



The threat to UK conifer forests posed by Ips bark beetles





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Research Report

Hugh Evans

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Executive summary

Of the many beetle pests that pose a threat to trees, bark beetles (Coleoptera: Curculionidae: Scolytinae) include many species which cause substantial damage, resulting in major tree mortality. Among these, the most destructive are *Dendroctonus* and *Ips*. In Europe, the most damaging *Dendroctonus* species is the great spruce bark beetle (*Dendroctonus micans*), which was previously absent from Great Britain until its establishment in the early 1970s. Although there have been interceptions of the more damaging North American *Dendroctonus* species, such as the mountain pine beetle (*Dendroctonus ponderosae*) and the spruce beetle (*Dendroctonus rufipennis*), neither of these are established in the UK. There are also damaging species in the *Ips* genus, in both Eurasia and North America, many of which have been transported by international trade. Globally, there are at least 37 species of *Ips*, with 10 recorded from Eurasia. Those with a more westerly distribution in Eurasia are regarded as a potential threat to woodland in the UK.

Reflecting the threat posed by Eurasian *Ips* species, the UK has Protected Zone (PZ) status under newly implemented European Union (EU) Regulation 2016/2031 (replacing EC Directive 2000/29/EC). Section 3, Article 32 of the new regulation sets out the restrictions and protective measures that aim to protect plant health within the EU. The species listed for UK PZ status are *Ips amitinus*, *Ips cembrae* (Northern Ireland only), *Ips duplicatus*, *Ips sexdentatus* (Northern Ireland only) and *Ips typographus*. This means that imports of all genera of conifer wood that could act as hosts for bark beetle species in the genus *Ips* must either be debarked or accompanied by a Plant Passport certifying that they come from a pest-free area. As part of the UK's PZ status, annual surveys are conducted nationwide to check for the possible presence of breeding populations of the aforementioned *Ips* species. These surveys are administered by the Forestry Commission Plant Health Service, which reports annually via Defra to the EU Standing Committee on Plant Health.

Knowledge of the threats posed by these pests, which are widespread in Europe and throughout parts of Asia, is an important government objective, and each one is listed in the new UK Risk Register of pests and pathogens. From a UK perspective, up-to-date knowledge of the biology and specific threats of the various species of *Ips* is therefore essential to assess the value of PZ surveys and their ongoing context, especially after the recent outbreak of *I. typographus* in Kent. In addition, the new EU Plant Health

regime introduced in December 2019 places an emphasis upon enhanced surveillance for key pests, and there are also implications to follow from the UK's exit from the EU with regard to moving from PZ status to becoming a Pest-Free Area, as defined in ISPM4 (International Standards on Phytosanitary Measures Number 4).

The risks to conifer forest estates in the UK consist of various phases of attack that are characteristic of mass-attack bark beetles, which result in 'boom and bust' population dynamics. These tree-attack strategies are almost invariably driven by random environmental or human-induced events. The principal drivers are wind storms and, increasingly, periods of severe drought, leading to an abundance of poorly defended potential breeding material upon which bark beetle populations can increase rapidly. If the numbers of pioneer beetles exploiting a weakened resource are sufficiently large, then attacks on living trees will further increase population size, resulting in major and rising tree mortality. This process is accelerated by the number of generations per year, which can range from one to three for most *Ips* species in the hottest and most southern parts of their ranges.

Dispersal of beetles tends to be very local, especially at low population densities, with most new attacks occurring within 500 m and frequently less than 100 m of the source. However, long-distance flights of greater than 50 km can also occur, in particular when they are wind-assisted. The transport of beetles in wood and wood products via trade is the main pathway for long-distance dispersal, as evidenced by interceptions of all the PZ *Ips* species in various countries.

Management of beetle attacks takes place principally through the removal of infested wood or of susceptible trees damaged by storms or felled as part of normal forest management. This strategy requires rapid action because beetles can complete their life cycles within 2–4 months and then re-emerge to attack standing trees. Major losses of trees, running to millions of cubic metres, have consequent losses on timber values, nutrient cycling, water supply and quality, carbon sequestration, biodiversity and recreation values. In certain situations, *I. typographus* is regarded as a keystone species, in that it affects whole ecosystems and their associated processes.

The widespread distribution of the various *Ips* species in Europe indicates that they have broad climatic tolerance and are all likely to establish in the UK if a sufficiently large

pioneer population is present. *Ips sexdentatus* and *I. cembrae* are already established in Great Britain, confirming their capacity to spread and colonise. However, both species are regarded as secondary and mainly responsive to the presence of already weakened trees.

Ips typographus is of particular concern in view of its track record as a major tree-killing pest and there have been many instances of interception in the UK. Although it has been regarded as having a relatively low likelihood of establishment, based on previous evidence of a lack of breeding and of a possible Allee effect requiring relatively large numbers to successfully establish, the recent discovery of a viable breeding population in Kent indicates that it could establish a foothold in the UK. Based on the assumption that threshold numbers for breeding by pioneer beetles are exceeded, the widespread availability of hosts and suitable climatic conditions along with a moderate likelihood of windthrow, suggest that mass attack and epidemic population growth with consequent tree mortality are possible in the UK. Measures to manage this possibility include improved surveillance based on the risk of windthrow, the rapid removal of weakened or infested host material and the potential establishment of internal quarantine. Increased awareness is an important part of integrated management of this pest. The scale of infestation is relatively difficult to predict, partially due to uncertainty about the number of generations per year and also as to whether dispersal between infested forest areas is likely, either by beetle flight or by human-assisted dispersal.

Introduction

The aim of this Research Report is to describe and assess the threats posed by bark beetles in the genus *Ips* that are subject to Protected Zone (PZ) status in the UK. Information from this report will be used to determine the efficacy of the UK's PZ status by assessing the value at risk from the various *Ips* species. In parallel to assessing measures to prevent the transport and potential establishment of these

pests, consideration is also given to possible management regimes, consisting of eradication, containment, slowing the spread of the pests and, ultimately, living with them.

A summary of the key factors likely to determine the dynamics of the main *Ips* species under UK conditions is provided in Table 1.

Table 1 Summary of the main parameters affecting the dynamics and impacts of *Ips* species with Protected Zone status.

Parameter	Pioneer population (1–3 years post-invasion)	Mass attack population (building from pioneer population)	Post-epidemic population (endemic state)	Notes on parameter	Uncertainty
Host area at risk	Random trigger (e.g. windthrow) ≤ 0.2 ha attack then extinction (Allee effect*) ≥ 0.2 ha. Population growth and potential for mass attack (see the section on 'Eradication and containment prospects' on page 29).	Any forest block with $>75\%$ spruce and >20 years old. 10-year duration in epidemic phase; 20 generations in the south, 10 generations in the north. In Great Britain, maximum area of 583 000 ha of spruce in this age class are vulnerable. Assume doubling time of 6 months (maximum). (Derived from Tables 11 and 13).	Return to random trigger but at higher background level. Background populations widely distributed and more hotspots for rapid increase.	Living spruce = Norway spruce and Sitka spruce >20 years old. Highest likelihood within 500 m of emerging adult source but long tail to distribution. Assume 200 m average spread. Range from 100–500 m. (Derived from Kautz <i>et al.</i> , 2016).	Populations must emerge together to overcome tree defences. Uncertainty: Medium for pioneer High for mass attack Low for post-epidemic These act in sequence and pioneer stage must take place.
Ecosystem services at risk					
Timber losses	Random losses of trees are mainly not human-influenced. Little additional loss from bark beetles. Most windthrows <2 ha.	Can be major for monocultural spruce. Rapid harvesting can mitigate losses, but yield could be down. Assume average loss for 40-years-old trees. Volume at risk in Great Britain = 160 million m^3 . (Extrapolated from Tables 12 and 13).	Some ongoing impact but very small in the average 10-year interval between outbreaks (European experience). Random trigger could return to epidemic phase at any time.	As above.	As above.
Nutrient cycling, water supply and quality	Some impacts from random losses. Little effect from pioneer beetles.	Crown condition ranging from green (healthy or no visible symptoms), red (dying or recently dead) and grey (long dead with loss of foliage) phases. Increase in soil NH_4 and NO_2 and cations. Dissolved organic carbon decline. Difficult to quantify. Assume the same as air quality. Average value $\pounds 470\ ha^{-1}$. (Extrapolated from ONS, 2017).	Recovery of all parameters, but potentially not to pre-epidemic phase.		
Carbon sequestration	As above.	Maximum is total loss of biomass. However, likely to harvest and remove as much as possible. Assume overall loss of carbon around $\pounds 70\ ha^{-1}$, but could be as high as $\pounds 490\ ha^{-1}$. (Extrapolated from ONS, 2017).	Overall will be net loss, even if replanting and grown to full rotation. Assume loss of 10% = $\sim\pounds 7\text{--}\pounds 49\ ha^{-1}$.		

Table 1 Summary of the main parameters affecting the dynamics and impacts of *Ips* species with Protected Zone status (continued).

Parameter	Pioneer population (1–3 years post-invasion)	Mass attack population (building from pioneer population)	Post-epidemic population (endemic state)	Notes on parameter	Uncertainty
Biodiversity	Small loss of canopy but insignificant.	Large loss of canopy and possible increase in invertebrates that rely on dead or decaying wood, and ground flora (more light). Average monetary value estimate for biodiversity loss = £146 ha ⁻¹ . (Estimated from Willis <i>et al.</i> , 2003.)	Some recovery and potential qualitative change in biodiversity mix. Restored value gradually over 10+ years to £146 ha ⁻¹ .		There is no consensus on valuing biodiversity. Another estimate from Willis <i>et al.</i> (2003) of £0.35 per household per 12 000 ha of Sitka spruce would give a value of £790 ha ⁻¹ .
Recreation and aesthetic values	No additional loss relative to natural random events such as windthrow.	Large loss of visual and recreational value, initially more severe than clearfell if reach grey phase in standing dead trees. Visitor time could be lost. Value per ha = £190. (Estimated from ONS, 2017).	Recovery from restocking or natural regeneration and gradual return to full value over 10–20 years. Average estimated to be ~£90 ha ⁻¹ .		
Spread rates with and without management					
Spread rate – do nothing	Initially slow from small centres. 1–3 years to spread without control.	Assume that all spruce forest areas in Great Britain are at risk. The Forestry Commission Tool does not allow time series and age structure. Assume doubling time of 6 months.	Return to low level local spread with beetles relying on limited supply of weakened trees.	Maximum possible. Local spread + human-assisted. High-medium certainty.	
Spread rate – remove fallen timber	Eradication possible if within 1 or 2 generations.	If >2 generations, population increase but at lower rate. Doubling time of 12 months.	If removal of infested timber continues, very low spread.		
Spread rate – remove standing killed trees	As above.	As above. Doubling time of 12 months.	If removal of infested timber continues, very low spread.		
Spread rate – impose quarantine	Not necessary if conditions above are met.	Essential if aim to protect from expanding infestation. Assume slowing of rate of mortality and doubling time of 24 months.	Effective quarantine will minimise likelihood of remote infestations.		
Effectiveness of control measures					
Minimum area below which pest eradicated	0.2 ha but could be greater if early location of new infestation and intervention.	Once epidemic population growth commences, eradication not possible. Move to containment.	For <0.2 ha patches expect local extinction. If >0.2 ha risk of returning to epidemic state.		
Control effort (areas managed)	0.2–0.5 ha or size of smallest windblow.	Whole of susceptible spruce estate.	Local infestations and tick-over populations.		
Natural enemies	No impact. Host population too small.	Potential impact from native natural enemies responding to pest population increase. Only likely to affect after large population increase. Could be as high as 50% population reduction (Wermelinger, 2002) but after pest population peak, hence little reduction in timber loss. Assume 90% loss relative to no control option.	Natural enemies will keep population down for period until their own numbers decline or they switch to more available hosts. Assume 5–10% impact.	Most activity is likely from generalist natural enemies whose background densities will depend on presence of other prey.	High uncertainty for UK situation where there is no prior interaction between pest and natural enemies.

Table 1 Summary of the main parameters affecting the dynamics and impacts of *Ips* species with Protected Zone status (continued).

Parameter	Pioneer population (1–3 years post-invasion)	Mass attack population (building from pioneer population)	Post-epidemic population (endemic state)	Notes on parameter	Uncertainty
Control efficiency under different regimes and areas infested	As for spread rate assumptions.	As for spread rate assumptions.	As for spread rate assumptions.		All control measures depend on reducing breeding by removal with some additional influence of natural enemies.
Control period	1–2 years if locate hotspots quickly.	Average rotation. Assume 50 years.	Return to 1–2 years.		The Forestry Commission Tool does not have temporal or spatial components. Hence use of averages. Medium uncertainty.

*Allee effect: a threshold in population growth and maintenance below which a population may tend towards extinction.

The UK has PZ status for a number of forest pests, which allows imposing controls on the importation of goods that could represent pathways for pests to reach forests in the UK. The pests subject to PZ status in the UK (i.e. Great Britain, Northern Ireland and the Isle of Man) are listed, with specifications for measures to prevent their arrival, in the newly implemented Regulation (EU) 2016/2031 of the European Parliament (replacing EC Directive 2000/29/EC).

The pests that have PZ status and are included in the current report are:

- *Ips typographus* – bark beetle principally associated with spruce and which, in its Eurasian range, occasionally reaches outbreak levels resulting in extensive tree mortality.
- *Ips amitinus* – bark beetle associated with spruce and pine and, to a lesser extent, fir and larch. It is distributed from western Europe to the western part of Russia and neighbouring countries. Although it causes limited tree mortality and is often regarded as a secondary pest, its severity and range appears to have increased in recent years.
- *Ips sexdentatus* – bark beetle associated with pine and occasionally spruce and fir. It has a Eurasian distribution. It is mainly regarded as a secondary pest, with occasional attacks on standing trees (along with other pests). It is present in the UK.
- *Ips cembrae* – bark beetle mainly associated with larch, and occasionally pine and spruce. It is present in Europe and parts of Russia and Ukraine. Locally, it is highly damaging, and is often linked to drought and high

temperatures. It is present in the UK and has caused limited damage to larch.

- *Ips duplicatus* – bark beetle principally associated with spruce, and occasionally pine and larch. It has a Eurasian distribution but is absent from the most western countries of Europe. Tree mortality has mainly been reported from Poland, Czechia and Inner Mongolia.

The UK's PZ status enables it to specify that all wood of host tree species must be free of bark and accompanied by a Plant Passport indicating origin, to ensure compliance with PZ requirements (Defra, 2020). To retain PZ status, annual surveys to check for potential breeding by the named pest species have to be carried out and reported to the EU (Fielding *et al.*, 1994). For *Ips* spp., the surveys are on a 15 km grid basis, and only include conifer woodland locations containing at least 25 spruce or pine trees aged >15 years old, and where trap logs, baited with the *Ips typographus* aggregation pheromone, are placed during the putative adult flight period (April to October). All baited logs are inspected in September or October and any bark beetles present are identified.

The results are collated and reported annually to the EU. Until 2018, when *Ips typographus* was found at a PZ survey site in Kent, there had been no evidence of successful breeding by the pest.

Pest characteristics

The biology of *Ips* species in a European context

The five species of *Ips* are all subject to PZ status; however, *I. cembrae* and *I. sexdentatus*, which are both already present in mainland Great Britain, only have PZ status for certain parts of the UK, namely, Northern Ireland and the Isle of Man (see the section on the 'Commission Implementing Regulation (EU) 2019/2072 listing for *Ips* spp.' on page 32). All five species are Coleoptera: Curculionidae, Scolytinae, and they overlap considerably in biology, distribution and host plants. There is extensive coverage of each species, with *I. typographus* receiving significantly more attention in both scientific and more general literature.

The key characteristics of each *Ips* species are summarised in Table 2. Because *I. typographus* is regarded as the most serious pest of the five species (Gregoire and Evans, 2004), it will be described in detail as an exemplar for the range of *Ips* species covered in this report. Details of the other *Ips* species will be provided where appropriate, with particular emphasis on any aspects which differentiate them from the detailed description of *I. typographus*.

