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ORIGINAL PAPER

# Evidence of cross-channel dispersal into England of the forest pest *Ips typographus*

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## Abstract
A breeding population of the tree-killing European spruce bark beetle *Ips typographus* was detected in England for the first time in 2018 and was initially assumed to have arrived with infested timber. To test the hypothesis that the beetles are dispersing naturally across the English channel, extensive trap networks were deployed in 2021 and 2022 to track the flight activity of the beetles from an outbreak hotspot in France and Belgium to southern England, including parallel 'coastal' traps on either side of the channel. Beetles were caught all along the transect, decreasing in abundance with distance from the outbreak area. Linear modelling indicates that beetles dispersed into England during 2021 and 2022, and that during a large-scale dispersal event in June 2021, beetles could have penetrated more than 160 km inland. The 2021 dispersal event initiated new incursions of the beetle in southeast England and demonstrates the extraordinary distance *I. typographus* may move under outbreak conditions. Our findings support the hypothesis of a damaging forest pest aerially dispersing across the barrier of the English channel and suggest that future incursions of this and other plant-associated pests may move via the same pathway.

**Keywords** Bark beetles · *Picea* · Pest management · Invasive species

## Introduction

*Ips typographus* (L.), the eight-toothed spruce bark beetle, is currently the most destructive and economically important forest insect pest in Europe, causing widespread mortality of spruce trees (*Picea* spp.). It typically colonises damaged or recently wind-felled hosts, but extensive wind-throw caused by severe storms may facilitate rapid population growth, leading to outbreaks and the killing of standing spruce trees (e.g. Komonen et al. 2011; Kausrud et al. 2012; Mezei et al. 2017). Over the past 2 decades, under the influence of climate change, the scale and longevity of outbreaks across Europe have been markedly increasing, with high summer temperatures and drought having an amplifying effect (Netherer et al. 2019; Netherer and Hammerbacher 2022; Trubin et al. 2022), and unprecedented population levels being reported across continental Europe. For example, in the Czech Republic alone, 23 million $m^3$ of spruce were killed in 2019 (Hlásny et al. 2021), while in the two most affected French regions (*Grand-Est* and *Bourgogne-Franche-Comté*), the damage in 2018–2021 amounted to 19 million $m^3$ (DSF 2022).

*Ips typographus* mostly attacks *Picea* spp. across its entire range from western France to Japan. Its original distribution in Europe coincided with that of Norway spruce *Picea abies* (L.) in the Boreal forests of Northern Europe and the subalpine regions of the Alps and the Carpathians (Taberlet et al. 1998; Caudullo et al. 2016). Spruce has been extensively planted outside of its original range since the nineteenth century and *I. typographus* has followed its host (Mayer et al. 2015), with variable time lags between the planting of spruce forests in new areas, the arrival of the beetle and the first outbreaks (usually triggered by extreme weather conditions). In Belgium, for example, spruce was introduced in 1894 (Scheepers et al. 1997) and *I. typographus* was first mentioned in the literature in 1926, supposedly arriving from Germany in the east (Dourojeanni 1971).

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It was widely present at low densities by the 1970s (Dourojeanni 1971), and after a gradual population build-up, the first outbreaks appeared in 1976 during an exceptionally hot and dry summer. Reflecting the widescale population growth across Europe, *I. typographus* populations in Belgium have increased and expanded, most notably resulting in more outbreak locations in the Ardenne forest in the south of the country, as well as progressively expanding their range and killing trees in more remote stands, parks and gardens around Brussels, and up to the coast.

Until recently no established breeding population was known in the British Isles, despite regular interceptions associated with imported spruce wood products (e.g. Winter 1985). The physical barrier of the English channel has been assumed to have restricted entry while an ‘Allee effect’, whereby small populations are unable to expand and persist (Taylor and Hastings 2005), prevented successful establishment. Additionally, emerging *I. typographus* adults tend to disperse widely (Franklin and Grégoire 1999; Franklin et al. 2000), reducing opportunities for mate location and the colonisation of new resources. It is likely that the dilution effect resulting from the wide dispersal of young adults explains why *I. typographus* has similarly failed to establish in North America, despite many interceptions (see “Discussion” section) and the large availability of suitable hosts (Pureswaran et al. 2022).

