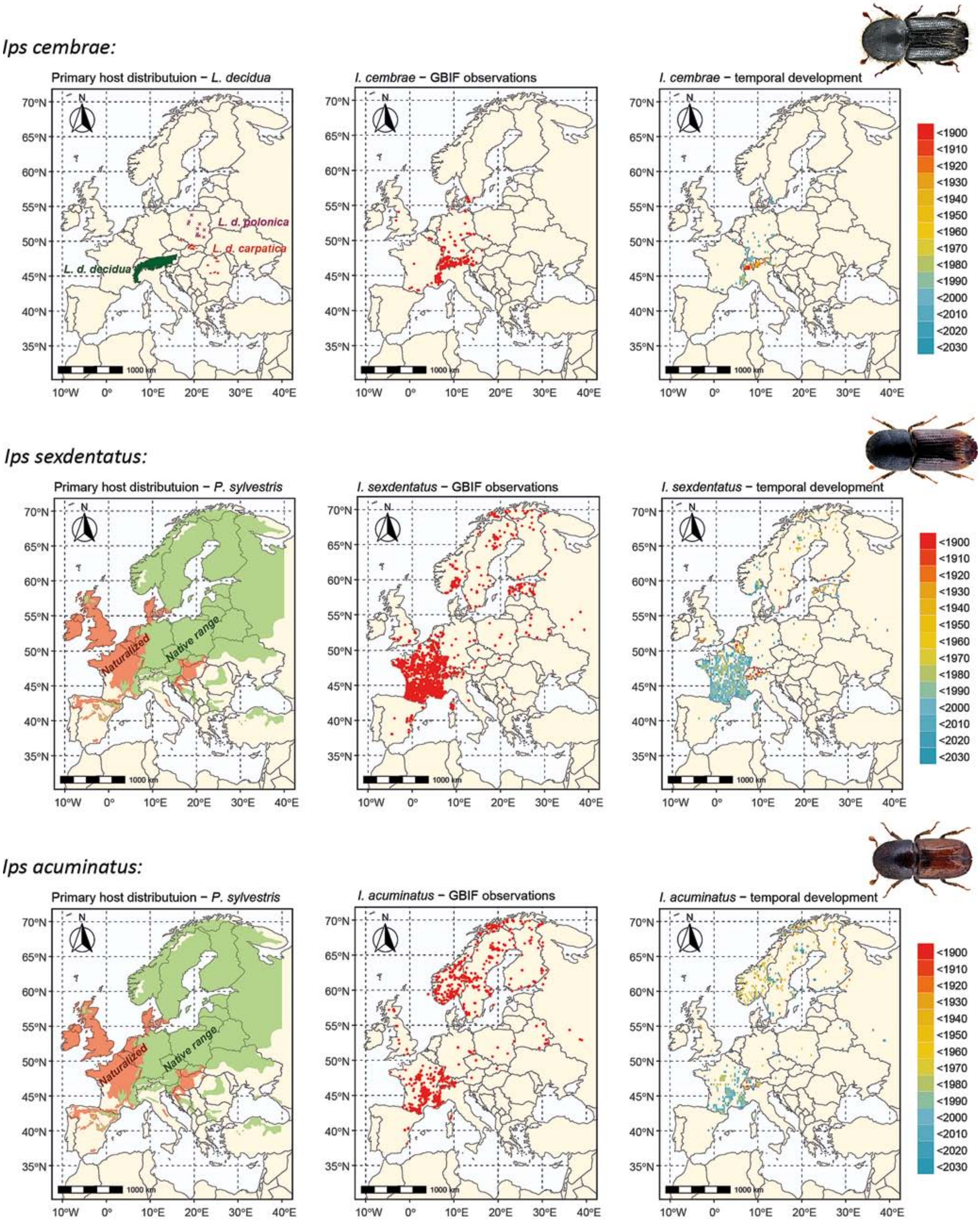

Fig. 2. Present status of *Ips cembrae, Ips sexdentatus* and *Ips acuminatus* in Europe.
Legend: see Fig. 1. Photos: Udo Schmidt.