Tree attack strategies

All five species of *Ips* can be described as aggressive or mass-attack bark beetles (Raffa *et al.*, 2008) in that they are able to overcome the constitutive and induced defence systems of living host trees (Lieutier *et al.*, 2004; Franceschi *et al.*, 2005). However, the dynamics of attacks on living trees are almost invariably driven by the initial availability of weakened or recently dead trees, which have a much lower defence capability than living trees (Wermelinger, 2004). In living trees, constitutive defences consist partially of the capacity of the tree to release pre-formed resin in response to physical damage caused by the entry of male beetles chewing through the bark to reach the phloem, and also partially of innate mechanical defences such as suberised and lignified cells, stone cells and calcium oxalate crystals. Secondary induced defence systems involve activation and production of defensive chemicals, including development-related proteins and enzymes. Induced defences act against ongoing pest attacks (hypersensitive responses and localised resistance) and potential future attacks (acquired resistance). These are reviewed in detail by Franceschi *et al.* (2005).

Table 2 The main biological characteristics of the five species of *Ips* with Protected Zone status for the UK.

Name	Generations per year	Overwinter		Adult emergence	No. of eggs	No. of instars*	Sister broods	Host list	Host size preference	Host trigger	Fungal associate?	Mass attack?
		Life stage	Location									
<i>Ips typographus</i>	1-3	Adults; larvae or pupae	Bark or litter	April-June	30-80	3	Yes	<i>Pinus; Abies, Larix, Picea</i>	Mature or pole	Weakened trees	Yes	Yes
<i>Ips amitinus</i>	1-2	Adults	Litter or bark	June-August	up to 60	3	Yes	<i>Picea abies, Pinus sylvestris, Abies alba, Larix decidua</i>	Small, thin barked	Weakened trees	Yes	Yes
<i>Ips duplicatus</i>	1-3	Adults	Litter, soil or bark	April-May	60 average	3	Yes	<i>Picea abies; Pinus, Larix, Abies, Juniperus</i>	Older trees on upper thinner bark sections. Standing trees only	Weakened trees	Yes	Yes, limited evidence
<i>Ips cembrae</i>	1-2	Adults	Bark or litter	May	50	3	Yes	<i>Larix; Picea, Pinus</i>	Larger trees	Weakened trees	Yes	Limited
<i>Ips sexdentatus</i>	1-5	Adults	Bark or litter	March/April in the south, May/June in the north	up to 60	3	Yes	<i>Pinus; Abies, Larix, Picea</i>	Larger trees with thick bark	Weakened trees	Yes	Limited - only in southern part of range

*Instars: different stages of development of immature (larval) stages.

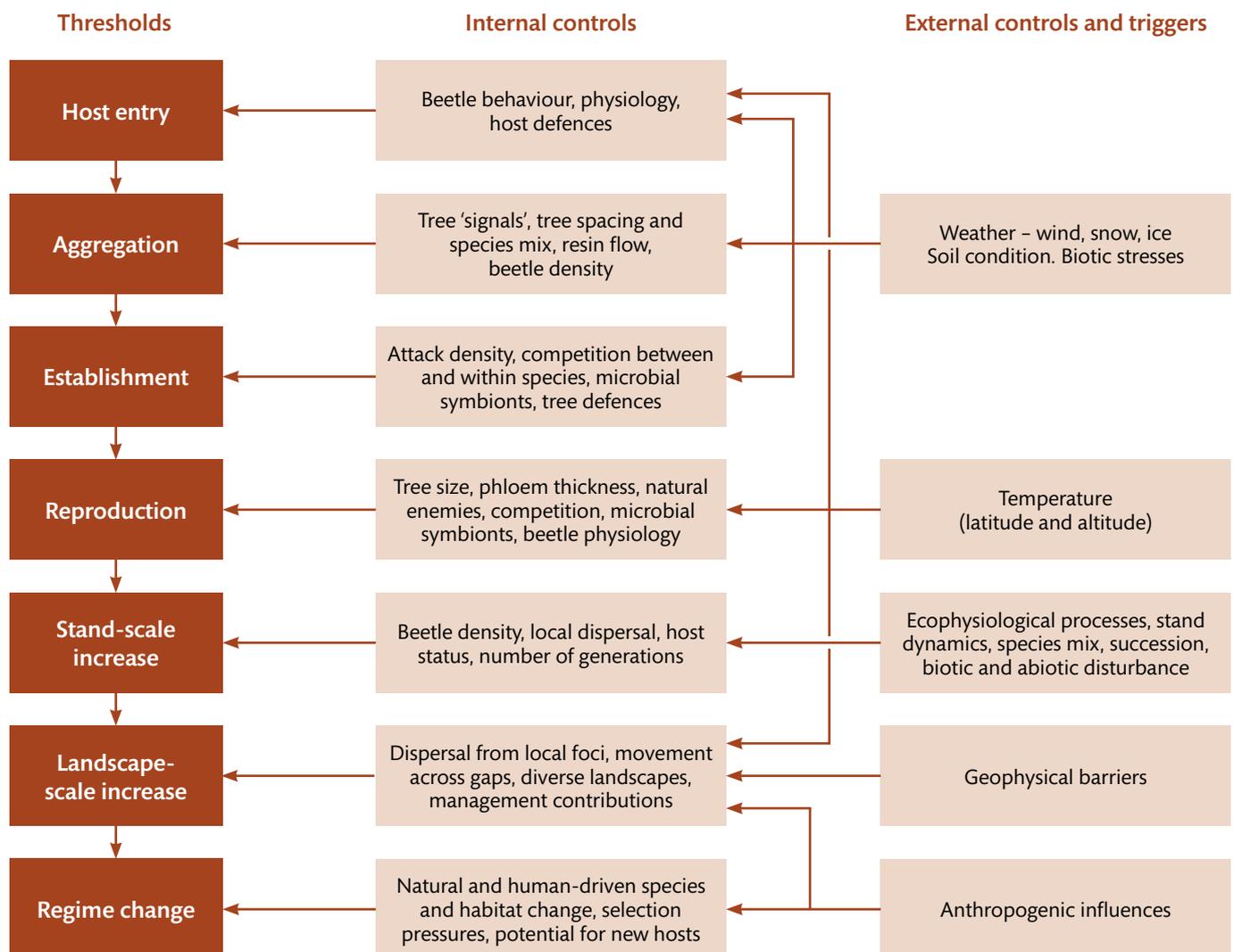
When relating epidemic population growth to random environmental events, a critical consideration is assessing how these factors affect the ability of bark beetles to increase population growth sufficiently to subsequently attack and breed in living trees. The general principles of bark beetle attack, especially for those considered to be aggressive, are well described by Raffa *et al.* (2008), although the case studies reported relate to North American species. In particular, the authors provide a conceptual framework with which to describe the key attributes of each stage of bark beetle attack, from initiation at the tree level to stand- and landscape-scale outbreaks. This framework has been reproduced and adapted to reflect those particular attributes that are key to the population dynamics of *Ips* spp. in Europe (Figure 1).

Thresholds for host entry, aggregation, establishment and reproduction, while sequential in concept, tend to work

in parallel, so that many of the controls, both internal and external, influence the entire process towards successful reproduction. Adult beetle behaviour is influenced by visual and olfactory cues and, apart from evidence of strong responses to beetle pheromones and host volatiles from weakened trees (Wermelinger, 2004), it is believed that attacks on living trees can also be a result of random landings of pioneer beetles, followed by testing for host suitability (Wood, 1982; Byers, 1989b; Saint-Germain, Buddle and Drapeau, 2007).

Successful breeding by low density populations of all five species of *Ips* is dependent on newly emerged adult male beetles (Figure 2) finding a suitable, weakly defended host tree, burrowing a nuptial gallery and then emitting a pheromone to attract up to five females to the gallery system. Flight periods and numbers of generations per

Figure 1 Factors driving the population dynamics of *Ips* spp. bark beetle.



Notes: Thresholds (boxes) are shown in sequence leading to increasingly large-scale population growth influenced by the controls (internal and external) that determine the population dynamics of the pests. Source: Adapted from Raffa *et al.* (2008).

Figure 2 Adult *Ips typographus*.



year are temperature-dependent, with typically up to two generations per year, one in spring and one in summer.

Eggs are laid on the sides of the gallery system, with each species of beetle having a characteristic pattern of gallery and egg niche, followed by larval feeding outwards from the central gallery, again in a species-characteristic pattern (Figure 3). Within an attacked tree, the thickness of the bark and the capacity for larvae to develop within individual systems without encountering other galleries is crucial to the overall breeding success of each *Ips* species. For example, *I. typographus* tends to concentrate attacks on the thicker barked areas of a trunk, primarily in older trees (Sauvard, 2004).

By contrast, *I. duplicatus* and *I. amitinus* tend to select thinner barked areas of trees and are also sensitive to the pheromone emissions from the more competitive *I. typographus* (Schlyter and Anderbrant, 1993).

Despite the low resistance of recently dead or highly stressed trees, there is still a minimum number of 'pioneer' beetles required to successfully establish in the tree and produce offspring for further attacks. For *I. typographus*, the minimum number of pioneer beetles required to breed successfully in a weakened tree varies between 110 per square metre of bark surface (Schlyter and Anderbrant, 1993) and around 700 per square metre (Hedgren and Schroeder, 2004), the upper band of which reaches the density needed to overcome healthy trees. At lower attack rates, there are no competition constraints within a species and bark beetles can potentially achieve their maximum reproductive rates. This varies by species but ranges from a mean of 142 per square metre for *I. sexdentatus* on pine (Pineau *et al.*, 2017) to 850 per square metre for *I. acuminatus* on pine (Langstrom *et al.*, 1992). The mean number of successful galleries, termed the Critical Threshold

Figure 3 Gallery system of *Ips typographus*. Central nuptial gallery with larval burrows extending from egg niches on the sides.



of Attack Density, was related to tree vigour for *I. sexdentatus* and ranged from <60 per square metre for weakened or dead trees to around 130 per square metre for trees with high vigour (Pineau *et al.*, 2017).

Because of the considerable variation among data for density thresholds for successful attacks by all five species of *Ips*, it is not possible to provide a definitive value for the number of adult beetles required to establish a pioneer population of beetles. In addition, high levels of colonisation can result in significant competition among larvae in their galleries and, at extreme levels, result in very low numbers of offspring. This is a density-dependent regulatory factor in the population dynamics of bark beetles, which has been studied and modelled for *I. typographus* and *I. duplicatus* population development on spruce (Schlyter and Anderbrant, 1993). Competition both between and within bark beetle species was observed: *I. typographus* population growth was reduced by adult *I. duplicatus* beetles which were avoiding those parts of the tree already colonised by *I. typographus*. However, competition within the *I. typographus* species was also high.

Such a restriction on breeding success is a result of 'scramble competition', described by Schlyter and Anderbrant (1993) as 'everyone loses'. Aggressive bark beetles are known to exhibit this type of population restriction, which is described in considerable detail by Byers (1989a), who developed the concept of minimum distance between galleries for attack by beetles colonising trees already subject to initial attacks. Initial attacks are moderated by reactions to pheromone signals given off by pioneer males (initially attractive and later repellent for other beetles) and, once new galleries are produced, larval behavioural mechanisms tend to avoid interaction with other galleries. Louis *et al.* (2016) highlight how attacking beetles must balance the low resistance from weakened trees, which encourages multiple attacks and competition within each species, against the intrinsic resistance but high nutritional quality provided by standing trees. The poor defence presented by weakened trees also exposes them to attack from a wide range of species that feed on dead or decaying wood, which also increases the likelihood of competition between species (Louis, Gregoire and Pelisson, 2014).

A further consideration with regard to the management of beetle populations are overwintering sites for the various species of *Ips*. Overwintering as adult beetles can take place under the bark or in the litter layer beneath infested trees (Jeger *et al.*, 2017). This has implications for management in that beetles might remain on site after infested trees containing beetles under the bark have been removed. However, overwintering survival in the litter layer may be less than under the bark in extremely cold conditions, resulting in beetles freezing (Kostal *et al.*, 2011), or under warm conditions when beetles are unable to hibernate and subsequently die through depletion of energy resources (Jonsson *et al.*, 2007; Kostal *et al.*, 2011). Under extremely cold conditions, mortality under bark can be high in the upper parts of the trunk above any snow layer, although this tends to be greater in immature or young adult stages rather than mature adults (Faccoli, 2019).

Association of *Ips* spp. with phytopathogenic fungi

An important feature of the attack strategies of *Ips* spp. is the almost universal association with phytopathogenic fungi (Table 3). The combination of numbers of attacking beetles and associated fungi is generally assumed to be a mutualistic mechanism to overcome the defence systems of host trees (Kirisits, 2004). Many species of fungi have been shown as associated with *Ips* spp. (Table 3). Beetles are

able to carry fungal spores when they emerge as immature adults, and this enhances their capacity to overcome the defences of living trees. The beetles are aggressive and their associated fungi add to the biological impact on the tree, which is why this pest (including *I. typographus*) is capable of overcoming a tree's defences.

Research into bark beetle-fungal associations explains how the combined effects of beetle numbers and phytopathogenic fungi overcome both pre-formed and induced defences in living trees (e.g. Kirisits, 2004; Lieutier, Yart and Salle, 2009). Six and Wingfield (2011) dispute this arguing that, instead of supporting bark beetles in tree killing, fungi themselves benefit by reducing competition with other fungi. Not all individuals of a bark beetle species carry fungal spores, and the rate of fungal development in a tree is too slow to help beetles in overcoming defences. Irrespective of the precise relationship with fungi, successful attacks on living trees are overwhelmingly driven by beetle numbers, both through pioneers emitting aggregation pheromones and established beetles emitting anti-aggregation pheromones to prevent further attacks.

Pioneer bark beetle populations: the numbers needed

Balancing the relative ease of attack on weakened trees versus the need for a mass attack to overcome healthy trees is an important consideration when assessing the dispersal of beetle populations and, in particular, the potential for establishment in new locations as an invasive species. Conversely, despite the evidence that bark beetles are capable of establishing in new locations—for example, *I. cembrae* and *I. sexdentatus* and, more recently, *I. typographus* in Great Britain—it is key to explore why some species have not yet done so or have had limited success in colonisation and expansion. Allee effects (Liebhold and Tobin, 2008) is a concept that is increasingly used to explain why certain bark beetle species have not established outside their home ranges, despite the evidence of carriage and flight after international trade. Allee effects, named after the author who originally coined the term (Allee, 1931), reflect a threshold in population growth and maintenance, below which a population may tend towards extinction. Taylor and Hastings (2005) have reviewed the potential roles of Allee effects in invasions and, quoting Stephens, Sutherland and Freckleton (1999), they distinguish between 'component' and 'demographic' Allee effects. A component Allee effect on a population arises when a particular component of individual fitness is positively related to density, especially when it is reduced at low population density, exhibiting

Table 3 Relationships between various conifer beetle species and their ophiostomatoid fungi.

		H					M			L												
		<i>Ceratcoystis polonica</i>	<i>Ceratcoystis rufipenni</i>	<i>Ceratcoystis laricicola</i>	<i>Leptographium terebrantis</i>	<i>Leptographium wingfieldii</i>	<i>Grosmannia clavigera</i>	<i>Ophiostoma minus</i>	<i>Ophiostoma bicolor</i>	<i>Ophiostoma ips</i>	<i>Ophiostoma brunneo-cillatum</i>	<i>Ophiostoma montium</i>	<i>Ophiostoma longiclavatum</i>	<i>Ophiostoma canum</i>	<i>Ophiostoma brevicomi</i>	<i>Leptographium abietinum</i>	<i>Ophiostoma penicillatum</i>	<i>Ophiostoma piceae</i>	<i>Ophiostoma pseudotsugae</i>	<i>Ophiostoma europhioides</i>	<i>Ophiostoma aimoe</i>	<i>Ambrosiella symbioticum</i>
H	<i>Ips typographus</i>	•						•								•	•		•	•		
	<i>Dendroctonus ponderosae</i>						•				•	•										
	<i>Dendroctonus frontalis</i>						•															
	<i>Dendroctonus brevicomis</i>						•							•								
	<i>Dendroctonus pseudotsugae</i>		•													•			•	•		
	<i>Dendroctonus rufipennis</i>		•													•						
	<i>Dendroctonus micans</i>													•								
	<i>Scolytus ventralis</i>																					•
M	<i>Ips cembrae</i>		•					•		•												
	<i>Ips sexdentatus</i>						•		•												•	
	<i>Ips acuminatus</i>						•		•												•	
	<i>Pityogenes calcographus</i>							•									•				•	
	<i>Orthotomicus erosus</i>									•												
	<i>Ips pini</i>									•												
L	<i>Tomicus minor</i>												•									
	<i>Dendroctonus valens</i>				•				•													
	<i>Dendroctonus terebrans</i>				•																	
	<i>Tomicus piniperda</i>					•	•															

Notes:

1. Bark beetles are grouped by level of aggressiveness: Furniss and Carolin (1977) and Dymerski, Anhold and Munson (2001) for North America, and Chararas (1962) and Gregoire and Evans (2004) for Europe. Fungi are grouped by level of pathogenicity. H = High, M = moderate, L = low aggressiveness/pathogenicity.
2. The four species of *Ips* on the UK Protected Zone list are presented on a grey background.