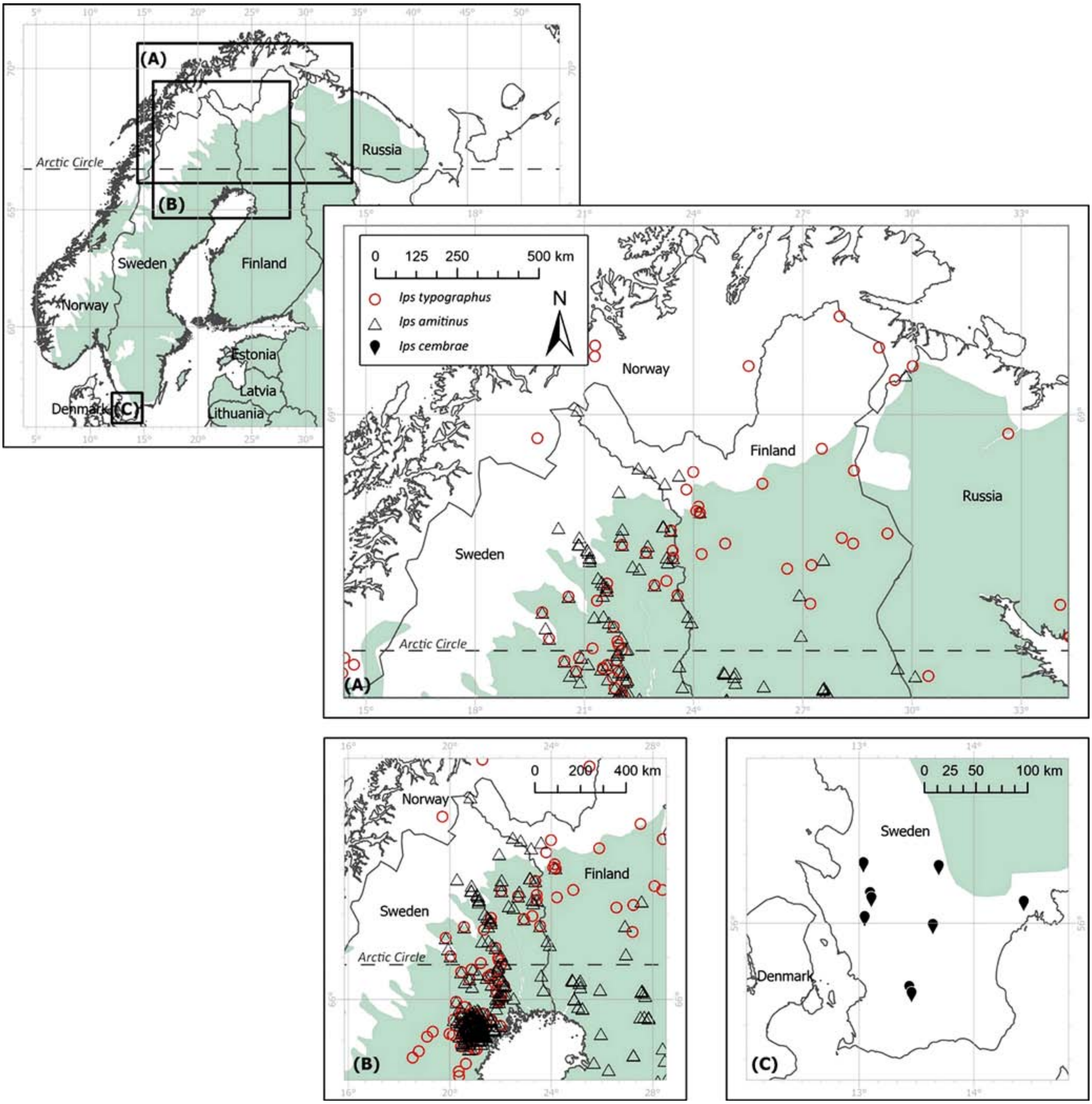

Fig. 3. (A) Previous records of *Ips typographus* and *I. amitinus* in northern Scandinavia. The green colour represents the geographic range of Norway spruce. The records do not represent complete distributions of the species (localities of occurrence taken from Økland et al. 2019, Artsdatabanken 2022, Shcherbakov et al. 2013, data from Sweden provided by M. Schroeder and D. Cocos.). (B) Locations with records of *Ips amitinus* from the 2016–2019 and 2023 surveys in northern Sweden (Cocos et al. 2023). (C) Records of *Ips cembrae* in southern Sweden from a trapping study in 2020.

stands (Göthlin et al. 2000; Lindman et al. 2023). Volume of spruce and amount of forest edges count among the most significant variables driving beetle attacks in an analysis of the yearly monitoring data of *I. typographus* in Norway (Gohli et al. 2024). Stand location is another factor promoting high *I. typographus* abundance. The largest volumes of spruce damage arising from drought and *I. typographus* attacks have been in the nemoral and boreonemoral vegetation zones in the southern part of Fennoscandia (Moen 1998), which historically are natural areas for deciduous and mixed forests and are less favourable for spruce during heat and drought periods. In the most recent outbreak, initiated by the extremely warm and dry summer of 2018 (Wilcke et al. 2020), enormous volumes of spruce (about 31 million m^3) were lost to beetle attacks in 2018–2022 in southern Sweden (Schroeder & Kärvemo 2022; Wulff & Roberge 2022). This corresponds to 70% of the trees killed by *I. typographus* during outbreaks since 1961.

The western part of Norway may become an arena of expansion for *I. typographus*. Spruce is a newcomer there due to planting during the last 100 years, but today there is a significant volume of spruce in this region (Svensson et al. 2021). However, *I. typographus* is still rarely found in the area, and the reasons for its absence are not clear.

Ips amitinus

Ips amitinus has expanded its range by approximately 14–20 km/year (Økland et al. 2019; Cocos et al. 2023) from central to northern Europe and Fennoscandia, reaching southern Finland in the early 1950s (Koponen 1975). The species has also expanded eastward and westward, being recorded in St. Petersburg Province in 1978 and in northern Sweden near the Finnish border in 2012 (Lindelöw 2013). It is now spreading southwest along the spruce range (Voolma et al. 2004) and is established throughout Finland (Økland et al. 2019). In Sweden, *I. amitinus* colonizes a higher proportion of Norway spruces compared to Scots pines, with higher reproductive success observed on this host (Cocos et al. 2023). According to surveys in 2016–2019 (Cocos et al. 2023; Cocos 2023), the species is distributed in 58% of all checked localities in northern Sweden (Fig. 3B). Above the Arctic Circle, the northernmost areas where *I. amitinus* was recorded were the Pasvik nature reserve on the Russian side in 2011 (Shcherbakov et al. 2013; Mandelshtam & Selikhovkin 2020) (Fig. 3A), and Kilpisjärvi, Finland (Økland et al. 2019), close to the Norwegian border. While maximum-entropy models predictions for *I. amitinus* show an optimal area in northern Europe and the mountain ranges of Central Europe, future predictions (2081–2100) present a reduction in the area of suitable habitat in the southernmost mountain ranges of Europe (Økland et al. 2019).