Source: Modified from Lieutier, Yart and Salle (2009).

inverse density-dependent growth. This can result in a demographic Allee effect, where population fitness as a whole is linked to density such that per capita growth rate of the species is reduced at low density. Demographic Allee effects can be weak or strong, thus affecting the equilibrium points around which populations either grow or decline.

Allee effects influence population change at lower densities when per capita growth is insufficient to sustain a viable population. At higher densities, populations tend towards extinction when they grow too much and become resource-limited.

Allee thresholds are regarded as important in reducing the spread of pests and explaining why some species have not established in a new area, despite there being

numerous arrivals of adults in that area. Haack (2001; 2006) analysed interception and establishment data for exotic bark beetles in the USA and reported that *I. typographus*, *I. sexdentatus*, *I. acuminatus*, *I. cembrae* and *I. amitinus*, in descending number order, had been intercepted during 1985–2000. However, none of these species are reported as having established in the USA. Similar results were reported in New Zealand, with *I. typographus*, *I. cembrae*, *I. amitinus*, *I. acuminatus* and *I. sexdentatus* in descending order (Brockerhoff *et al.*, 2006). Liebhold and Tobin (2008) speculated that the lack of establishment is a consequence of arriving populations being too small to exceed the Allee threshold for each bark beetle species.

Interceptions of *I. typographus* in the UK have also been frequent, with incidences of the capture of adults in

pheromone traps linked to changes in trade patterns. Traps baited with the pheromone mix for *I. typographus* were deployed by the Forestry Commission at ports from 1985 to 2008, and revealed that this pest had arrived and left various ports each year (Forest Research annual survey data). Initially, annual totals were extremely low but increased significantly in 1994, and then again in 1995, reflecting poor debarking standards from trading with the Baltic states; however, annual totals returned to lower levels once debarking practices improved (Figure 4). No trapping took place from 2007 to 2014. Limited trapping in the Humber ports has been carried out since 2015, with annual captures of 2, 21, 4 and 15 beetles in 2015, 2016, 2017 and 2018 respectively, confirming the regular arrival of *I. typographus*, despite PZ rules specifying that all conifer wood should be debarked.

Considering that the capturing efficiency and zone of attraction of pheromone traps is <10 m (Byers, 2009), most beetles arriving in the UK would have escaped detection.

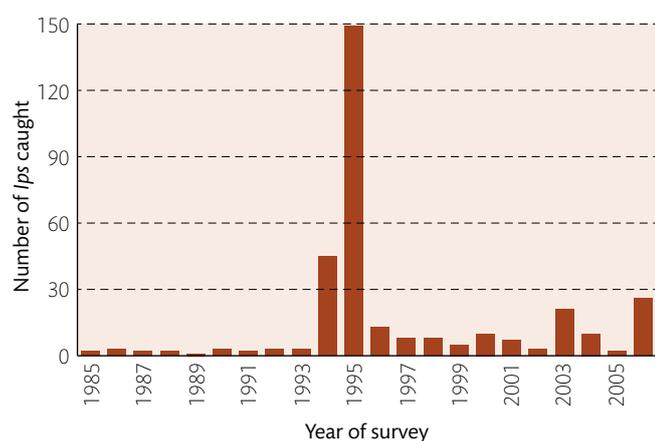
However, the movement of goods away from the ports and the potential for beetles to appear at numerous end points of pathways dilutes the emergent local populations at final destinations, which might explain the absence of evidence of establishment of *I. typographus*. Trade with European countries, before the introduction of debarking requirements under EU rules, would have introduced cohorts of exotic *Ips* spp. in the 20th century, suggesting that there were barriers to the initial establishment of viable populations. This was recognised shortly after the Second World War when *I. typographus* was discovered emerging from Norway spruce logs that had been imported from Germany (Laidlaw, 1947). It was noted that larval development had been

completed by early July, suggesting that the beetle may have emerged as adults and also that a second generation would have been possible. Laidlaw (1947) indicated that both *I. typographus* (mainly on spruce but also on Scots pine) and *I. sexdentatus* (on Scots pine) were found on shipments at ports in England, Scotland and Wales, with 200–300 beetles found in some logs. Recognising the threat posed by such large imports of infested material, the Forestry Commission arranged for trap logs of Norway spruce to be placed near ports and high-risk areas (e.g. spruce forests) but did not find any infestations by the pest.

Whether the lack of establishment in the UK of the most aggressive bark beetles (notably *I. typographus*) is a consequence of Allee effects on initial batches of pioneer adults remains uncertain. The thresholds for successful attacks, even at the individual tree level, suggest that relatively large numbers of beetles (initially males, followed by females responding to aggregation pheromones) must arrive at the same time in close proximity to suitable host trees. It is unlikely that sufficient beetles would arrive to overcome well defended healthy trees, but attacks on weakened or recently dead trees provide a potential resource for initial establishment. Although still subject to investigation, the discovery of a breeding population of *I. typographus* in Kent in November 2018 confirms that a source of pioneer beetles and weakened trees available for colonisation coincided at the affected location. While there is no certainty regarding the origin or pathway for arrival of the beetles, the proximity of the affected site to routes leading from channel ports and the poor condition of Norway spruce host trees at the site suggest that pioneer beetles were able to locate weakened trees for breeding after their arrival in the UK. It is also possible that adult beetles could have flown directly from France or Belgium since the distances are less than those recorded for flights of *I. typographus* (e.g. 43 km; Nilssen, 1984). Populations of *I. typographus* in Belgium and western France in 2018 and 2019 were high, suggesting that a ‘cloud’ of beetles could have flown to Kent, which extensive captures in a network of pheromone-baited traps in the area have confirmed (Inward, pers. comm.).

There has been relatively little quantitative research to investigate the minimum pioneer population needed to establish viable populations of *I. typographus*. However, the evidence that both *I. sexdentatus* (early 20th century) and *I. cembrae* (1950s) (Crooke, 1955; Crooke and Bevan, 1957; Redfern *et al.*, 1987) and, more recently, *I. typographus*, have successfully established in Great Britain, indicates that sufficient numbers of those species arrived in the ‘right place at the right time’. Because *I. sexdentatus* and *I. cembrae* are

Figure 4 Interceptions of adult *Ips typographus* at ports in Great Britain.



Note: The bars represent annual totals from pheromone-baited traps.

regarded as less aggressive than *I. typographus*, and because both of these species have mostly remained as secondary pests since they were first recorded, this suggests that the thresholds for establishment are lower in these species and that they can easily find and exploit relatively scarce resources of weakened or felled trees. For *I. typographus*, the continuing gradual expansion in western parts of Europe indicates that the pest does not readily colonise new areas, especially if spruce resources are scattered and a more stringent coincidence of emergent adults and weakened trees is necessary for establishment. To assess the specific dispersal of *I. typographus* from infested to non-infested areas, Jacquemin (2008) set up a 150 km long transect of pheromone traps from infested Bouillon and the Belgian Ardenne to Champagne in France, a predominantly spruce-free area. Captures along the transect indicated that *I. typographus* was found up to 100 km from the source occupying small, isolated spruce stands. Mark-recapture studies in a beetle- and spruce-free area in Champagne-Ardenne indicated a rapid dilution of released beetles, suggesting that Allee effects would preclude establishment in similar situations.

Because timber imports invariably arrive in urban environments, and knowing that adult beetles may emerge anywhere from the arrival point through to the final destination of the imported goods, there could be a continuous gradient of flying beetle presence in urban and peri-urban environments. Data from Piel *et al.* (2005) provide some context to the British pheromone trap data on *I. typographus* captures. The authors set up a transect of baited pheromone traps across Brussels, from the southeast to the city centre, and also at the Port of Brussels. As expected from the known presence of *I. typographus* in the nearby spruce forests in Wallonia, a gradient of captures going from high at the outer periphery of Brussels to low in the beech-dominated Sonian Forest at the city's edge and the city centre, an area influenced by the vertical structures of its buildings. A surprising finding was that captures at the Port of Brussels were high, especially in the second year of sampling; the two traps captured up to 170 individuals, representing 9.5 adults per day, compared with 0.4 adults on average at the other locations. The authors investigated the general area around the port and concluded that these beetles originated from imported timber arriving from the Baltic states and European Russia, which do not have to debark for internal trade to mainland EU member states. These capture rates are much higher than those recorded in the Great Britain pheromone-trapping regime, but indicate the potential for high numbers of flying adult beetles to arrive over a short time period. Interestingly, an inspection of possible host trees in Brussels did not uncover any evidence of active *I. typographus* attacks.

The influence of temperature and daylight period on *Ips* life cycles

Ips undergo 1–5 generations per year depending on species, location and altitude (Table 2). The number of generations is driven by temperature although day length also influences emergence and, in particular, the start of overwintering, usually by the adult stage (Sauvard, 2004; Baier, Pennerstorfer and Schopf, 2007; Jonsson *et al.*, 2007). For *I. typographus*, spring emergence starts when air temperatures exceed 16.0°C, but an accumulated temperature of ~140 degree-days (dd) from early April is also required (Baier, Pennerstorfer and Schopf, 2007). Once attacks take place and eggs are laid, larvae emerge as new adults when temperatures under the bark reach 8–39°C. The emergence of a new generation of adults occurs between 500–700 dd.

Faccoli (2009) carried out a detailed field assessment of *I. typographus* flight periods and used data from Wermerlinger and Seifert (1998) to estimate the thermal sums required to complete the F1 generation for 1996–2005 in the southeastern Alps.

The data from Faccoli (2009) agree in general with observations of the dd required for development of the first generation of *I. typographus* in any given year, with the exact starting date of development being dependent on spring temperatures exceeding a threshold of ~10–15°C. The data were typical for a population that would complete two generations per year. Temperature and day length are the two triggers for the overwinter phase of the life cycle, when beetles hibernate for either environmentally or genetically driven reasons (Schebeck *et al.*, 2017).

The various *Ips* species are distributed across a wide temperature range (see the section on 'Native and invaded ranges for the five species of *Ips*' on page 21). Their capacity to tolerate temperatures as low as –32°C arises from a phenomenon called supercooling; the temperature at which ice formation takes place is called the supercooling point (SCP) (Zachariassen and Kristiansen, 2000). The ability to supercool comes from the presence of chemicals that prevent the freezing of tissue or damage to cells. These chemicals are found in beetle species that have adapted to very cold climates. SCPs occur during hibernation in winter; they range from –25°C in central Europe (Schopf and Kritsch, 2010) to –32°C further north (Annala, 1969). Only fully formed adults possess these very low SCPs; beetles at developmental stages have higher SCPs than adults, and pupae are more resistant to cold temperatures than larvae (Annala, 1969; Schopf and Kritsch, 2010).

Impacts of *Ips* species in their natural and invaded ranges

Large outbreaks of *I. typographus* have occurred periodically over most of its known range (see the section on the 'Host range of *Ips* species in Europe' on page 22); the triggers for outbreaks include random environmental and climate events such as major wind storms, heavy snowfalls, ice storms and, increasingly, consecutive annual periods of severe drought (Netherer *et al.*, 2019).

Schelhaas, Nabuurs and Schuck (2003) estimated that ~8% of tree mortality in Europe between 1850 and 2000 was attributable to bark beetle activity, principally from *I. typographus*. Other estimates for attacks post-2000, linked to major wind storm triggers, included losses of 8 million m³ during 2000–2009 in Switzerland (Stadelmann *et al.*, 2013), 18 million m³ during 2002–2012 in Austria (Jeger *et al.*, 2017) and 223 047 m³ in the high Tatra Mountains of Poland/Slovakia (Mezei *et al.*, 2014). The latter case is an example of the link between high winds and changing temperatures in mountainous regions as drivers of bark beetle population fluctuation, however, with an important limitation to breeding being that only one generation per year is possible under these conditions.

Dispersal of *Ips* spp.

Dispersal of the five species of *Ips* under PZ status is, in common with most other bark beetles, the result of local beetle flight and longer distance human-assisted transportation.

Beetle-mediated dispersal

There has been considerable research into *Ips* flight behaviour, partially to understand how beetles move after their emergence as new adults, but also how they locate and select trees for mating and laying eggs (Wood, 1982; Bakke, 1989; Sauvard, 2004; Wermelinger, 2004; Raffa *et al.*, 2008). Several mark-recapture studies on flight behaviour have been conducted, in which adult beetles marked in some way are released from a central point and then are subsequently recaptured by pheromone traps placed at different distances from the release points. For example, Duelli *et al.* (1997) studied recaptures in concentric rings of pheromone traps around a central release point of *I. typographus* that were either newly emerged or which had flown previously. Recaptures tailed off rapidly from the release point and only accounted for ~50% of released beetles. Modelling the trend of recaptures, the authors reported that beetles which had previously flown would

migrate by up to ~1 km, whereas newly emerged beetles would fly up to ~5 km. The experiment was carried out in a Scots pine stand ~6 km from the nearest spruce source. Despite the absence of any apparent breeding source for *I. typographus*, >14 000 unmarked beetles were captured in the traps, indicating relatively long-distance flights to reach the experimental site. Other data from captures of *I. typographus* in remote locations, such as islands and isolated woodlands, indicate that adults can fly long distances. Nilssen (1984) placed trap logs into areas north of a natural spruce range in Finland and found *I. typographus* 43 km away from the nearest spruce. It was assumed that the beetles had been carried on wind, rather than by purely directed flight. Other similar studies in areas without natural spruce suggest that aerial dispersal of >10 km is common for many bark beetles, including *Ips* spp. (e.g. 18 km; Forsse and Solbreck, 1985).

New attacks tend to be initiated when weakened and recently dead trees are available, and *Ips* species have evolved strategies to detect potentially scarce resources in order to breed and maintain population levels. The capacity to disperse long distances, whether in directed flight or by movement with wind, ensures that cohorts of adult beetles are airborne and can 'sample' large areas using a combination of visual and olfactory cues, which entice them to land and attempt to colonise potential host trees. From this presumption, any woodland containing potential hosts, particularly spruces, within at least 50 km of a source of *Ips* spp. could be vulnerable to attack, which could have been an important factor influencing the infestation in Kent. Duelli *et al.* (1997) provide evidence that newly emerged adult *I. typographus* tend to have a migration phase, in which a proportion of the population fly long distances from their points of emergence.

Apart from direct studies of adult flight, remote sensing of the progression of new outbreaks has provided inferences on the rates and frequencies of infestations in relation to random triggering events, such as windthrow and beetle-induced incidences of tree mortality. There has been growing interest in the use of remote sensing aided by improved multi-spectral cameras, new satellites and unmanned aerial vehicles (UAVs) (Senf, Seidl and Hostert, 2017). Most of the early studies concentrated on visual stages of infestation in red trees (those displaying a reddening of foliage shortly after death) and grey trees (dead trees where needles have been shed). While these are comparatively easy to detect, they have the disadvantage of being too late to initiate any remedial action since the beetles have already bred and dispersed from the trees.

Lausch *et al.* (2013) investigated hyperspectral remote sensing at a range of scales to assess *I. typographus* outbreaks using a scale of 1 (dead trees) to 5 (healthy). Overall, the accuracy for classes 1–4 was low (28–48%) compared with 62% for class 5. Visible and near infrared wavelengths (400–800 nm) were best for differentiation, but it remained difficult to differentiate class 4 (a green attack with no visible symptoms upon ground survey) from class 5. This was made more challenging by natural changes in reflectance due either to phenology or to non-beetle-induced stress factors

Landsat has been the main sensor for mapping bark beetle infestations, with an emphasis on achieving the highest resolution possible over a time series, especially when outbreaks last several years (Meigs, Kennedy and Cohen, 2011; Meddens *et al.*, 2013; Meddens and Hicke, 2014; Meigs *et al.*, 2015; Senf, Seidl and Hostert, 2017). This suggests that spatial resolution is a key feature for mapping bark beetle infestation. These studies reflected the large footprint of *Dendroctonus ponderosae* outbreaks in North America. Similarly, Oeser *et al.* (2017) demonstrated that Landsat time series helped classify major disturbances arising from windthrow and bark beetle attacks (principally *I. typographus*) in central Europe. The short-wave infrared part of the electromagnetic spectrum is particularly important for detecting bark beetle infestations that arise from its sensitivity to changes in needle water content, a characteristic of the shift to red or grey phases of beetle outbreaks (Senf, Seidl and Hostert, 2017). With high and very high spatial resolution data, however, an analysis of single-date images is still the usual approach (Pontius *et al.*, 2008; Hicke and Logan, 2009). Landsat imagery tends to be used for long, inter-annual, time series, but this is often supplemented by direct observation and local airborne very high-resolution data to assess sub-pixel mortality, such as the percentage of a Landsat pixel that is infested.