Ips cembrae

The first record in Sweden dates to 2011 (18 specimens caught in two larch stands in the most southern part of the country, the province of Skåne). Inspections of dead standing larch trees in these stands in late 2011 revealed old, empty brood systems corresponding to attacks since 2007 or 2008. No individuals were caught further north (Lindelöw et al. 2015). One explanation for the lack of increase in population density and spread after the initial establishment may be the highly fragmented occurrence of larch stands. In southern Sweden (Götaland), larch constitutes 0.2% of the total growing stock including all tree species (Anonymous 2022).

One plausible explanation for the establishment of *I. cembrae* in Sweden is natural spread from Denmark, with the shortest distance over the sea being less than 5 km (Fig. 3C). In addition, in 2012–2014, all positive records except one occurred in the western part of Skåne closest to Denmark. In Denmark, *I. cembrae* was first reported in 1995 (Ravn & Harding 1995) and it is currently established over large parts of the country (Ravn 2012; Cocos 2023). Imports of larch timber may also have contributed to establishment of *I. cembrae* in Sweden. The most eastern record in Sweden (from the province of Blekinge) is situated less than 3 km from the port of Karlshamn, to which large quantities of timber have been imported.

Ips sexdentatus

This pine specialist was widely distributed in Sweden up to the early 1900s, although it was rare in the south (Lekander et al. 1977). It has been recorded south of 58 °N before 1900 and between 58 °N and 62 °N before 1920–40. From 1970–2010 onward, the only records are mostly north of 65 °N (Pettersson 2013). The last records of reproducing *I. sexdentatus* in northern Sweden date from the mid 1990s (Pettersson 2013).

A similar decline of the distribution area of *I. sexdentatus* has been observed in Finland (Lekander et al. 1977). After 1925, the species was considered rare south of 66 °N. Löyttyniemi (1975) suggests that the few specimens colonising pine logs placed out in southern Finland originated from timber imported from abroad or transported from northern Finland. After 2000, there is only one record in Finland, close to the arctic circle 67 °N (Finnish Expert Group on Coleoptera 2024). In southern Norway, *I. sexdentatus* has long been known to occur in limited areas (Lekander et al. 1977), with records before 1900. Recently, the species seems to have expanded its range (Artsobservasjoner 2023). Two hypotheses have been proposed for the decline of *I. sexdentatus* in northern Fennoscandia (Löyttyniemi 1975; Bakke 1968): i) increased competition with *Tomicus piniperda* for breeding material; ii) climatic constraints, *I. sexdentatus* being present in areas where it is univoltine (Bakke 1968) and the survival of a second generation is not possible because of low winter temperatures killing the larvae and pupae. In contrast to this decline, *I. sexdentatus* has increased its range in southern Fennoscandia. In recent years, it colonised Denmark where it is now widely distributed in the country and observed reproducing in *Pinus nigra* (Hansen et al. 2012) and *P. sylvestris*.

Ips acuminatus

The species has historically been considered of minor economic importance with few instances of tree mortality (Colombari et al. 2013). Recently, however, *I. acuminatus* has significantly contributed to the decline of Scots pine stands in localised areas in continental Europe (Wermelinger et al. 2008; Colombari et al. 2012; Papek et al. 2024) and in Fennoscandia (Siitonen 2014). In southern Finland, populations disappeared from large regions after the 1950s. Therefore, a recent survey that discovered large occurrences that played a primary role in the mortality of pines in southern Finland was unexpected. The previous hot and dry summers probably increased the susceptibility of the pines and contributed to population growth (Siitonen 2014). Recent literature on *I. acuminatus* may not provide evidence of substantial or true range expansion for this species, however it does suggest that climatic influences can increase damage for this beetle, with increases possible under future climatic scenarios.

2.2 Central Europe (Czechia, Slovakia, Hungary, Poland, Austria, Germany)

In Central Europe, natural forests have been largely replaced by spruce monocultures over the past several centuries (Pretzsch 2019). This has led to millions of trees being attacked by spruce bark beetles annually (Dávidková et al. 2023). As a result of this extensive planting of spruce, the diverse forest landscapes that once acted as barriers to pest spread have been eliminated, leading to widespread outbreaks.

Ips duplicatus

In Central Europe, *I. duplicatus* was recorded before the 20th century (Mrkva 1994; Steyrer 2019; Wermelinger et al. 2020). Since the 1990s, it has become a serious pest (Holuša et al. 2010; Lubojacky et al. 2022). Currently it occurs in 22 European countries (CABI 2021) and has recently spread to Switzerland and Liechtenstein (Wermelinger et al. 2020) and Slovenia (Kavčič et al. 2023). The transport of *I. duplicatus* with infested timber has been observed in Switzerland, Liechtenstein, Germany and Austria (Holzschuh 1989; Steyrer 2019; John et al. 2019; Wermelinger et al. 2020). The pest was also intercepted in Belgium, close to a fluvial port where infested timber was transiting (Piel et al. 2006). In Romania, the initial discovery occurred in 1948, and the first outbreak was reported in 2008 (Duduman et al. 2011; Olenici et al. 2022). Although *I. duplicatus* is not considered a significant pest in its native countries (Krokene & Solheim 1996), it has become a widespread pest in new areas, resulting in losses of thousands to millions of cubic meters of spruce yearly at the country scale, killing trees and degrading timber value due to blue staining by fungi. In Slovakia, annual harvests of trees damaged or killed by *I. duplicatus* range from 10–50 thousand m^3 (Vakula et al. 2018), while in the Czech Republic, 2.9 million m^3 were harvested between 2019 and 2021 (Lubojacký et al. 2022). Current climatic conditions promote the spread and proliferation of *I. duplicatus* and are likely to make this pest increasingly damaging (Olenici et al. 2022).

Ips amitinus

The species was associated with conifers at higher altitudes in the western Carpathians, while being less frequently found at lower elevations (Holuša et al. 2012). It can survive extremely low winter temperatures, and it has been hypothesized that higher temperatures during diapause could negatively impact survival rates, body size, and life cycle synchronization (Økland et al. 2019). Joint attacks involving both *I. amitinus* as a secondary pest in conjunction with *I. typographus* have been noted in the northwestern region of Slovakia, an area invaded by *I. duplicatus* during the 1990s (Vakula et al. 2015). It is possible that the recent climate warming trends have been beneficial to the spread of *I. duplicatus*, partly displacing *I. amitinus*. Similarly, *I. duplicatus* appears to be gaining ecological prominence in the Czech Republic, while the incidence of *I. amitinus* is diminishing (Knižek 2023 personal communication).

2.3 The Netherlands

Forest cover was under severe anthropological pressure until the 1850s. Since then, large scale commercial plantings have taken place (Staatsbosbeheer 2021). *Pinus sylvestris* was initially popular on sandy heathland (Van Goor 1993) but *Picea abies* was more widely planted in the 1900s (NDFF & FLORON 2023). Afforestation increased in the 1900s with the establishment of the state agency Staatsbosbeheer. Over time, the focus changed from predominantly commercial forestry to woodland managed for its recreational, ecological, and cultural values (Staatsbosbeheer 2021). In 2021, total forest cover was ca. 364,000 ha (Schelhaas et al. 2021).

Ips typographus was first reported in 1918, from Eindhoven (Everts 1920) and noted as a rarity. No established populations were known at that time, though nearby German populations were noted. The natural history museum in Leiden contains multiple specimens, the earliest collected in the Netherlands in 1945, with several more from various locations dating from the 1950s. Voûte (1950) mentioned increased reports of local populations likely resulting from the frequent importation of spruce wood with attached bark from Germany after World War II. Breeding populations of *I. sexdentatus* were apparently already present in dead *P. sylvestris* in Hoenderloo in 1939–1942 (Voûte 1942). *I. typographus, I. cembrae* and *I. sexdentatus* did not seriously come to the attention of Dutch foresters as pests until the aftermath of severe storms in 1972 and 1973, when numbers of the two formers in particular increased dramatically (Doom 1975; Luitjes 1977). *Ips acuminatus, I. amitinus* and *I. duplicatus* are not known to be present in the Netherlands.

2.4 Belgium

Ips typographus

Spruce has been planted in Belgium since 1810, but large-scale plantations only started around 1894 (Claessens 2001; Scheepers et al. 1997). Presently, *P. abies* is the most widely distributed conifer in the country. In Wallonia, there were 126,000 ha of spruce plantations in 2021 (Lejeune et al. 2022). *Ips typographus* has followed its host (Mayer et al. 2015) in three consecutive phases, first between host tree planting and the first establishment of the beetles, second between first establishment and spread to larger areas, and third between wider establishment and the first outbreaks. *Ips typographus* was first mentioned in the literature in 1859 (Mathieu 1859), with the first individual in Belgian collections dating from 1933 (Dourojeanni 1971). By the early 1970s, *I. typographus* was present at low densities everywhere in the south, where spruce is grown (Dourojeanni 1971). The first outbreaks appeared in 1976, during the hottest and driest spring and summer of the century (RMI 2024), among pure, even-aged, 60–80 years old stands (Lecomte et al. 1992). Later, a succession of storms favoured population growth. The 1990 storms had a particular impact, with about five million m^3 of windfalls and wind breaks. In 1999–2000, *I. typographus* was trapped in most of the 43–65 pheromone traps deployed in the city of Brussels, about 50 km from the closest important spruce plantations (Piel et al. 2005). The hot and dry springs and summers after 2018 contributed to population increases and range expansion. By 2019, most of the spruce trees in Brussels had been killed and, in 2022, beetles were caught in pheromone traps up north at the seaside (Inward et al. 2024).

Ips sexdentatus

This species was first mentioned by Mathieu (1859). The first individual in the Belgian collections dates from 1874 (Dourojeanni 1971). Although now present everywhere in the country, *I. sexdentatus* is not abundant and is considered harmless.

Ips amitinus

This species was first mentioned in 1926 (Service des Recherches et Consultations en Matière forestière 1926). The first individual in the Belgian collections dates from 1924 (Dourojeanni 1971). The species is not considered a pest.

Ips acuminatus

It was first mentioned by Mathieu (1859). Dourojeanni's catalogue (1971) only records *I. acuminatus* twice (1931 and 1933). No further occurrences were published. Establishment in Belgium is thus doubtful.

Ips cembrae

The species was unknown in Belgium until 1991, when it was found attacking a few standing and felled *Larix decidua* and *P. abies* in the south of the country (Grégoire, unpublished) and was later reported by Moucheron (2011). Because of their morphological similarity to *I. typographus*, specimens caught earlier might have been misidentified (Moucheron 2011). Currently, except in hot and dry years, *I. cembrae* is secondary.

2.5 Great Britain

The British landscape has been shaped both by the post-glaciation re-establishment of several tree species and by more recent human activity (Holmes 1975). The only conifer species that had some relict presence after the end of the last glaciation (ca. 12,000 years ago) was Scots pine (*P. sylvestris*), mainly restricted to Scotland and some parts of southern England (e.g. the New Forest). Increases in land conversion to agriculture and land clearances, especially in Scotland, resulted in tree cover for the whole of the UK (including Northern Ireland) declining to 4.7% by the first decade of the twentieth century. Subsequent plantings in Wales and Scotland have been dominated by conifers with the total percentage land cover being slightly higher than for the UK as a whole. There was little change in overall tree cover until the period after the Second World War (Gambles 2019). From the late 1940s onwards, there was a large increase in planting of non-native conifer species (Harmer et al. 2015). Although there has been a recent increased trend to plant broadleaved and mixed woodlands, woodland cover is still dominated by conifers, particularly Sitka spruce (*Picea sitchensis*).