Recognising that most remote-sensing technology has a lag phase that precludes early remedial measures to reduce further attacks, Abdullah *et al.* (2018) assessed the potential of hyperspectral measurement of foliar chlorophyll and the nitrogen concentration of healthy or beetle-infested trees, and found that wavelengths of between 730 and 790 nm (red-edge) were the most accurate for detecting variation in chlorophyll concentration arising from bark beetle green attack. This technology could be scaled up by using a UAV-based platform or newly available multispectral satellite data, such as Sentinel-2, World View-2 or 3 RapidEye. Nasi *et al.* (2018) were able to demonstrate the potential of UAV-mounted hyperspectral cameras for small-scale assessment

of *I. typographus* attacks in an urban setting in Finland. Although the authors were able to differentiate infested from healthy trees, this was during the red phase of attack and hence would need further refinement to assist with early detection.

Recently, Abdullah *et al.* (2019a) assessed Landsat 8 spectral vegetation indices (SVIs) and canopy surface temperature (CST) from the satellite-acquired thermal infrared band and concluded that CST was a viable measure of early bark beetle attack on apparently green trees. This offers potential for remote sensing of bark beetle-induced stresses before they become apparent to the naked eye. In addition, SVIs from Sentinel-2 satellite imagery (notably red-edge dependent indices 2 and 3) and water-related indices (Short Wave Infra Red, Normalized Difference Water Index, Disease Water Stress Index, and Leaf Water Content Index), were shown to discriminate healthy from infested plots of spruce trees (Abdullah *et al.*, 2019b). Landsat-8 water-related indices were less effective in distinguishing healthy from infested trees. When compared with high-resolution aerial photography, percentage matching for early infestations was higher for Sentinel-2 (67%) than for Landsat-8 (36%), suggesting that the former is likely to be more effective for remote early detection of attacks by *Ips* spp.

Remote sensing has the potential to detect triggering events such as windthrow and snow damage and for tracking the development of bark beetle attacks following these events. Recent work shows potential to utilise satellite-based remote sensing of 'green' early stage attacks on healthy trees, enabling early intervention to minimise the scale of local outbreaks.

Human-mediated dispersal

Long-distance movement of bark beetles with traded goods is a well-documented pathway that can result in establishment of these pests in new locations (Hulme, 2009; Douma *et al.*, 2016). As indicated in the section on 'Pioneer bark beetle populations: the numbers needed' on page 7, there is ample evidence that some of the most damaging bark beetle species, including the five species of *Ips*, are frequently intercepted in different countries.

Pest categorisation of *I. typographus* carried out by the European Food Standards Agency (EFSA) (Jeger *et al.*, 2017) identified different categories of coniferous wood as pathways for human-mediated movement of the pest. Those pathways were:

- Wood of *Abies*, *Larix*, *Pinus*, *Picea* and *Pseudotsuga* from countries where the pest occurs;

- Wood chips of conifers from countries where the pest occurs;
- Bark of conifers from countries where the pest occurs;
- Wood packaging material and dunnage from countries where the pest occurs.

In all cases, the presence of bark was essential for survival of the pest through transport and for eventual emergence as adult beetles. The EFSA panel did not consider plants for planting to be viable pathways for dispersal of the beetle on the basis that small plants are usually not attacked by the pest or, if they were attacked, would be killed and, therefore, not moved by trade. However, if large specimen trees are moved in trade then they could be regarded as potential pathways, but would represent an insignificant proportion of the volume of material being moved. For example, Haack (2001) analysed interceptions of *I. typographus* in the USA during 1985–2000 when the pest was only found on wood packaging material associated with heavy goods contained in crating (230 cases), dunnage (166) and pallets (34).

In response to assessments of pathways, international measures to reduce the incidences of bark beetle and other wood-dwelling pests moving in trade have been strengthened in recent years. For example, IPPC ISPM 15 – *Regulation of wood-packaging material in international trade* (IPPC, 2019), deals with procedures to reduce the presence of a range of bark- and wood-boring pests in packaging wood. This was introduced to account for the fact that most traded goods have some form of wood packaging associated with them, ranging from wooden pallets and crates to dunnage. In theory, all wood packaging moved internationally should be compliant to ISPM 15 standards but, as indicated by Haack *et al.* (2014), records of interceptions pre- and post-introduction of ISPM 15 in 2002 suggest only an ~50% reduction. However, these data have high uncertainty and are also strongly influenced by some countries having lower compliance rates than others.

Despite improvements in the standards relating to the health of wood and wood products being moved internationally, there are many records of new establishment of pests across a range of taxa (Aukema *et al.*, 2010). These reflect massive increases in global trade and the development of new trading relationships that introduce additional pathway sources to the global picture of pest movements.

In general, it can be said that both the volume and speed of trade increase the likelihood of pests surviving in transit and eventually arriving in relatively close proximity to potential host trees.

Management options: removal of weakened or infested trees

Outbreaks of *Ips* spp. are difficult to predict since they are almost invariably triggered by major events such as storms. Management is, therefore, usually a retrospective damage limitation exercise rather than a pre-emptive strategy to prevent outbreaks.

Most of the management processes employed in the current ranges of all five *Ips* species focus on the removal of infested material or material suitable for breeding that has not yet been attacked (Bakke, 1989; Wermelinger, 2004). Reflecting the ‘6 week rule’ for the removal of felled conifers from logging sites, as recommended by the Forestry Commission (Grayson, 1989), rapid removal of damaged trees is necessary to reduce beetle population growth (Bakke, 1989; Jonsson *et al.*, 2012; Stadelmann *et al.*, 2013; Okland *et al.*, 2016). The removal of damaged and fallen trees provides two benefits in pest reduction: the immediate removal of trees that have just become infested, but before emergence of a new generation, and the removal of poorly defended trees that could act as foci for further infestation. The timing of removal is more critical when beetles are in climate zones where two and possibly three generations can be achieved. For example, up to three generations were observed in the *I. sexdentatus* outbreak in the Landes area of France after the 1999 wind storm (Rossi *et al.*, 2009). The slow removal of salvage logging in this forest resulted in aggregated attacks of *I. sexdentatus* near to log storage areas, which were significant up to 1 km from the storage area.

Regarding *I. typographus*, the use of trap trees to attract beetles to manageable centres of infestation, thus enabling selective removal of infested material to prevent further population increase, has been the preferred method for managing beetle outbreaks in central Europe (Holusa *et al.*, 2017). Trees with thicker bark were the most effective trap trees but their performance declined if they were left in direct sunlight, suggesting that they should be introduced just before the flight period of targeted bark beetles if exposure to sunlight is a potentially limiting factor.

A comparison has also been made between the efficacy of standing versus felled trees in trapping beetles before removing the infested material. Hedgren and Schroeder (2004) studied *I. typographus* attacks at both low and high beetle population densities and showed that reproduction was more successful in standing trees compared with felled material. Another interesting observation was that natural

enemies were more abundant in standing compared with cut trees, even although species richness was the same in both categories.

From Hedgren and Schroeder (2004):

'A total of 72 872 beetles, 4174 parasitoids, 13 273 flies and 1591 bugs (Heteroptera) emerged from the stem sections. The beetles were numerically dominated by bark beetles (93%), whereas other beetles, mostly Staphylinidae, constituted 7%. Three bark beetle species were dominating: *P. chalcographus* (36% of all emerged beetles), *I. typographus* (34%) and *Crypturgus* spp. (23%). Among parasitoids, the most abundant family was Pteromalidae (98%), in contrast to Braconidae (2%). Most of the flies belonged to Sciaridae (89%), whereas *Medetera* flies constituted 11%.'

These are interesting results indicating that deadwood arising from bark beetle-induced mortality is a rich source of biodiversity. The presence of *Medetera* flies also signifies that predation under bark was likely to be high because larvae of dolichopodid flies feed on the larvae, pupae and immature adults of bark beetles (Kenis, Wermelinger and Gregoire, 2004).

According to Eriksson, Neuvonen and Roininen (2008), one of the reasons why forests in Finland have not suffered from the high levels of *I. typographus* attack, as experienced in neighbouring Scandinavian countries, is the government's policy of insisting on the removal of groups of ≥ 20 damaged conifers. This is time-constrained, requiring removal of the trees before completion of a generation of bark beetles, thus preventing further flights and attacks. Further investigation into intervention limits led to the conclusion that, in agreement with Hedgren and Schroeder (2004), small groups of ≤ 20 damaged spruce trees do not increase tree mortality from *I. typographus* attacks. However, a larger number of damaged trees (i.e. >20 in a small area) did increase the risks to standing healthy trees (Schroeder and Lindelow 2002; Eriksson, Neuvonen and Roininen, 2007).

An additional factor is whether to prioritise salvage logging ahead of sanitation felling of damaged (but not yet attacked) trees when dealing with new infestations. Stadelmann *et al.* (2013) investigated this in a population of *I. typographus* reproducing at the rate of one generation per year. The authors studied beetle infestations that arose following Storm Lothar, which affected 71% of forest districts in Switzerland. The results revealed that there was relatively little benefit from salvage logging (i.e. removing the easily attacked trees damaged by the storm). Sanitation felling was

more effective because it removed beetles as well as the felled trees, but only if this was done quickly during the first year of attacks, otherwise beetles emerged from the attacked trees and colonised other living trees. Overall, the most significant factor was the proportion of spruce in the plantation, especially in sites where spruce had been planted.

These data support findings from other studies that indicate an increased risk of infestation with a greater proportion of spruce in a forest location (Netherer and Nopp-Mayr, 2005; Schroeder, 2010; Lausch, Fahse and Heurich, 2011; Stadelmann *et al.*, 2013). Spruce in lower elevations in the Pre-Alps are on sites that would have supported mixed woodlands, but have been planted as a single species of the same age. Stadelmann *et al.* (2013) regard these as more susceptible to storm damage than mixed forests, a view which is also supported by data from Mayer *et al.* (2015) and Jurc *et al.* (2006).

In preparing for potential infestations, examining forest structure with respect to species mix, total standing volumes, local climate variables and the likelihood of damaging wind storms, could help identify where the most damaging attacks could take place. This information could be used in risk-based surveys, rather than a grid-based system, where pheromone-baited traps and trap-trees are placed in conifer sites close to grid points.

Management options: natural enemies

The role of natural enemies in bark beetle dynamics has been reviewed by Kenis, Wermelinger and Gregoire (2004). Many predators and parasitoids attack the five species of *Ips* that are subject to PZ control. For example, *I. typographus* has a wide range of recorded natural enemies (Table 4). Many of these records are associations rather than of capability to reduce beetle populations. Assumptions regarding impacts on beetle populations were obtained from records of types of natural enemies through different gradations of epidemic to endemic pest levels.

Wermelinger (2002) studied *I. typographus* over a two-year period and noted that predators were dominant when beetle population density peaked in the first year, whereas parasitoids were more prevalent in the second year as beetle populations declined. The author estimated the impacts of the natural enemy groups, which suggested an increasing effect as populations of parasitoids increased during the second year.

Table 4 Natural enemies recorded for *Ips typographus*.

Type of natural enemy	Family	Number of species
Parasitoid (Hymenoptera)	Braconidae	7
	Pteromalidae	8
	Eupelmidae	1
	Eurytomidae	3
Predators (Coleoptera)	Cleridae	3
	Histeridae	3
	Nitidulidae	7
	Rhizophagidae	5
	Salpingidae	5
	Staphylinidae	9
	Tenebrionidae	1
	Trogossitidae	1
Predators (Diptera)	Asilidae	3
	Dolichopodidae	11
	Lonchaeidae	5
	Muscidae	2
	Palopteridae	1
	Stratiomyidae	1
Predators (Heteroptera)	Anthocoridae	1
Predators (Neuroptera)	Chrysopidae	1
Predators (Raphidioptera)	Raphidiidae	3
Predators (Acari)	Acarophenacidae	1
	Pyemotidae	1
	Tarsonemidae	1
Predators (Aves)	Fringillidae	1
	Picidae	1

Source: Derived from Kenis, Wermelinger and Gregoire (2004).

Not all of the observed mortality could be attributed to the activities of natural enemies (Wermelinger, 2002). However, ~80% of *I. typographus* were killed by natural enemies, principally from the families Pteromalidae (most numerous) and Dolichopodidae. The relative 'consumption rates' were more important than density alone and, on the basis of higher consumption, Dolichopodidae (notably the *Medetera* species) was the main cause of mortality.

Although regulatory impacts from natural enemies are important, these are difficult to factor into management plans, other than to ensure that sufficient prey are available for successful breeding by those natural enemies which are already present in the environment occupied by the pests. This implies a trade-off between leaving deadwood in the forest, with benefits both for biodiversity and for

increasing natural enemy presence, and the likely increase in populations of bark beetle with potential increases in tree mortality. Most of the information on the natural enemies of *Ips* spp. relate to how they fluctuate with density of the beetle pests, usually in the lag phase, so that peak natural enemy activity tends to be recorded close to or soon after peak bark beetle density. While this has relatively little impact on immediate damage from the pests, it can result in delaying the return time of the pest, which remains at endemic levels while natural enemy activity is high. However, the density-dependent nature of the relationship also results in a decline in natural enemy numbers when the pest population declines, leading to a further lag in activity when pest numbers increase again.

Management options: water storage

Log storage under water sprinkling or by immersion in water courses after wind storms, to protect them from bark beetle attack and to reduce bark beetle population growth, has been practised against various species of bark beetles. Lindelow and Schroeder (2008) described responses to the Gudrun wind storm in Sweden, which included the storage of millions of cubic metres of damaged timber, to protect it from beetle attacks and decay. Storage in lakes was limited. In general, this procedure is only practical when large volumes of felled timber are at risk, for example, following the 1987 storm in Thetford forest when huge volumes of pine were blown over (Grayson, 1989).

Management options: alteration of tree species mix

Apart from the availability of weakened trees as initiators of bark beetle infestations and potential outbreaks on nearby living trees, one of the key factors in *Ips* population dynamics is the proportion of host trees in surrounding forests, particularly the volume and proportion of spruce in a given forest stand (see the section on 'Management options: removal of weakened or infested trees' on page 13).

The relative values of mixtures versus monocultures for a wide range of ecosystem services (ES) have been a subject of debate (Jactel *et al.*, 2012). For *Ips* species, vulnerability to attack increases when there is a high proportion of a favoured host in a forest block. In addition to species composition, the structure of the overstorey influences vulnerability. Jactel *et al.* (2009), in an analysis of several studies, attributed this to impacts on the local microclimate, the provision of fuel and resources to biotic and abiotic hazards, increased biological control from natural enemies

and the effects on tree physiology and development. Karvemo *et al.* (2014) studied infestations of *I. typographus* in a 130 000 ha managed forest in southern Sweden. Among the variables assessed, the most significant was the volume per hectare of Norway spruce (*Picea abies*), with a strong positive correlation reported up to 200 m³ ha⁻¹, and a further positive contribution from increased tree height (10–15 m). Other predictive variables were the distance to the nearest harvested area in the previous four years and the volume of birch, which reduced attacks when it exceeded 25% of the standing volume.