Ips acuminatus

Though when and how it established in Great Britain is unknown, *I. acuminatus* was the first *Ips* species recorded in Great Britain in northern England (listed as *Tomicus acuminatus* by Munro 1920, 1926). However, despite establishing in Great Britain over 100 years ago, the species is still only found in northern England and southern Scotland in small numbers (Blake et al. unpublished).

Ips sexdentatus

The distribution of *I. sexdentatus* appears restricted to southern Britain. The first record in the NBN Atlas (2024) is an unverified observation in 1891 in Wales. Later records from Wales and England include 26 findings from 1919 onwards. Absence of the pest in Scotland has been confirmed through survey (Scottish Forestry 2021). There has been no recorded impact on living trees, although populations have occasionally been very large, particularly in the east of England following the 1987 hurricane in Thetford forest (Grayson 1989).

Ips cembrae

The species was first found in 1955, breeding on larch trees in northeast Scotland (Crooke & Bevan 1957). It was believed to have been imported on larch logs following the Second World War, and until 2018 it was considered to only be present in Scotland, the Forest of Dean, and sporadically between those extremes. However, after an extremely hot, dry summer in England in 2018 *Ips cembrae* was found to have caused significant larch mortality at a number of sites in England across the south and east (M. Blake, D. Inward & N. Fielding, pers. obs.), with reports peaking in 2019. This spread may have been accelerated by infection of larch, particularly Japanese larch *Larix kaempferi*, caused by *Phytophthora ramorum* increasing the availability of weakened or dying hosts, particularly in the western side of Britain where larch has been planted extensively (N. Fielding, pers.

obs.). However there have still been several reports of tree mortality from *Ips cembrae* well away from areas infected by *P. ramorum*, and though attacks are still associated with trees which are already declining from various causes (Redfern et al. 1987) it is likely to remain a significant cause of mortality on sites with predisposed larch. In east England and Scotland, where the conditions are dryer and *P. ramorum* struggles, with continued climate change *Ips cembrae* may emerge as a significant mortality factor in larch stands.

Ips typographus

Incursions have been recorded throughout the last 100+ years, particularly soon after the Second World War when *I. typographus* and *I. sexdentatus* were found, often in hundreds, at ports in England, Scotland and Wales on Scots pine and Norway spruce timber imported from Germany (Laidlaw 1947). Following these finds, the Forestry Commission placed trap logs of Norway spruce near ports and spruce forests, but no *I. typographus* infestations were found. As part of EU Plant Health regimes, surveys to verify the absence of several *Ips* species have been carried out since the early 1980s, initially as Protected Zones under EU phytosanitary legislation and, since 2021 post-Brexit, as Pest Free Areas (https://planthealthportal.defra.gov.uk/resources/plant-health-protected-zones/). In addition to within-forest surveys using pheromone-baited trap logs, pheromone trap surveys at ports were also carried out. *Ips typographus* was caught in pheromone traps almost annually between 1985 and 2018, usually only a few individuals, with peaks in 1994 (45 individuals) and 1995 (149 individuals) (Evans 2021).

Despite the frequent arrival of *I. typographus* in Britain, the first breeding population on weakened Norway spruce wasn't detected until 2018 (Forestry Commission 2023; Blake et al. 2024) in a woodland in Kent, during an annual survey as part of the UK Protected Zone requirements. Extensive surveys have been carried out since 2018 to delineate the infested area and attempt eradication (Forestry Commission 2023). The demarcated area has increased as new infestations were detected. A study based on pheromone trap transects in England, France, and Belgium, on both sides of the English Channel, provides strong indications that *I. typographus* flies over the sea from large population reservoirs on the continent, with a capacity to enter at least 265 km inland into England (Inward et al. 2024).

3 Discussion

Drawing from the country narratives and from the literature, two categories of factors favouring expansion are identified: the amount of suitable host trees and, to some extent, the biological characteristics of each species. Similarly, three expansion mechanisms can be listed: active flight, semi-passive, wind-borne flight, and transportation on infested material (wood with bark, solid wood packaging material).

3.1 Factors favouring expansion

3.1.1 Suitable host trees

More susceptible hosts provide increased resource availability and resultant larger beetle populations with a higher capacity to spillover and colonise margins around their ranges. Two elements contribute to increasing the numbers of suitable hosts.

i) The extension of forest areas. This occurs from a combination of natural recolonisation since glaciation and artificial plantations such that, conifers occupied increasing areas in Europe particularly during the 20th century (Figs. 1–2). After they had reached susceptible ages and sizes, they were colonised with a variable success by the six *Ips* species. Host shifts sometimes facilitated establishment. In the Caucasus, *I. sexdentatus* started aggressively attacking oriental spruce, *Picea orientalis* Carr (EFSA 2017). In west Siberia, *I. amitinus* infested new hosts: *Pinus sibirica, Picea obovata* and the introduced *Pinus koraiensis* (Kerchev et al. 2019; Kerchev & Krivets 2021). Within a short period of time, *I. amitinus* infested a few thousand hectares of Siberian pine in West Siberia and its spread continues (Kerchev et al. 2022).

ii) Environmental and anthropic drivers. Climatic events (droughts and storms) and forest management options (monospecific, even-aged stand plantations, clear-cutting) favour population growth (e. g. Marini et al. 2016; Hlásny et al. 2021), increasing spillover by flight (active or wind-borne) into adjacent territories, and travel on infested material (wood with bark, solid wood packaging material) beyond geographic barriers. The ability to exploit these pathways varies between the six *Ips* species.

3.1.2 Biological characteristics of the Ips species

Major life history traits do not markedly differ between species (Supplementary Table 1). It is possible however that climatic constraints affecting voltinism or diapause, or suboptimal host species reducing fecundity could locally hamper range extension. An additional trait that may have an influence, though, is the proportion of mated pre-emergent females. Inbreeding Scolytinae are over-represented among the species that have successfully expanded their ranges over geographic barriers (Grousset et al. 2020; Lantschner et al. 2020; Grégoire et al. 2023). *Ips* species are not inbreeding, but it has been recently shown recently that 15–25% of emerging *I. typographus* females have been fertilised by a neighbour or a brother (Dacquin et al. 2023) and, respectively, 72%, 57% and 29% of emergent *I. acuminatus, I. sexdentatus* and *I. cembrae*, have also been found fertilised (Dacquin et al. submitted). Pre-emergence mating could influence expansion success by reducing the need to find mates after emergence and lowering Allee thresholds, at the risk of inbreeding depression. The pseudogamous habits of *I. acuminatus*, which produces a proportion of parthenogenetic females (Kirkendall 1990), also lowers the Allee threshold for this species.

3.2 Expansion mechanisms

A summary of the expansion mechanisms relevant for each of the six *Ips* species is provided in Supplementary Table 2.

3.2.1 Active flight

All *Ips* species are capable of dispersing by flight, but this capacity is still incompletely assessed. Flight duration and distance have been measured by flight mills and release-recapture experiments.

Flight mills

Jactel & Gaillard (1991) showed that, within a sample of 38 *I. sexdentatus* beetles, 98% flew more than 5 km, 50% more than 20 km and 10% more than 45 km. In a study of *I. typographus*, Forsse & Solbreck (1985) observed that "a one-hour flight (which many of the beetles can do daily) with the beetle moving at 5 m/s relative to the ground (a conservative estimate of wind speed plus active flight speed of the insect) would take the beetle 18 km". Both species thus display a capacity to cover tens of kilometres by active flight.

Release-recaptures

This approach provides interesting information, not only on distances flown, but also on the response of emerging beetles to pheromones. Jactel (1991) recaptured 20–30% of released *I. sexdentatus* at 100 m from the release point; 45–50% were caught at 600 m. In contrast, Franklin & Grégoire (1999) recorded 1.2% spontaneous landing of *I. typographus* (no pheromone lures) in a 1-ha stand surrounding the release point. In two other experiments with pheromone traps, Franklin et al. (2000) recaptured only small proportions of the released insects, respectively 2.3% (in 64 traps over 12 ha) and 7% (in 100 traps over 20 ha). Byers (1999) summarized the results of other experiments more explicitly measuring recapture distances (data from Botterweg 1982; Zumr 1992; Zolubas & Byers 1995; Duelli et al. 1997): Fig. 4A. The overall results are conflicting: in two studies, ca. 40% of the released insects were caught between 5 and 40 m, whilst in the two other reports, the recapture rates were much lower (maximum ca. 8% at 50 m). It cannot be excluded that these divergent results were influenced by different responses to pheromones.

Most of the gradual, continuous spread of *Ips* spp. reported in the country narratives probably relate to active flight. For example, one likely explanation for the establishment of *I. cembrae* in Sweden is natural spread from Denmark over the short stretch of sea (<5 km) separating both countries. The 14–20 km/year spread of *I. amitinus* in Fennoscandia (Voolma et al. 2004; Økland et al. 2019; Cocos et al. 2023) is also likely due to natural spread.

3.2.2 Semi-passive, wind-borne flight

In this category of flight, insects are taken by air currents above the atmospheric boundary layer and are drawn over long distances exceeding their own flight capacities. Chapman et al. (2015) report many cases of high-altitude semi-passive insect flights. Scolytinae also appear capable of being wind-transported over long distances. Using trap logs along a road in the tundra in Finland, Nilssen (1984) recorded *Dryocoetes autographus* (Ratz.), *Hylastes cunicularius* (Erichs.) and *H. brunneus* (Erichs.) at 171 km, and *Ips typographus* at 43 km from the nearest forests.