These findings indicate that in forests which are relatively close to previous infestations, the risk from bark beetles tends to be higher when the proportion of suitable hosts is high (>75%; Karvemo *et al.*, 2014). In addition to the easily measured parameters of volume (numbers and size) and the proportion of host trees, the heat sum in an area drives the speed of an infestation. Following major storms, temperature becomes less important because there is an abundance of breeding material, which means that beetles do not have to move far to find poorly defended trees (Marini *et al.*, 2016). Accounting for these factors is now part of forest management in all areas where bark beetles are important agents of change. In Austrian forests, episodes of *I. typographus* infestation have been assessed to improve future management regimes. Pasztor *et al.* (2014) analysed infestations over a 20-year period, during which beetle damage ranged from 0.6 to 3.0 million m³. It was concluded that, since it was not possible to control climatic drivers (i.e. temperature, rainfall and storm events), management options should concentrate on decreasing the proportion of spruce, shortening rotation length and moving felled timber quickly. The authors acknowledged that these were 'slow drivers', which implied a substantial time lag before these measures became effective, thus requiring pre-emptive and early adoption if they were to be successful. Climate trends are part of the 'slow driver' concept; for example, outbreaks of *I. typographus* in Sweden were mainly linked to standing volumes of trees during 1850–1950, followed by growing climate influence (i.e. higher temperatures and increased storms) during 1961–2014 (Tudoran, Marquer and Maria Jonsson, 2016). Note that a relationship between *I. typographus* attacks and larger trees (Netherer and Nopp-Mayr, 2005) has not always been reported and attacks may be driven by a range of related factors. For example, Blomqvist *et al.* (2018) found that attacks were frequently associated with smaller, non-dominant trees and predominantly driven by moderately steep slopes with an eastern aspect and soils with high fertility and C/N ratios.

Effects on Ecosystem Services

In recent years there has been growing interest in the concept of ES to provide a framework with which to assess a range of factors on ecosystem functioning, whether in the natural or human-influenced environment. The UK National Ecosystem Assessment (UNEP-WCMC, 2011) and its follow-ups (2017) have provided substantial material and a basis for debate on the values of ES and how they can be managed. The four primary services recognised in ES described by the UK NEA are reproduced in Box 1.

Forests and woodlands encompass all four services but have particular linkage and influences for provisioning, regulating and cultural services, with the assumption that supporting services are essential for all other ES. Although there is an interaction between the habitat types, the woodland habitat has a pivotal position for many of the other habitat types because of its longevity and capacity to modify regulating services.

While the obvious outcomes of high attacks from *Ips* spp. have been recorded frequently, less attention has been given to the inter-related effects on ES in the environments where beetles are important components of the fauna.

Timber losses

As indicated in the section on 'Impacts of *Ips* species in their natural and invaded ranges' on page 11, episodes of damage and high tree mortality have been frequently associated with attacks by *Ips* spp., in particular by *I. typographus*. The majority of studies of impact have provided data for volumes of standing timber killed by beetles (Bakke, 1989; Gregoire and Evans, 2004; Wermelinger, 2004). There are also estimates of areas destroyed, but there has been little quantification of the monetary values lost to bark beetle attacks in Europe.

Extrapolating to potential impacts in the UK and making an assumption that *I. typographus* in particular could establish here, the volumes of timber at risk are linked to the key factors of tree species mix, tree age, vulnerability to windthrow and temperature. These are discussed in detail in the section on 'Measures to manage *Ips* species if they establish successfully' on page 28.

Effects on nutrient cycling, water supply and quality

Influences on water supply and quality arise when trees die because of a loss of canopy and alteration in water and nutrient uptake. This, in turn, leads to changes in hydrology and biogeochemical cycling. While there are

Box 1 The UK's ecosystem services.

Supporting services provide the basic infrastructure of life. These include primary production (the capture of energy from the sun to produce complex organic compounds), soil formation, and the cycling of water and nutrients in terrestrial and aquatic ecosystems. All other ecosystem services (ES)—regulating, provisioning and cultural—ultimately depend on them. Their impacts on human well-being are indirect and mostly long-term in nature; the formation of soils, for example, takes place over decades or centuries.

Supporting services are strongly interrelated to each other and generally underpinned by a vast array of physical, chemical and biological interactions. Our current understanding of exactly how such ecological interactions influence ecosystem processes and the delivery of supporting services is limited.

Regulating services provided by ecosystems are extremely diverse and include the impacts of pollination and pest and disease regulation on the provision of ecosystem goods such as food, fuel and fibre. Other regulating services, including climate and hazard regulation, may act as final ES, or contribute significantly to final ES, such as the amount and quality of available fresh water. As with supporting services, regulating services are strongly linked to each other and to other kinds of services. Water quality regulation, for example, is primarily determined by catchment processes and is thereby linked to other regulating services, such as the control of soil and air quality and climate regulation, as well as to supporting services such as nutrient cycling.

Provisioning services are manifested in the goods people obtain from ecosystems such as food and fibre, fuel in the form of peat, wood or non-woody biomass, and water from rivers, lakes and aquifers. Goods may be provided by heavily managed ecosystems, such as agricultural and aquacultural systems and plantation forests, or by natural or semi-natural ones, for example in the form of capture fisheries and the harvest of other wild foods. Supplies of ecosystem goods are invariably dependent on many supporting and regulating services. Historically, provisioning services have been a major focus of human activity, therefore are closely linked to cultural services.

Cultural services are derived from environmental settings (places where humans interact with each other and with nature) that give rise to cultural goods and benefits. In addition to their natural features, such settings are imbued with the outcomes of interactions between societies, cultures, technologies and ecosystems over millennia. They comprise an enormous range of so-called 'green' and 'blue' spaces such as gardens, parks, rivers and lakes, the seashore and the wider countryside, and include agricultural landscapes and wilderness areas. Such places provide opportunities for outdoor learning and many kinds of recreation; exposure to them can have benefits such as aesthetic satisfaction, improvements in health and fitness, and an enhanced sense of spiritual well-being. People's engagement with environmental settings is dynamic: meanings, values and behaviours change over time in response to economic, technological, social, political and cultural drivers, and change can be rapid and far-reaching in its implications.

Source: The UK NEA.

outcomes that are specific to local tree species, soil type, geology and climate, some generalisations are relevant to the effects on aquatic ES in the UK. Mikkelsen *et al.* (2013) provide a useful review of the impacts of mountain pine beetle (*Dendroctonus ponderosae*) in North America on nutrient cycling, water quality and interdependent hydrological effects. The authors compare their results with those from other studies reporting the effects of bark beetles and describe the main changes to processes following major beetle outbreaks.

The authors describe three phases from immediate post-infestation when the canopy is still green, through the red

phase after tree death to the grey phase with standing decaying trees. Soil ammonia (NH_4) and nitrates (NO_3), Al^{3+} and cations all peak in the red phase over time then tail off once full decay of the trees (in the grey phase) takes place. The trends in soil water dissolved organic carbon (DOC) are opposite for the first 1–3 years then increase to a peak above the baseline. This trend is in contrast to the abrupt changes in parameters when clear fells are carried out in planned timber harvesting. Soil buffering and surviving vegetation may partially compensate by decreasing nutrient loss and hydrological impacts.

Therefore, damage to nutrient cycling and water parameters from bark beetles can be considered as similar to (but slower than) planned felling operations and, if early removal of beetle-killed trees is instigated, may closely mimic a normal felling sequence. Consequently, the effects of bark beetle infestations depend on management responses to attacks. The study by Mikkelsen *et al.* (2013) represents a situation in which there is little removal of material and forests are allowed to regenerate naturally. This is unlikely to be the case in the UK, where retrieval of any marketable material would take place as soon as possible, as occurred following the 1987 great storm (Grayson, 1989). In addition, most commercial or amenity forest plantations would be subject to clearance and restocking if there was a catastrophic event such as a bark beetle attack.

Effects on carbon sequestration

Trees are important contributors to carbon sequestration in the UK and, reflecting the increased rates of planting and continuing growth of standing trees, display increased carbon equivalents since 1990 (Table 5). Within woodlands, soil contributes ~75% of the stored carbon and therefore is vulnerable to carbon loss during felling operations or after bark beetle attacks.

Attacks by bark beetles can alter the carbon balance in both unmanaged and managed woodlands. In the latter, the contributions from attacks will have different impacts, depending on when in the rotation of the tree the attacks take place. Thus, for Sitka spruce (*Picea sitchensis*), the main commercial conifer crop in the UK, beetle attacks are likely to be most significant from pole stage onwards within a rotation. Morison *et al.* (2012) comprehensively reviewed the roles of trees in carbon sequestration and illustrated how different management regimes for *Picea sitchensis* affected the carbon stock over several 50-year rotations. The stand is assumed to be planted on bare ground with an initial spacing of 2 m, felled and replanted on a 50-year rotation. Attacks by *I. typographus* would be expected to occur when trees have reached the age of first thinning or any time from then to the end of rotation. Thus, the window

Table 5 Forest carbon stock.

Source of carbon (million tonnes CO ₂ equivalent)	1990	2000	2005	2010	2015
Carbon in above-ground biomass	360	471	527	583	639
Carbon in below-ground biomass	129	170	190	210	230
Carbon in dead wood	9	10	10	10	10
Carbon in litter	165	175	179	182	187
Soil carbon*	2366	2533	2594	2629	2715
Total forest carbon	3029	3359	3500	3614	3781

*Carbon in soil depth 0 to 100 cm. Source: Forestry Commission.

of carbon loss arising from no further growth in the tree would extend from ~18 to 35 years post-planting for yield classes 24 (fastest growing) to 6 (slowest growing, and which would probably have a longer rotation). The earlier in a tree growth cycle that a beetle attack takes place, the lower the impact on actual carbon loss at that stage, but further losses could occur from delays to future carbon sequestration, with economic losses from a lower yield and the expense of clearance and replanting.

Quine *et al.* (2011) summarised the monetary values estimated for ES in UK woodlands (Table 6), differentiating softwood from hardwood production, but combining both to estimate overall net carbon sequestration. Intervention from bark beetle attacks would, therefore, impact these totals, but on a case-by-case basis, including the yield class of the affected tree(s) and at which stage in a rotation the attack took place, also accounting for tree species which were vulnerable to attack, windblow or other events that weaken trees. The scale of the attack would also be driven by the proximity of the initially attacked woodlands to other vulnerable woodlands.

An interesting example of the effects of a bark beetle outbreak on carbon budgets was provided by Kurz *et al.* (2008), who assessed the effects of *Dendroctonus ponderosae* on changes in the carbon stock of pine forests in North

Table 6 Changes in values of ecosystem services from UK woodlands.

Ecosystem service	Annual value (in millions of £)				Annual value (£ per ha)		
	1945	1976	1990	2009	1990	2001	2009
Softwood production		112	145	105	95	55	68
Hardwood production			110	8–26	120		7–25
Net carbon sequestration by woodlands	124	563	642	680	246	270	239
Net carbon sequestration in harvested wood products	0	13	77	119	29	8	42

Note: Figures at 2010 prices. Source: from Quine *et al.* (2011).

America. The authors assessed three scenarios: control (no beetle infestation but with some harvest and fires), beetle infestation (additional to the control scenario) and an increased harvest during 2006–2016 (as well as a beetle attack). Beetle infestation resulted in large carbon emissions to the atmosphere with a gradual recovery over time, but never reaching the level of the control scenario, which gradually became a carbon sink.

Effects on biodiversity

When trees are killed by bark beetles, there is a trade-off in terms of overall impact on biodiversity. Soon after tree mortality, the population of animals and, in the understorey, plants and other biota, will lose an important habitat presented by the living tree. For spruce and pine, the tree genera typically affected by bark beetles, the biodiversity on the living trees will be linked primarily to those biota directly utilising components of the living tree and others at different trophic levels that rely on the primary utilisers. There is also a perception that plantation woodlands are not as biodiverse as ‘natural’ woodlands; Brockerhoff *et al.* (2008) reviewed the case of woodlands in the UK which, after massive deforestation prior to the 20th century, has increased forest cover to its current level of ~13% (Forestry Commission, 2018b). Despite being

dominated by exotic tree species (conifers, in particular), the authors concluded that there is increasing biodiversity value from the mixtures of tree species and range of ages now present in the UK.

Biodiversity context in the UK is therefore influenced by whether the tree species that could support *I. duplicatus* and *I. amitinus* and already support *I. cembrae*, *I. sexdentatus* and *I. typographus* provide valuable biodiversity, considering that they are primarily present in plantations rather than natural woodlands. In general, it appears that plantation woodlands offer positive habitats for a wide range of species and that their value increases as they age. Quine *et al.* (2007) showed that value for bird diversity increased as woodlands aged, particularly from mid-growth into mature and old-growth stages. While there is undoubtedly conservation value in old-growth woodlands (Humphrey, 2005), the proportion of UK woodlands in this category which would be vulnerable to *Ips* attack is small. Of wider relevance to the potential impacts of beetle attack on standing trees are the outcomes of the Forestry Commission’s Biodiversity Assessment Project (Humphrey, Ferris and Quine, 2003), which indicated that there was considerable variation between the three conifer species studied (Sitka spruce, Norway spruce and Scots pine), and that this was tempered by forest structure and tree age (Table 7).

Table 7 Selected factors affecting the biodiversity of planted stands.

Taxon groups	Tree species type	Forest structure/age
Canopy invertebrates 225 species	Sitka spruce much less diverse than other species; Norway spruce exceptionally rich.	Diversity in Scots pine plots lower in mature and over-mature stands compared with mid-rotation stands. Diversity negatively correlated with vertical cover index.
Sub-canopy invertebrates 420 species	Norway spruce stands had high species-richness of Cicadomorpha.	Positive relationship between field layer vertical cover, syrphid and cicadid diversity.
Ground beetles (Carabidae) 53 species	Spruce plots more diverse than pine, especially Norway spruce.	Increase in proportion of forest specialist carabids in over-mature stands. Mid-rotation Sitka spruce plots poorest of all stand types; mid-rotation Scots pine plots richer than pre-thicket plots.
Songbirds 41 species	No recorded effects.	Pre-thicket plots had distinctive communities.
Ground vegetation 239 species	Indirect effects mediated by soil fertility.	Compared with the other stand types, mature and over-mature pine and spruce stands in the north had communities most closely matching the species composition of semi-natural woodland.
Fungi 677 species	No difference in species counts between semi-natural and plantation stands.	Positive correlation between mycorrhizal species-richness and increased lower canopy cover.
Lichens on deadwood 106 species	Northern pine and oak stands had richest lichen communities. Semi-natural stands had richer communities than planted stands.	Pre-thicket and over-mature plots were far richer than mature and mid-rotation plots, especially in Sitka spruce.
Bryophytes on deadwood 77 species	Spruce stands had significantly richer communities than pine stands.	Over-mature spruce stands, characterised by high upper canopy cover values, had richer bryophyte communities than the other stand stages.
Soil microbes	Foothills Scots pine stands had higher fungal-derived microbial diversity than the other stand types.	Mid-rotation and mature plots tended to have higher microbial diversity than the other stand stages.

Source: based on data from the Forestry Commission Biodiversity Assessment Project.

These results show that conifers in the UK provide valuable habitats for a range of taxa, and that some of these are canopy specialists which would be negatively affected if trees were lost to bark beetle attack. However, biodiversity value could increase if deadwood was left after beetle attacks, as is the case in spruce forests affected by *I. typographus*, for example in Europe, where Coleoptera increased in openings created by bark beetle tree mortality (Muller *et al.*, 2008). In this study, which examined gaps in the forest created after *I. typographus* attacks, the authors concluded that it was a keystone species which created biodiversity opportunities, and although there were positive outcomes from the creation of forest gaps and edges (particularly valuable for endangered species that feed on dead or decaying wood), it was acknowledged that care needs to be taken in how to manage beetle infestations. Similar results were reported by Thorn *et al.* (2016), who suggested leaving branches cut from salvaged trees, as well as deadwood of a larger diameter, so as to encourage species adapted to these disturbance-created microhabitats.

Effects on biodiversity are time-driven because any impacts depend on the stage of growth the host tree reached before its death and also on the potential 'return time' for restoration of habitat by replanting or natural regeneration. Provision of deadwood is a positive outcome for biodiversity, and this can be an offset benefit of tree mortality depending on how much is left during forest operations to clear beetle-killed trees.

Effects on recreation and aesthetic values

Extensive tree mortality is one of the more tangible outcomes from bark beetle attacks. During the different phases of beetle attacks, from green through red to grey, their impact becomes more evident. This probably affects the values that visitors to forests expect (Table 8).

The frequent and highly visible infestations of *I. typographus* in Europe mean that forest managers have to balance a range of requirements when considering the perceptions of visitors to forested areas. Also, other land uses within the forest environment may cause negative perceptions if the views of recreational visitors are not taken into account. To assess potential conflicts in the Bavarian Forest National Park in Germany, Arnberger *et al.* (2018) conducted an image-based, discrete choice experiment to gauge visitors' visual preferences and trade-offs. The study addressed the following questions:

Table 8 The wide range of cultural ecosystem values for trees and woodlands from a meta-synthesis and analysis of 31 woodland focused studies.