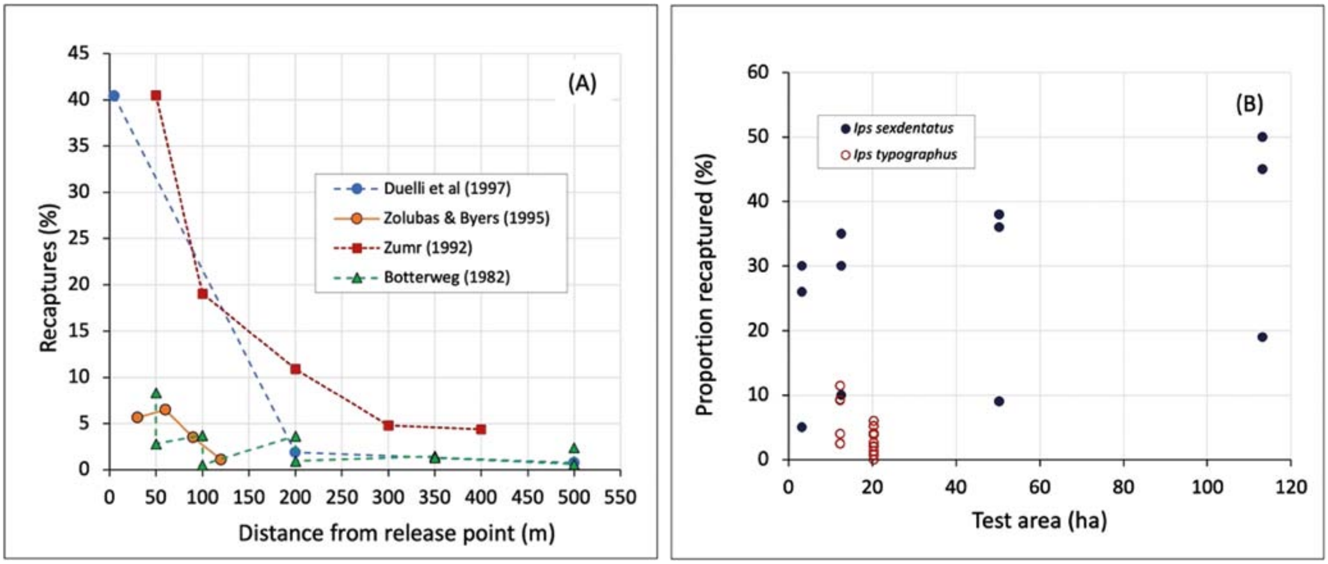

Fig. 4. (A) A synthesis of release-recapture experiments with *Ips typographus* (after Byers 1999), (B) Response of *Ips sexdendatus* and *Ips typographus* to trap networks deployed over different areas. Redrawn from Jactel (1991; *I. sexdentatus*) and Franklin et al. (2000; *I. typographus*).

Observations of *I. typographus* and *I. amitinus* (and one *I. duplicatus*) in northern Fennoscandia (Fig. 3A) suggest a similar phenomenon. In British Columbia, Jackson et al. (2008) used a weather radar and a drogue net towed by an aircraft to study high altitude flight of *Dendroctonus ponderosae* Hopk. and concluded that some of the beetles flew up to more than 800 m above forest canopy over distances of 30–110 km/day, at maximum densities of 18,600 insects/ha. High altitude, wind-borne semi-passive flight probably explains the recent movements of *I. typographus* from the European continent to Britain. According to the model developed by Inward et al. (2024), the beetles were able to fly 427 km from an outbreak hotspot in France (upper 95% confidence limit: 735 km) and could thus have moved at least 265 km inland into England.

3.2.3 Movements of infested material

Ips cembrae, I. typographus, I. sexdentatus, I. acuminatus and *I. duplicatus*, in decreasing numbers, have been intercepted worldwide (Turner et al. 2021). The impact of trade on the movements of non-native forest insects has been extensively reviewed (see, e.g., Lantschner et al. 2020; Turner et al. 2021; Ward et al. 2022). Within these pathways, bark- and wood borers are commonly associated with wood packaging material, firewood, logs, and unprocessed wood. Marini et al. (2011) identified importation of infested woods as a strong predictor of the numbers of exotic Scolytinae species established in 20 European countries and the 48 continental US states. In Britain, Bevan & King (1983) showed, using dendrochronology, that *Dendroctonus micans* detected in the early 1980s probably entered via a sawmill that had imported large volumes of timber from the continent.

Whilst *I. cembrae* and *I. sexdentatus* proved capable to cross geographic barriers with commercial shipments and establish outside of their native range, *I. typographus*, although a highly intercepted pests worldwide, has never established permanent populations outside its native range, apart from Britain where it likely arrived via semi-passive flight (see 3.2.2.). Despite the continuing trade flow, most introductions are not successful. These differences probably depend on each species' propensity for dispersal upon emergence and on its early or delayed response to pheromones.

3.3 How our comparisons explain the lack of invasive success of *I. typographus*

Adult activity upon emergence, particularly flight behaviour before responding to pheromones, strongly influences spread and constitutes a confounding factor in release-recapture experiments (see 3.2.1). Up to 99% of the *I. typographus* caught in release-recapture experiments are not part of the released batches (Weslien & Lindelöw 1989, 1990; Franklin et al. 2000). This behaviour varies between different *Ips* species: *I. sexdentatus* appears to respond more rapidly to pheromones than *I. typographus*, as respectively measured by Jactel (1991) and Franklin et al. (2000) (Fig. 4B). These differences may explain why *I. typographus* is not a successful invader. When an infested batch of host material lands in a new area, the transported insects disperse widely upon emergence and lose track of their conspecifics, which prevents "aggregation behaviour and polygamy that require a critical threshold of individuals infesting a tree to ensure population growth" (Pureswaran et al. 2022). As a commercial introduction is a discrete event, any successful establishment by a pioneer beetle is not followed by conspecifics responding to pheromones because all conspecifics have already scattered. An infested batch in new territory therefore behaves differently from a whole, established population capable of generating and dispatching large numbers of individuals which respond to pheromone cues during a protracted period, allowing pioneer beetles to recruit conspecifics.

Propagule pressure, Allee effects, and Ips typographus

How propagule pressure and Allee effects shape the capacity of *I. typographus* to establish beyond a geographical barrier is poorly understood and should be discussed.