ES category	
Trees and woodland as important environmental spaces; e.g. destination woodland with facilities, local woods, community woods, parks, street trees, trees as part of green infrastructure, copses.	
Value categories	Value types
Health	Physical well-being
	Mental restoration
	Escape and freedom
	Recreation, enjoyment and fun
Nature/landscape connections	Sensory stimulation
	Nature connectedness, biodiversity
	Landscape improvements
	Screening/shelter
	Gathering non-timber forest products
Education/learning	Sense of place
	Personal development
Economy	Education/learning
	Livelihoods
Social connections	Contribution to local economy
	Strengthening/building existing relationships
	Building new relationships
Cultural and spiritual significance	Participation and capacity building
	Symbolic/cultural/historic
	Sense of ownership
	Meaning and identity
	Religious, spiritual, artistic inspiration

Source: O'Brien, Morris and Raum (2017).

- What are the visual preferences of national park visitors for technical and recreational infrastructures, bark beetle-impacted and non-impacted forest stands, and visitor numbers and composition?
- Do visitor preferences vary by viewing distances of technical infrastructures and forest stands in the landscape?
- What trade-offs do visitors make between technical, forest, infrastructural and social factors, and which factors influence visitors' preferences the most?
- Are there differences in visual landscape preferences between tourists and local residents?

It was noted that >90% of the visitors were aware of *I. typographus* activity in the area. Responses to realistic images indicated strong preferences.

Overall, visitors were most concerned by visual impacts, preferring not to see clear cuts, wind turbines (single or multiple), or impacts of bark beetles near to visitor trails. Encountering other visitors or dogs or recreational infrastructure was regarded as positive. Trade-offs between the visual attributes were mainly between the immediate forest surroundings and the presence of wind turbines, to the extent that turbine absence could partially offset the impact of bark beetles.

These findings confirm the negative impacts of any factor that reduces the visual amenity of recreational visits to the forest, which presumably would also negatively affect the other value categories listed in Table 8. This suggests that clearing dead trees in close proximity to trails in woodland parks should be a priority, although this was less urgent in more remote locations, especially if that resulted in greater biodiversity.

Native and invaded ranges for the five species of *Ips*

Ips typographus as a proxy for the other species

In both the native and invaded ranges of *I. typographus* (still expanding in Europe; Jeger *et al.*, 2017), the principal host species are in the genus *Picea* (Figure 5). *I. typographus* has the widest geographical distribution of the various *Ips* spp. Maps for the other species are shown in Figures 6–9.

Figure 5 Global distribution of *Ips typographus*.



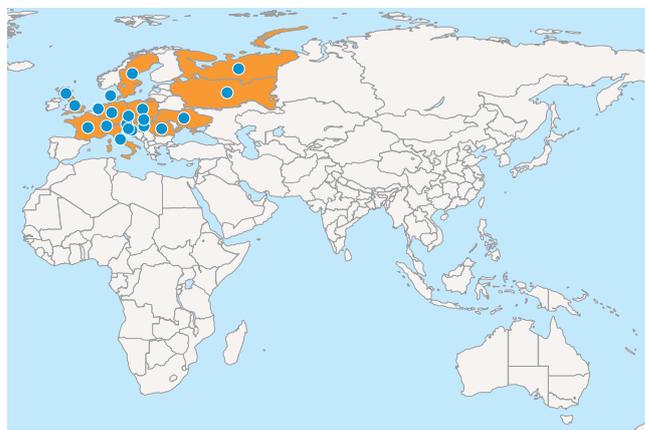
Note: The 2018 finding of the beetle in Kent is shown in purple as transient (under eradication). Source: EPPO Global Database, November 2020. © EPPO <https://gd.eppo.int>.

Figure 6 Global distribution of *Ips amitinus*.



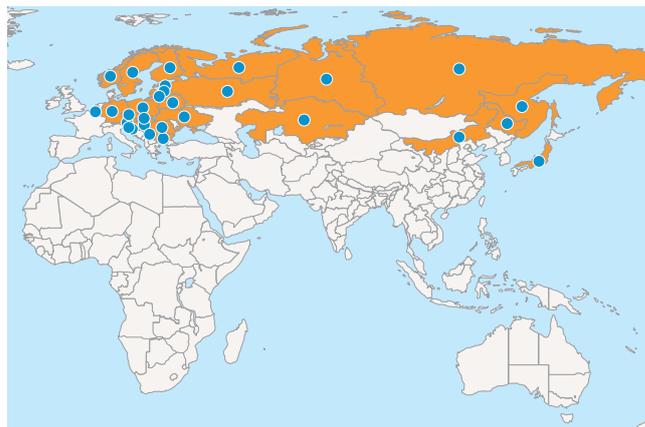
Source: EPPO Global Database, September 2018. © EPPO <https://gd.eppo.int>.

Figure 7 Global distribution of *Ips cembrae*.



Source: EPPO Global Database, September 2018. © EPPO <https://gd.eppo.int>.

Figure 8 Global distribution of *Ips duplicatus*.



Source: EPPO Global Database, September 2018. © EPPO <https://gd.eppo.int>.

Figure 9 Global distribution of *Ips sexdentatus*.

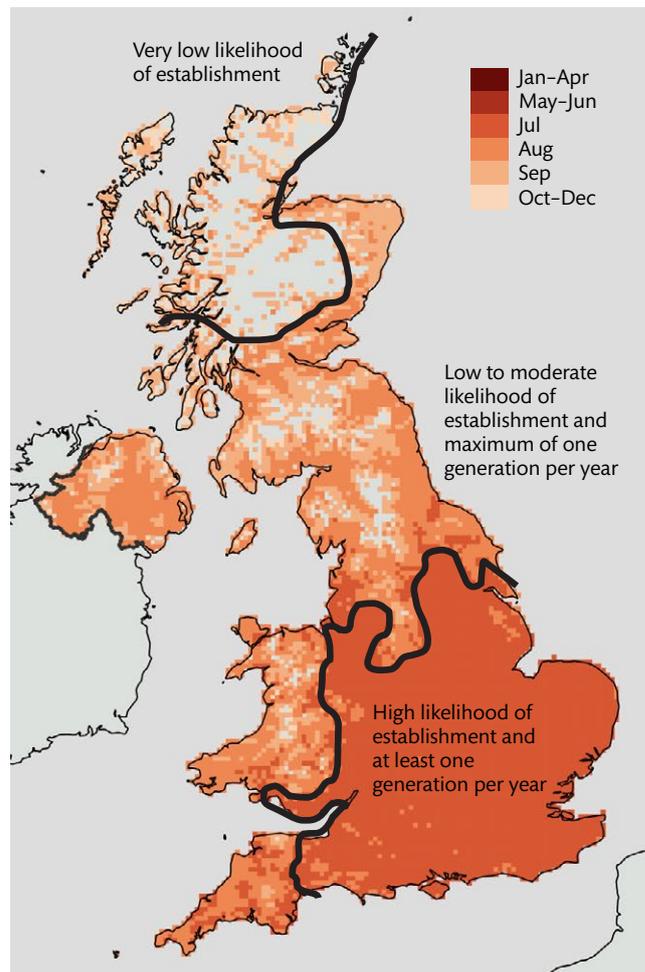


Source: EPPO Global Database, September 2018. © EPPO <https://gd.eppo.int>.

Climatic suitability of the UK for *Ips* colonisation

From Figures 5–9, wide geographic colonisation and development is evident, especially for *I. typographus* and *I. sexdentatus*. In all cases, tolerance to wide climatic variation is indicated by the distribution across a range of weather zones. In these situations, both more rapid development at high summer temperatures and tolerance to temperatures as low as -32°C during winter (see the section on 'The influence of temperature and daylight periods on *Ips* life cycles' on page 10), confirm the adaptability in development of the various *Ips* species. In common with many other species of bark beetle, the thermal requirement for full development from egg to emergent adult is driven by dds above a certain threshold, $\sim 10^{\circ}\text{C}$ on average (Wermelinger *et al.*, 2011). As indicated in the section on page 10 mentioned above, the dds required for *I. typographus* to complete its life cycle can also be used as estimates for the other *Ips* species, where such data are usually lacking (Bentz and Jonsson, 2015). Extrapolating from the average data presented in the same section on page 10 mentioned above, the likelihood of survival by *I. typographus* and the other species of *Ips* (with existing proof of establishment for *I. cembrae*, *I. sexdentatus* and *I. typographus*) can be estimated from the thermal requirements presented by the UK climate. A map of expected emergence dates for adult *I. typographus* using the average dd data from Faccoli (2009) to parameterise the pest day degree tool from the UK Meteorological Office (Everatt, pers. comm.) is shown in Figure 10. This is useful for assessing the potential development and number of generations of *I. typographus* in the UK and is also pertinent in light of recent establishments of several invasive species in the south-east of England (e.g. Inward,

Figure 10 Degree-days from a 10°C base in the UK with estimated zones for *I. typographus* establishment and number of generations.



Source: Produced using the UK Meteorological Office pest day degree tool.

2020). This has been carried out in Figure 10, with zones for estimated emergence dates for 2006 (an exceptionally hot year in the UK), and indications of the likelihood of establishment, development and number of generations for *I. typographus*.

The degree of uncertainty is low for the southern part of the UK and moderate for the more northern parts. The latter uncertainty is based on the relatively northern distribution of *I. typographus* in Europe, which suggests that factors other than temperature alone could enable the pest to establish in the northern parts of the UK.

Host range of *Ips* species in Europe

Ips typographus is known to attack spruce (*Picea* spp.), especially *Picea abies*, *Picea excelsa*, *Picea omorika* and *Picea orientalis*, all of which are native to Europe (Jeger *et al.*, 2017). In addition, a number of exotic spruce species are planted, both in commercial forestry and for

ornamental use. These include *Picea sitchensis*, *Picea glauca*, *Picea engelmannii*, *Picea jezoensis* and *Picea pungens*. *I. typographus* has also been reported attacking *Pinus sylvestris* and *Pseudotsuga menziesii* (Jeger *et al.*, 2017).

Various observations of *Ips* spp. attacks in arboreta and experimental plantings suggest that, when populations of the pest are high, attacks on a wider range of potential hosts are possible. Okland *et al.* (2011) found that *I. typographus* attacked and bred in *Picea rubens*, *Picea engelmannii*, *Picea sitchensis* x *Picea glauca*, *Picea mariana* and *Picea glauca*. Lakatos and Kovacs (unknown), examined beetle attacks on a wide range of tree species at Budafapuszta Arboretum in Hungary. The authors categorised attacks as light, moderate or heavy and suggested that large populations of *I. typographus*, arising from Norway spruce stands bordering the arboretum, had invaded and attacked trees. Those tree hosts in the light and medium attack categories had entrance holes but no successful maternal galleries, and all survived. However, heavy attacks resulted in successful colonisation and tree death in many cases.

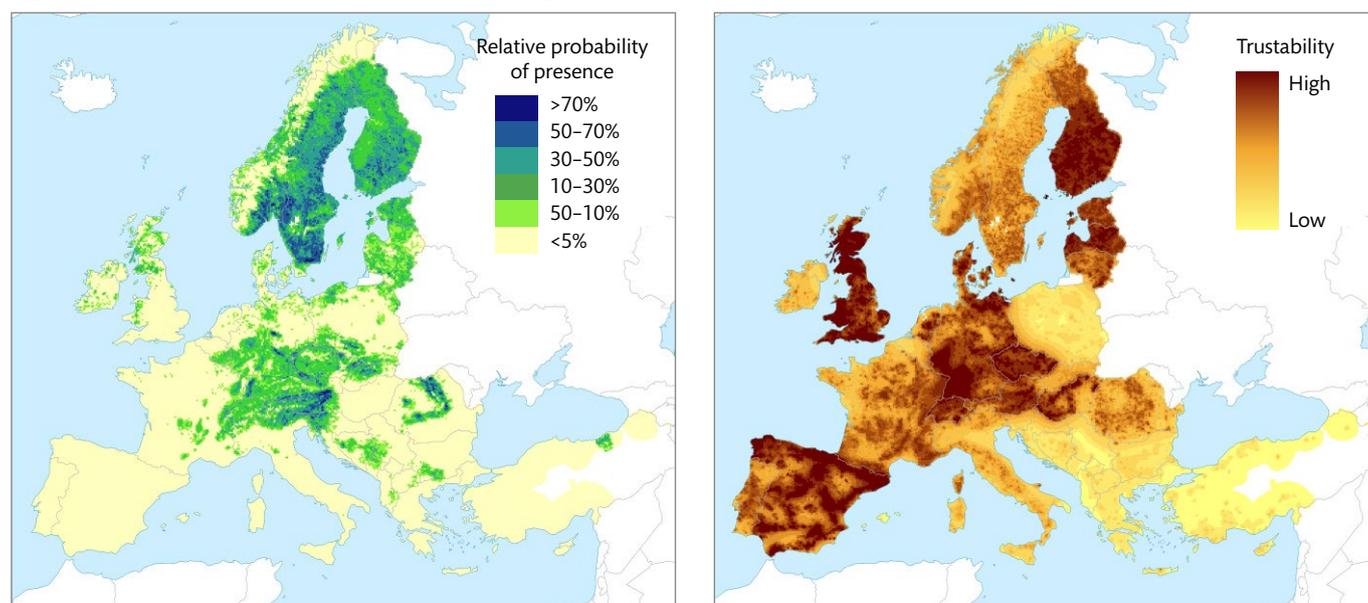
Conifer species in this category included *Abies alba*, *Abies cephalonica*, *Abies nordmanniana*, *Abies numidica*, *Larix eurolepis*, *Larix laricina*, *Larix leptolepis*, *Picea abies*, *Picea engelmannii*, *Picea glauca*, *Picea glauca* (Alberta), *Picea glauca* (Ontario),

Picea glauca (Saskatchewan), *Picea glehnii*, *Picea mariana*, *Picea omorika*, *Picea polita*, *Picea rubens*, *Picea sitchensis*, *Pinus aristata*, *Pinus banksiana*, *Pinus contorta*, *Pinus contorta latifolia*, *Pinus flexilis*, *Pinus monticola*, *Pinus nigra* var. *pallasiana*, *Pinus pinaster*, *Pinus ponderosa*, *Pinus ponderosa scopulorum*, *Pinus resinosa*, *Pinus silvestris*, *Pinus strobus*, *Pinus wallichiana*, *Pseudotsuga menziesii viridis*, *Taxodium distichum* and *Thujaopsis dolobrata*.

These data suggest that overspill from large populations of *I. typographus* on its principal hosts (*Picea abies* and *Picea orientalis*) can result in successful breeding on a wide range of conifer hosts, which would act as potential reservoirs for population maintenance in the absence of the preferred spruce species.

With regard to the distribution of hosts, while there would be high expectations of attack on *Picea abies*, *Picea excelsa*, *Picea omorika* and *Picea orientalis*, the planting of exotic spruces and a range of pines and other conifer species would act as reservoirs for population establishment and growth. For example, Jeger *et al.* (2017), in a pest categorisation for *I. typographus*, provided maps for the distribution of potential hosts at a European level (Figure 11). Comparison with Figure 5 indicates that *I. typographus* has been recorded over much of the range of potential hosts in Europe and has a considerably wider distribution including Asia.

Figure 11 European Union distribution maps for the genus *Picea*.



Notes:

1. The maps are based on data from the species *Picea abies*, *Picea sitchensis*, *Picea glauca*, *Picea engelmannii*, *Picea pungens*, *Picea omorika* and *Picea orientalis*.
2. The relative probability of presence (RPP) maps for each genera are mapped at 100 km² resolution. The underlying data are from European-wide forest monitoring datasets and from national forestry inventories based on standard observation plots measuring in the order of hundreds of m². RPP represents the probability of finding at least one individual of the taxon in a standard plot placed randomly within the grid cell. Courtesy of the Joint Research Council.
3. The trustability of the RPP expresses the strength of the underlying information in each grid cell and varies according to the spatial variability in forestry inventories. The colour scale of the trustability map is obtained by plotting the cumulative probabilities (0–1) of the underlying index. From Jeger *et al.* (2017).

As indicated in the section on 'Host availability in the UK' below, the principal commercial conifer in the UK is *Picea sitchensis*, which is not widely planted in the known range of *I. typographus* in Europe. An important issue is whether *Picea sitchensis* is likely to be attacked to the same extent as its usual hosts, notably *Picea abies*. Flo *et al.* (2018) confirmed that *I. typographus* attacked, formed galleries and emitted clusters of pheromones on *Picea sitchensis*. Egg laying and successful larval development were also demonstrated, although the total numbers of offspring were significantly lower than in the native host, *Picea abies*; this was attributed to fewer eggs being deposited because fewer adults selected *Picea sitchensis*, rather than being a consequence of poorer larval performance arising from those eggs that were actually deposited. The authors concluded that *I. typographus* would pose a threat to *Picea sitchensis*, especially where there are extensive plantings as an exotic species.

Host availability in the UK

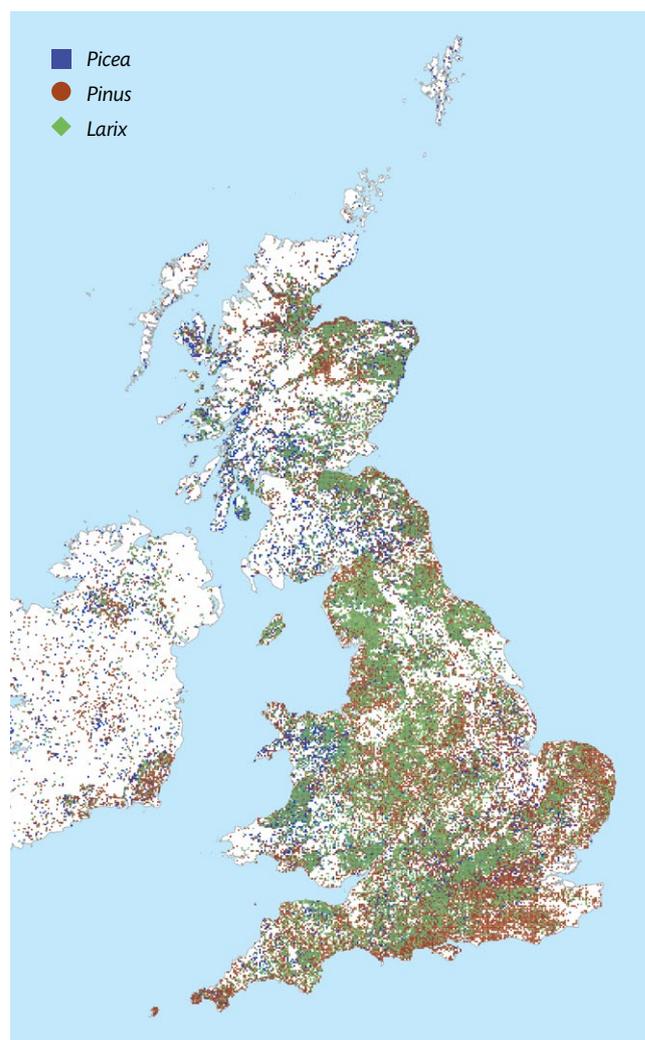
In relation to risks to the UK, there is a wide range of suitable hosts, principally in the genera *Picea* and *Pinus*, including both commercial and non-commercial plantings of trees in forested and other locations. This mix of conifers encompasses the known host ranges of all five species of *Ips* subject to PZ control. The Botanical Society of Britain and Ireland provide an interactive means of assessing presence or absence at a range of scales, summarised for the main hosts (*Picea*, *Pinus* and *Larix*) of *I. typographus*, *I. amitinus*, *I. cembrae*, *I. duplicatus* and *I. sexdentatus* for 2 km tetrads in Figure 12.

To add to the very high level of detail for *I. typographus* arising from the extensive literature on this pest, the host ranges recorded for the other *Ips* spp. in this report are shown in Tables 2 and 9.

The widespread distribution of potential hosts for *I. typographus* (Figure 12) indicates that, if the pest is able to establish itself in the UK, it will be able to locate suitable breeding material virtually anywhere. This is supported by the recent finding of a breeding population of *I. typographus* in Kent on *Picea abies*. The close proximity of the site to routes from the channel ports and the Channel Tunnel, the potential for direct flight from France or Belgium and the very poor quality of the trees on an essentially waterlogged and windblown site, suggests that several of the 'trigger' requirements for establishment of the pest were fulfilled.

In terms of areas of forests and woodlands at risk from potential establishment of *I. typographus*, the 2018 Forestry

Figure 12 Distribution of trees in the genera *Picea*, *Pinus* and *Larix* in Great Britain and Ireland on a 2 km tetrad basis.



Source: The Botanical Society of Britain and Ireland.

Commission Woodland Area, Planting and Publicly Funded Restocking report (Forestry Commission, 2018a), provides data on the total area of conifers in public and private ownership. From these data, the areas of major forests and woodlands at risk for each country are summarised in Table 10.

From Forestry Facts and Figures 2018 (Forestry Commission, 2018b), a more detailed breakdown by area (Table 11) and volume (Table 12) for the main conifer species confirms that Sitka spruce and Norway spruce make up the bulk of the conifer holding potentially at risk from *I. typographus*.

These data refer to total areas and standing volumes of trees. Not all trees are susceptible to attacks by *Ips* spp. *Ips typographus*, in particular, mainly attacks pole stage or older trees. Thus, the area at immediate risk is dependent on tree age as well as total area. In the UK, the age structure of conifer woodlands is shown in Table 13.

Table 9 Host ranges for *Ips amitinus*, *Ips cembrae*, *Ips duplicatus* and *Ips sexdentatus*.

Species of <i>Ips</i>	Host range	Reference
<i>Ips amitinus</i>	<i>Picea abies</i> , <i>Picea pungens</i> , <i>Pinus sylvestris</i> ; <i>Pinus cembra</i> , <i>Pinus mugo</i> ; <i>Pinus heldreichii</i> and <i>Pinus peuce</i> and occasionally on other <i>Picea</i> spp.; <i>Pinus</i> spp., <i>Abies alba</i> ; <i>Abies</i> spp.; <i>Larix decidua</i>	Jeger et al. (2017)
<i>Ips cembrae</i>	<i>Larix decidua</i> , <i>Larix kaempferi</i> , <i>Pinus cembra</i> , <i>Pinus</i> spp. and <i>Picea</i> spp.	Cabi (2020) EPPO (2020)
<i>Ips duplicatus</i>	<i>Picea abies</i> , <i>Picea obovata</i> , <i>Picea jezoensis</i> , <i>Pinus sylvestris</i> , <i>Pinus cembra</i> , <i>Pinus sibirica</i> , <i>Larix decidua</i> , <i>Larix sibirica</i> , <i>Larix dahurica</i> and, rarely, <i>Abies</i> and <i>Juniperus</i>	Holusa and Grodzki (2008)
<i>Ips sexdentatus</i>	<i>Pinus brutia</i> , <i>Pinus halepensis</i> , <i>Pinus heldreichii</i> , <i>Pinus koraiensis</i> , <i>Pinus leucodermis</i> , <i>Pinus nigra</i> , <i>Pinus nigra</i> subsp. <i>salzmannii</i> , <i>Pinus pallasiana</i> , <i>Pinus peuce</i> , <i>Pinus pinaster</i> , <i>Pinus pithyusa</i> , <i>Pinus radiata</i> , <i>Pinus sibirica</i> , <i>Pinus strobus</i> , <i>Pinus sylvestris</i> , <i>Pinus sylvestris</i> var. <i>mongolica</i> , <i>Pinus tabulaeformis</i> , <i>Picea orientalis</i> , <i>Picea abies</i> and <i>Picea schrenkianai</i> . It has also been recorded on <i>Larix decidua</i> and <i>Abies</i> spp.	Jeger et al. (2017) Chararas (1962)

Potential sequences and consequences of establishment and breeding of *Ips* spp.

The data on the biology, dispersal and availability of hosts enable an assessment of the potential sequences and consequences of attacks by various *Ips* species, with particular emphasis on *I. typographus* as the most damaging of the five species in their European ranges. Although the emphasis in such an exercise is on the likelihood of establishment and quantification of subsequent tree mortality, the impacts must also be placed in the context of ES effects.

Table 10 Area of woodland, 2018.

Ownership	England	Wales	Scotland	Northern Ireland	UK
Forestry Commission Natural Resources Wales Northern Ireland Forest Service	151	98	429	56	733
Private sector	189	54	635	11	888
Total	340	151	1064	66	1622

Note: Figures in thousands of hectares.

Likelihood of establishment

Historically, and from recent experience, there have been frequent arrivals and flights by adult *Ips* spp. (see the section on ‘Pioneer bark beetle populations: the numbers needed’ on page 7). Most evidence of such incursions comes from interceptions of *I. typographus*, which has worldwide ‘circulation’ with trade (Haack 2006). Both *I. cembrae* and *I. sexdentatus* have been intercepted in world trade and have also been able to establish in Great Britain with the recent addition of *I. typographus*. This provides evidence that sufficient pioneer beetles were present to initiate breeding and eventual successful establishment and limited spread. Of three *Ips* species established in Great Britain as exotics, only *I. typographus* is regarded as posing a significant threat from mass attacks on living trees.

The prospects of catastrophic increases in populations make *I. typographus* a potentially serious pest and this has justified the setting up of PZ status, with accompanying restrictions on import of wood with bark present. In the context of limited evidence of successful establishment outside its known range, consideration should be given as to whether the measures applied to wood imports are effective, both financially and ecologically, or whether a different strategy should be employed to manage the threat from this and related pests. The fact that *I. typographus* has established a limited breeding population in Kent indicates that the criteria for initial successful breeding have been fulfilled. In this report, the main factors would appear to be a pathway for carriage of beetles, the close proximity of suitable host trees to transient or final end points of pathways, and suitable climatic conditions. Specifically with regard to Kent, these factors are: close proximity to routes from the channel ports and the Channel Tunnel; being within the flight distance of adult beetles; the presence of *Picea abies* on a poor site; and a climate zone that indicates at least one, possibly two, generations per year (Figure 10).

As discussed in the section on page 7 mentioned above, up to several hundred beetles have to emerge at the same time and in the same place to exceed the threshold for successful colonisation of a potential host tree. In addition, it

Table 11 Principal conifer woodland areas in Great Britain by ownership and country.

Principal species	England	Wales	Scotland	Great Britain
Forestry Commission				
Sitka spruce	49	50	225	323
Scots pine	17	2	45	64
Corsican pine	27	2	2	30
Norway spruce	7	5	11	23
Larches	10	12	26	48
Douglas fir	10	5	5	20
Lodgepole pine	4	3	49	56
Other conifers	5	3	3	11
All conifers	128	82	367	576
Private sector				
Sitka spruce	32	27	282	341
Scots pine	45	1	109	154
Corsican pine	14	0	1	15
Norway spruce	21	3	15	38
Larches	30	8	39	78
Douglas fir	15	3	7	25
Lodgepole pine	3	1	39	44
Other conifers	19	2	8	29
All conifers	179	47	505	732
Total				
Sitka spruce	80	77	507	665
Scots pine	61	3	154	218
Corsican pine	40	2	3	46
Norway spruce	27	8	25	61
Larches	40	20	66	126
Douglas fir	25	9	12	46
Lodgepole pine	8	4	88	100
Other conifers	24	5	11	40
All conifers	307	129	872	1 308

Note: Figures in thousands of hectares.

is extremely unlikely, given the even higher numbers of adult beetles required, that attacks from a defined and relatively small cohort of beetles could overcome the defences of a living tree (see the section on 'Tree attack strategies' on page 4).

Successful attacks by pioneer beetles therefore require the presence of a cluster of adults and the availability of weakened or recently dead trees (e.g. initial attacks from *I. typographus* are heavily influenced by random events such as windthrow or other forms of damage or stress). Another key factor, which has been studied in relation to attacks by *I. typographus*, is proximity to weakened trees when adults emerge. This could involve adults flying considerable distances

Table 12 Principal conifer woodland standing volume in Great Britain by ownership and country.

Principal species	England	Wales	Scotland	Great Britain
Forestry Commission				
Sitka spruce	8.9	11.1	52.1	72.0
Scots pine	4.0	0.5	8.8	13.3
Corsican pine	5.5	0.6	0.4	6.4
Norway spruce	1.7	1.5	3.5	6.7
Larches	1.7	2.7	4.8	9.2
Douglas fir	2.7	1.3	1.4	5.4
Lodgepole pine	0.8	0.6	8.2	9.6
Other conifers	1.5	1.1	1.0	3.6
All conifers	26.8	19.4	80.2	126.4
Private sector				
Sitka spruce	11.4	9.5	88.0	108.9
Scots pine	14.7	0.3	24.5	39.4
Corsican pine	4.7	0.2	0.3	5.3
Norway spruce	7.1	1.3	5.9	14.4
Larches	10.7	3.3	12.3	26.3
Douglas fir	6.4	1.6	3.5	11.5
Lodgepole pine	1.0	0.3	7.4	8.7
Other conifers	7.6	1.1	3.0	11.7
All conifers	63.7	17.9	146.7	228.4
Total				
Sitka spruce	20.3	20.6	140.0	180.9
Scots pine	18.6	0.8	33.3	52.7
Corsican pine	10.2	0.8	0.7	11.7
Norway spruce	8.8	2.8	9.4	21.1
Larches	12.4	6.0	17.1	35.6
Douglas fir	9.1	2.9	4.9	16.9
Lodgepole pine	1.8	0.9	15.5	18.3
Other conifers	9.1	2.2	4.1	15.4
All conifers	90.5	37.4	226.9	354.7

Note: Figures in millions of cubic metres overbark.

Table 13 Age distribution of conifers in the UK and risk of attack by *Ips* spp.

Age (years)	Conifers (thousands of ha)	Risk of <i>Ips</i> attack
0–20	285	Low
21–40	514	Moderate
41–60	389	High
61–80	82	High
81–100	22	High
100+	16	High

Notes:

1. Stocked area only; exc. felled areas and (for private sector land) open space.
2. Areas at 31 March 2012.

Source: Forestry Commission, 2014a and 2014b (supporting data).

and detecting potentially scarce weakened trees in an otherwise healthy forest. Long-distance dispersal in directed flight or by carriage on wind indicates that beetles can travel at least 50 km. Although this suggests that it would be easy for beetles emerging from imported infested wood to find suitable host trees, as shown in Figure 12, dilution of an emergent population of beetles would probably prevent successful colonisation and breeding in the majority of such hosts. In reality, invasion is driven by the number of beetles released into an area to which they are not native (Lockwood, Cassey and Blackburn, 2005); this has been modelled for *I. typographus* and other bark beetles by Skarpaas and Okland (2009). It is highly relevant that timber sources containing bark beetles provide a point source for dispersal and that movement from this source towards woodland locations tails off rapidly over a distance of <1 km. Skarpaas and Okland (2009) recommended that increasing the distance between wood storage sites and local forests would help manage the risks from beetles emerging from imported timber. Low numbers of beetles are still expected to arrive in forests that are far away from storage sites, but their establishment is likely to be low due to Allee effects (Taylor and Hastings, 2005). Increasing the separation distance would also provide enclosures for stored timber, to help prevent initial adult flights. This study assumed that large volumes of imported wood are stored prior to further movement and processing. Another assumption, which is of particular relevance to the UK, is that there is no pre-existing attraction caused by the emission of clusters of pheromones from trees that have already been attacked by *I. typographus* (Helland, Anderbrant and Hoff, 1989).

Conclusions on the likelihood of establishment of *I. typographus*, *I. amitinus* and *I. duplicatus*

The steps in the invasion process that could result in establishment of *Ips* species each carry different levels of confidence, as summarised in Table 14.

Table 14 assumes that the numbers of adult *Ips* species arriving in the UK will remain at current levels, although precise numbers are unknown. Previous episodes of *I. typographus* arrivals relate to particular events that increased the levels of ‘invasion’, including large volumes of un-debarked wood from Germany immediately after the Second World War (Laidlaw, 1947) and increased imports from the Baltic States in the 1990s (Figure 4). The latter example provides a partial measure of the value of debarking under the PZ scheme, with initial poor standards of debarking resulting in greatly increased captures of *I. typographus*, followed by higher standards, which substantially reduced annual pheromone trap captures.

The potential source of the successful breeding population of *I. typographus* in Kent is still under investigation and may provide information on the likely pathway for arrival in Great Britain. Clearly, a sufficient number of pioneer beetles must have located vulnerable spruce resources in Kent. Since the site was actually part of the annual PZ survey regime and included trap logs baited with the *I. typographus* attractant lure, it is possible that the combination of emissions by the cluster of pheromones from the artificial lures and the presence of weakened spruce may have resulted in a concentration of adult beetles from a widely distributed ‘cloud’ of flying beetles, which came from imported wood or by direct flight from Europe. This has parallels with the situation noted by Piel *et al.* (2005) in Brussels, where flying beetles were trapped in all parts of the city, indicating a ‘cloud’ of adults sampling the environment for potential host trees. This could also have been the case in Kent in 2019, as suggested by captures of beetles in extensive pheromone trapping.