Lockwood et al. (2005) define propagule pressure as "a measure of introduction intensity (…) comprising both the number of individuals of a species introduced per introduction (propagule size) and the frequency of introductions". Brockerhoff et al. (2014) and Ward et al. (2022) consider interception frequency as a convenient proxy for introduction intensity. Liebhold et al. (2017) use the relative abundance of each species in the invasion pathway. For Lantschner et al. (2017), the proxy is a species' relative abundance in its native range. These metrics, that involve discrete introductions, do not consider the behaviour of the introduced species. In the case of *I. typographus* (wide dispersal upon emergence and delayed response to pheromones), the fate of any individual starting a gallery on a new host will be different according to whether the insect is in new territory beyond a geographic barrier or is in its distribution range. Within the species' range, the signals emitted by an early settler reach a whole population reservoir constituted by conspecifics dispersing from other sources. Contrastingly, in a new area devoid of conspecifics, the individual beetle (if any) lucky enough to find a suitable host is extremely likely to call in the void, as its conspecifics would have flown away. Because of this need for the backing of a whole reservoir, protracted over time, propagule pressure for *I. typographus* should thus be expressed as a continuous process, a flow (e.g. density/air volume/day), instead of as an instantaneous, discrete event such as the arrival of a wood consignment. The absence of a reservoir backing could probably explain why *I. typographus* was detected only once in traps in Pennsylvania in the early 1990s, in Indiana in 1995, and in Maryland in 2002, but was never trapped again (Ward et al. 2022). The emerging offspring of lucky settlers would have dispersed too widely for colonising new resources. For other species which responds more readily to pheromones (e.g., *I. cembrae* in Britain, Denmark and Sweden, *I. duplicatus* in Switzerland, Austria and Germany, or *I. sexdentatus*), shipment volume or frequency, or interceptions, could still prove valuable metrics for predicting establishment.

Because of the above, Allee thresholds for *I. typographus* should also be seen as quantities in a flow. Within the pest's range, these thresholds vary according to population densities and to the breeding resources available. At low densities, *I. typographus* preferentially attacks weak or fallen trees. At the extreme, even one single female fertilised before emergence can start a new brood (Dacquin et al. 2023). When populations grow, *I. typographus* shifts to standing trees (Kausrud et al. 2011). In new territories, instantaneous values such as "a sufficiently high number of conspecifics […] required for *I. typographus* to overcome host resistance of live trees" (Ward et al. 2022) would not be adequate because of their discrete arrival and the absence of a local reservoir.

3.4 The risks for Ireland

Though widespread in Europe, none of the *Ips* species have reached Ireland to date.

Out of all their host species, only *P. sylvestris* is considered a native tree in Ireland. After a probable interim period of extinction, it was re-introduced in the early 1800s (Smith & Goddard 1991; Hall 1995) and was mainly used as a nursery tree for other species in reafforestation programmes or confined to marginal land. Ireland remained largely devoid of trees after the retreat of the glaciers until re-afforestation programmes actively ran trials of non-native species suitable for timber production in the early 1900s (Fitzpatrick 1966; Neeson 1991). Re-afforestation with Sitka spruce, larch and several pine species proceeded rapidly (Neeson 1991; O'Carroll 2004). Currently, the Republic of Ireland has just over 800,000 ha of forest, of which 360,850 ha is comprised of Sitka spruce (DAFM 2023). With such a large area available, often planted in monocultures, the question is then: why none of the *Ips* species, particularly *I. typographus*, colonised the island. Other conifer bark beetles, such as *Dryocoetes autographus*, did successfully establish in Ireland and are now considered common and widespread (Alexander & Anderson 2012; NBDC 2023).

Despite regular plant health inspections, interceptions of *Ips* species have been low in Ireland, with just three interceptions of *I. typographus* in the Republic of Ireland and one in Northern Ireland. Despite annual trapping taking place across the island to fulfil EU protected zone requirements, no detection has occurred.

Susceptible hosts of suitable ages and sizes are present in Ireland. However, it is possible that this condition is not optimal, as forestry in Ireland is often fragmented, with relatively few extensive, continuous forest tracts. Furthermore, the dominant spruce species *P. sitchensis* may be less susceptible to at least *I. amitinus* and *I. typographus* (Flø et al. 2018).

3.4.1 Colonisation by flight and biological constraints

The sea surrounding the island imposes a substantial distance (ca. 20–200 km) that beetles would be either required to fly or to bridge via trade movements. While experiments have clearly demonstrated the capacity for *Ips* species to fly very long distances, particularly using semi-passive flight (easily far enough to fly from Britain to Ireland) it is also apparent that the vast majority of individuals do not fly much further than a few hundred metres (see section 3.2.1). Prevailing winds in Ireland are south-westerlies and windows where both temperature and wind direction are suitable for mass dispersal to Ireland would be relatively rare (Met Éireann 2024). Furthermore, lower temperatures in summer reduces voltinism compared to most locations in mainland Europe and thus it might be more difficult for the beetle to establish from a pioneer population. The lack of cold winters could possibly prevent successful completion of diapause and be disruptive to the lifecycle of *I. amitinus* (Økland et al. 2019). Fecundity may also be affected by sub-optimal conditions (Bakke 1968).

3.4.2 Factors favouring expansion

Climatic events have become more frequent in Ireland in recent years, particularly severe storms and flooding (Noone et al. 2017; OPW 2024; Sweeney 2000). Windthrow is an increasing risk in creating potential colonisation sites for pioneers (Ní Dhubháin & Farrelly 2018). Interceptions through trade have been low and while *I. sexdentatus, I. cembrae* and *I. duplicatus* appear able to spread through trade, the low frequency and numbers that have arrived so far have not permitted the establishment of these species. A range of biosecurity measures are in place, including the regulation of trade and inspections of imported material and this will no doubt have contributed towards preventing incursions. *Ips typographus*, which appears to require a consistent stream of incoming beetles moving by semi-passive flight to establish itself, is unlikely to establish in Ireland as long as a large reservoir of beetles does not exist in Britain. Should this become the case, monitoring of weather conditions and targeted trapping and surveys should be able to provide early warning and hopefully facilitate the continued protection of Ireland's conifer forests against *Ips* species.

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