Table 14 The steps needed to establish a successful population of *Ips* bark beetles in the UK.

Parameter	Evidence	Level of confidence
Arrival of adult beetles in imported wood	Interceptions of adult beetles many times, despite PZ requirements for debarking	High
Arrival by adult flight from continental Europe	Multiple records of long flights in Europe and many adults captured in network of pheromone traps across Kent despite only a small number of infested trees recorded	Medium
Flight capacity under British conditions	Flight takes place at temperatures >16°C Captures in pheromone traps at ports and timber yards – direct evidence of flight	High
Dispersal from import source to nearest woodland with host trees	Local flights tend to be very short (~500 m) Long-distance flights can be up to 50 km Host trees of suitable age occur throughout UK. Probable that beetles will land in sites with suitable host trees	High
Attacks and successful breeding in host trees	Climate in most of UK is suitable for one, possibly two, generations per year	Medium

Measures to manage *Ips* species if they establish successfully

Reflecting its status as one of the most damaging insect pests in Europe, the literature on *I. typographus* is extensive and far exceeds the information available on other species of *Ips*. Therefore, discussion of impact will concentrate on *I. typographus* (with reference to the other species where appropriate).

Direct effects on trees

Tree mortality arising from mass attack by *I. typographus* can result in enormous losses of living trees (see the section on the 'Impacts of *Ips* species in their natural and invaded ranges' on page 11). Millions of trees can be killed in large outbreaks triggered by events such as windthrow, snow damage and extensive drought. In the absence of such triggering events, the 'return time' between outbreaks when populations of the beetle gradually build up naturally was estimated to be as high as 75 years in Scandinavia, with the duration of each outbreak being ~10 years, whether triggered by random events or natural increase (Okland and Bjornstad, 2006).

On the basis that *I. typographus* has been able to establish in the UK at a local level, the scale of any outbreak is subject to the range of triggering events outlined in the section on 'Tree attack strategies' on page 4. The principal factors likely to influence population growth in the UK are random damaging events such as windthrows (outbreak initiators), followed by tree age and scale of host tree density in monocultures or mixtures (factors affecting mass attack once populations have increased in poorly defended trees).

Prediction of sites most likely to experience windthrow can be carried out accurately for the UK using ForestGales (Forest Research, 2020). This provides the means to assess individual stands of trees and accounts for local variation in soil type, rainfall and wind hazard. If it was present in the UK, *I. typographus* would have had an abundance of breeding material; there have been relatively few major episodes of windthrow but local windthrow would have been more common at higher elevation. For example, Quine and Bell (1998) provided data on major storms in the UK since 1945. These all encompassed large forest areas and resulted in a massive destruction of standing trees, especially in the expanded areas of upland forestry that were planted in the 20th century.

Areas such as these would be expected to provide foci for breeding by *I. typographus*, which would increase in the 2–3 years after the windthrows, first utilising the residue of the windblown trees and then, when numbers of beetles were large enough and the supply of weakened trees was depleted, attacking and killing standing trees. Comparative data from Europe suggest that once initial colonisation of weakened trees takes place there is a direct influence on the mortality of living trees in the close vicinity. Karvemo *et al.* (2014) assessed this effect and compared field data from their study with an earlier study by Schroeder and Lindelow (2002).

Expansion of initial infestation foci

The implication from the pattern of attacks reported by Karvemo *et al.* (2014) is that attacks extend outwards from initial foci on the wind-felled trees, demonstrating local dispersal that scales in metres rather than kilometres. Similar results were obtained by Kautz *et al.* (2011), who tracked the progression of infestations in outbreak and non-outbreak populations of *I. typographus*. In both populations, new attacks took place predominantly within 100 m of the initial infestation and ~96% of new attacks occurred within 500 m, in particular for the higher outbreak population. If initial attacks are successful, then the implications for the UK are that the onward progression of the outbreak on living trees will be local and driven by the numbers of beetles entering the local population. Thus, the main requirement in potentially managing overall impacts on trees in the UK is early detection of 'starter populations' of beetles, with emphasis on sources of poorly defended trees. Except for wind damage, any other factors which substantially weaken trees can be regarded as predisposing for attack by all species of *Ips*. These factors include snow damage, ice storms, drought, the edges of large fire events, growing host trees on unsuitable sites (as was the case for *I. typographus* in Kent) and leaving felled timber for a sufficiently long period to support one generation of the beetles.

Attacks on surrounding living trees are also driven by other factors such as density, which requires ≥ 700 beetles per square metre of bark to overcome tree defences. In addition, the species mix in the surrounding area and the sizes of suitable tree species affect the choice of tree for initial colonisation by pioneer male beetles (Wermelinger, 2004). Monocultures of a given species of host tree are more likely to be attacked than mixtures of trees where host trees are in the minority (see the section on 'Management options: alteration of tree species mix' on page 15).

Kautz *et al.* (2016) investigated distributions of 'susceptible' (weakened), 'resistant' (healthy, well defended) and scattered trees (those randomly scattered in a patch of resistant trees) relative to colonisation by dispersing *I. typographus* from a point source. The outputs from their observations and model simulations confirm the highly local dispersal and colonisation strategies employed by *I. typographus* and also indicate that dispersing adults have to move further when trees are better defended or when susceptible trees are scattered in sets of resistant trees.

Eradication and containment prospects

The prospects of eradicating new infestations of *Ips* in the UK are heavily dependent on early detection of beetle attacks, as was the case with the Kent infestation, indicated by early surveys of the extent of the infested area. A strategy of felling infested trees and potential host trees in the immediate area has been applied followed by intensive monitoring to determine the outcome of the management programme. Emergency measures were enacted introducing restrictions on movement of potentially infested wood from the site and immediate area (including East Sussex as well as Kent) (Forestry Commission, 2019).

Long-term strategies to improve the prospects of eradication should include pre-emptive management to maximise detection. As indicated in the section on 'Management options: removal of weakened or infested trees' on page 13, a risk-based survey of sites predisposed to attack factors (e.g. in close proximity to import pathway end points) would optimise survey resources and maximise the likelihood of locating new infestations. If infestations can be located shortly after they start, the prospect of eradication increases, especially if the hypothesis of an Allee effect (see the section on 'Pioneer bark beetle populations: the numbers needed' on page 7) is correct and localised removal of beetles to below a viable population size is achieved.

Based on experiences of population growth and decline in Finland, a minimum area for eradication in the UK could be a threshold of ≤ 20 infested trees in a forest 'patch' (see the section on 'Management options: removal of weakened or infested trees' on page 13); assuming that all the trees are in close proximity but not directly adjacent, and are pole stage or larger, then they could be located within a patch of ≤ 0.1 ha. A study by Quine and Bell (1998) of the frequency and size of forest gaps created by windblows in spruce forests provides an insight into the expected range of storm damage in the UK. Over the six-year study period the frequency and size of gaps was highly

skewed to smaller sizes, with the majority between 1000 and 2000 m², which equates closely to the range implied by the threshold in Finland.

Therefore, it would be reasonable to consider a minimum area for increased risk of population growth at ~ 2000 m² (~ 0.2 ha). Areas larger than this would require intensive management to remove all the infested and non-infested (but susceptible) trees within a generation (approximately six weeks) to prevent further population increase in an isolated infestation by *I. typographus*. Although there is less information on critical numbers, a similar threshold is likely to be applicable to the other *Ips* species. While this is a threshold that could apply in more northern locations such as Finland, it is too early to assess whether such an approach can be applied in the infested zone in Kent.

Any successful attacks would require surveys covering 100–200 m from the point of infestation. Reflecting the key drivers for beetle attacks, efforts should concentrate on weakened trees, which may not necessarily display obvious signs of attack. As outlined in the section on 'Beetle-mediated dispersal' on page 11, there has been progress in using remote sensing for early detection of attacks at the green stage, and this merits further assessment. Although neither direct nor quantitative, baited pheromone traps can be used to supplement visual surveys.

Slowing the spread

Established infestations tend to decline to low levels, particularly if the supply of easily colonised trees (damaged or freshly felled trees) is exhausted and further progression can only continue by mass attacks requiring large numbers of beetles. Reducing local spread by the dispersal of flying beetles would involve the same tactics as eradication because the infestations would be contained within a relatively small area. Longer distance movement is more probable through human-assisted transport of infested wood, which is likely to be concentrated in timber yards, where there may be an abundant supply of suitable host material (i.e. weakened trees). Provided the material on site is processed within the time frame of a single beetle generation, there is no danger of population growth. However, if material is not processed quickly enough, beetle populations could increase significantly, with possible further dispersal to local woodlands. Therefore, slowing the spread is partially achievable by managing local populations of *Ips* as well as raising awareness of the danger of longer distance spread with felled timber.

Living with the pest

If eradication measures fail, which is highly probable unless initial infestations are found within one or two generations of arrival, then any of the *Ips* species could become part of the UK's beetle fauna. Impacts will vary with species, and those circumstances described earlier could trigger population increases and mass attacks on living trees. In Great Britain, experience of *I. cembrae* since the 1950s, and *I. sexdentatus* from even earlier in the 20th century, indicate that both species have had little or no impact on living trees. *Ips sexdentatus* populations increased following the 1987 great storm, confirming that this species is a secondary pest in the UK, whose main impact is carrying blue-staining fungi, which reduce the value of wood if visual defects are detrimental. There was no evidence of a switch to mass attack, as has occasionally been reported in Europe (Rossi *et al.*, 2009). *Ips cembrae* has gradually spread south from its original first location in Scotland and it is now present in the Forest of Dean (Alexander, 2007). Apart from limited tree mortality reported in Scotland shortly after its discovery, there has been little direct impact on living trees (Crooke and Bevan, 1957; Redfern *et al.*, 1987).

Ips typographus is by far the most damaging of the remaining three species and would require a more robust awareness and monitoring regime to 'live with it'.

Building on the strategies proposed for slowing the spread, early warning systems of possible attacks could be developed around known triggering events: for instance, by tracking wind events, any significant amounts of windblown trees, or, via ForestGales, indications of windthrow at a forest or forest block level. These data could be combined with phenology modelling, such as PHENIPS (Baier *et al.*, 2007), to assess potential flight periods and durations of larval development, thus providing a time window for clearance of damaged, infested trees before the emergence of the next generation of beetles. Based on experiences in Finland, where ≤ 20 damaged trees are acceptable without increasing beetle damage (Eriksson, Neuvonen and Roininen, 2008) (see the sections on 'Management options: removal of weakened or infested trees' on page 13, and 'Eradication and containment prospects' on page 29), it may be possible to establish a similar threshold under UK conditions. In all cases, supplementing visual assessment with deployment of pheromone traps baited with a suitable lure would help to confirm the presence of flying beetles, but would have minimal influence on beetle population density in a given area.

Awareness campaigns as part of surveillance and management

All the strategies to manage *Ips* populations could be enhanced by awareness campaigns targeted principally at those working in the timber industry (e.g. sawmill and forest owners, felling contractors) but also at members of the public visiting forest locations (e.g. >90% of visitors to the Bavarian Forest National Park in Germany were aware of *I. typographus*; Arnberger *et al.*, 2018). Information on the pest is available on the Forestry Commission website and, to a limited extent, the Defra Plant Health Information Portal. Initiatives such as Observatree (Observatree, 2018), provide heightened awareness and encourage citizen science as a means of surveillance and reporting. However, currently the only pest of spruce on the Observatree website is *Dendroctonus micans*. Other portals for raising awareness at public level should be explored.

An awareness of the importance of maintaining forest health, and who is responsible for this, remains a contentious issue. For *I. typographus*, several studies have investigated as to whether a Payment for Ecosystem Services (PES) strategy should be adopted at a national level. Sheremet *et al.* (2018) conducted a preference study of forest owners in Finland to assess their willingness to enter a PES scheme, including measures to manage *I. typographus*. When offered different value contracts and different lengths of contracts with which to maintain forest health, their preference was for shorter contracts and higher value. The authors emphasised the importance of cooperation and also of balancing actions to reduce both the risks and associated costs of invasive pests with multiple forest management objectives. The willingness of the general public to fund PES schemes was dependent upon which benefits (e.g. recreation, commercial, carbon sequestration) would be most impacted by a particular pest. Thus, any PES scheme for invasive pests must be consistent with maximising net social benefits from a forest; the costs of participation must also be economically justifiable for forest owners. As pointed out by Epanchin-Niell (2017), each stage of the process in managing an invasive species (i.e. prevention, early detection, eradication and coping with established populations), has scope for optimisation, which is driven by both ecological and financial considerations. Keeping a pest out (prevention) is often the starting point for managing invasive species and this can be achieved in several ways, each of which imposes some restriction on trade, and may ultimately prove ineffective. Carrasco *et al.* (2010) developed a model including prevention, detection and control of a range of invasive species. The authors

reached the conclusion, one which is highly relevant to bark beetle management, that there should be less expenditure on prevention but more on post-invasion control of invasive species characterised by Allee effects, a low rate of spread and low numbers of non-native species. From this report, it appears that the early stages of development by *I. typographus* fulfil these criteria.

Commission Implementing Regulation (EU) 2019/2072 listing for *Ips* spp.

Commission Implementing Regulation (EU) 2019/2072 of 28 November 2019 establishing uniform conditions for the implementation of Regulation (EU) 2016/2031 of the European Parliament and the Council, as regards protective measures against pests of plants, and repealing Commission Regulation (EC) No 690/2008 and amending Commission Implementing Regulation (EU) 2018/2019 of 28 November 2019. EL = Greece; F = France; IRL = Ireland.

(a) *Ips amitinus* Eichhof

- Plants of *Abies* Mill., *Larix* Mill., *Picea* A. Dietr. and *Pinus* L., over 3 m in height, other than fruit and seeds
- Wood of conifers (*Coniferales*) with bark
- Isolated bark of conifers

Countries with Protected Zone: EL, F (Corsica), IRL, UK

(b) *Ips cembrae* Heer

- Plants of *Abies* Mill., *Larix* Mill., *Picea* A. Dietr., *Pinus* L. and *Pseudotsuga* Carr., over 3 m in height, other than fruit and seeds,
- Wood of conifers (*Coniferales*) with bark,
- Isolated bark of conifers

Countries with Protected Zone: EL, IRL, UK (Northern Ireland, Isle of Man)

(c) *Ips duplicatus* Sahlberg

Plants of *Abies* Mill., *Larix* Mill., *Picea* A. Dietr. and *Pinus* L., over 3 m in height, other than fruit and seeds, wood of conifers (*Coniferales*) with bark, isolated bark of conifers

Countries with Protected Zone: EL, IRL, UK

(d) *Ips sexdentatus* Börner

- Plants of *Abies* Mill., *Larix* Mill., *Picea* A. Dietr. and *Pinus* L., over 3 m in height, other than fruit and seeds
- Wood of conifers (*Coniferales*) with bark
- Isolated bark of conifers

Countries with Protected Zone: IRL, UK (Northern Ireland, Isle of Man)

(e) *Ips typographus* Heer

- Plants of *Abies* Mill., *Larix* Mill., *Picea* A. Dietr., *Pinus* L. and *Pseudotsuga* Carr., over 3 m in height, other than fruit and seeds
 - Wood of conifers (*Coniferales*) with bark
 - Isolated bark of conifers
- Countries with Protected Zone: IRL, UK

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Conifer forests and woodlands thrive in most of Europe and into Asia, particularly in more northerly latitudes, but can be attacked by several species of bark beetle in the Coleoptera sub-family Scolytinae. The island status of the UK has helped to protect our mainly exotic conifer woodlands from invasion by non-native bark beetles but, over time, several species have established here, notably great spruce bark beetle (*Dendroctonus micans*) and several species in the genus *Ips* (*Ips sexdentatus* on pine, *Ips cembrae* on larch and, from 2018, *Ips typographus* on spruce). Among these, *I. typographus* is the most destructive and has periodically killed millions of spruce trees across Europe and Asia. This Report describes the biological and environmental factors that influence attack frequency and severity from *Ips* bark beetles and assesses strategies for their management, with emphasis on the major threat posed by *I. typographus*.