In Britain, *Picea* is an important component of commercial forestry, particularly Sitka spruce (*P. sitchensis* (Bong.) Carr.), which comprises 54% of all planted conifers (Forest Research 2023). Another spruce pest, *Dendroctonus micans,* was accidentally introduced to Britain (Bevan and King 1983) and has become widespread, but to date, it has caused only localised damage due to a successful biological control programme (Fielding and Evans 1997). Any new threat to *Picea* is therefore of considerable concern to the forest industry. As such, *I. typographus* is regulated as a quarantine pest in Britain and Ireland, with measures implemented to prevent entry, including requirements for imported conifer wood to be bark free, originate from an area free from the pest, or be suitably heat-treated (Forestry Commission 2018). Additionally, pest-free area (PFA) surveys have been conducted annually across Britain (Fielding et al. 1994). In December 2018, a routine PFA survey detected a breeding population of *I. typographus* in southern Kent for the first time, in an area of windthrown Norway spruce and on nearby live standing trees. In accordance with regulations, an intensive programme of eradication activities began: delimitation-, aerial- and ground-based surveys; wider environment monitoring with pheromone traps; and the establishment of a demarcated area (initially covering parts of Kent and East Sussex, but subsequently expanded) to limit movement of susceptible *Picea* material within or out of the region (Plant Health England 2019).

All recent incursions of *I. typographus* identified in southern England have been small, and geographically isolated populations exhibiting one or more breeding galleries. This study aims to test the hypothesis that these incursions result from natural long-distance dispersal from a large population reservoir in continental Europe, rather than originating from imported, infested host material.

## Methods

### Site design and selection

The trap networks set up in this study were designed to test the hypothesis of a large population reservoir of highly mobile *Ips typographus*, centred around an outbreak hotspot and dispersing outwards (including across the channel) at distances proportional to the reservoir size. Pheromone-baited bottle traps were deployed along a series of transects in France, England and Belgium, to monitor the presence of *I. typographus*, as used in previous bark beetle surveys (Franklin et al. 2000; Piel et al. 2005; Meurisse et al. 2008). The continental transects originated in hotspots in France (2021 and 2022) and Belgium (2022 only) and were oriented north-west to end at the channel coast. An additional transect in France was arranged parallel to the coastline in the Pas-de-Calais region. In southern England, transects were arranged parallel to the channel coast (2021 and 2022), with a larger geographic span in 2022 to determine whether dispersal activity was concentrated near the narrowest part of channel, or could be detected more widely (Fig. 1).

The 2021 trap network was arranged as follows:

1. An inland French transect originating at Revin, Champagne-Ardenne region, and extending 230 km north-west to the channel coast (11 sites; A-K, Fig. 1). Revin is located in the south-west of a densely planted spruce growing region (Ardenne forest) extending across southern Belgium to Germany. Large populations of *Ips typographus* have developed in the area, resulting from a sequence of very dry and hot years, as confirmed by regular monitoring of beetles and records of associated damage in France (Department de la Santé des Forêts) and Belgium (Observatoire Wallon de la Santé des Forêts).
2. A coastal French transect along the Côte d’Opale (Pas-de-Calais), at the narrowest part of the channel, from Wimereux to Wissant (6 sites; L-Q).
3. Two parallel transects in England, each 25 km long and directly opposite the French coastal trapping sites and consisting of a ‘coastal transect’ originating at Dover (2021 sites 1–10, located 2.5 km from the sea on average) and an ‘inland transect’ (2021 sites 11–20, located 12 km from the sea on average).

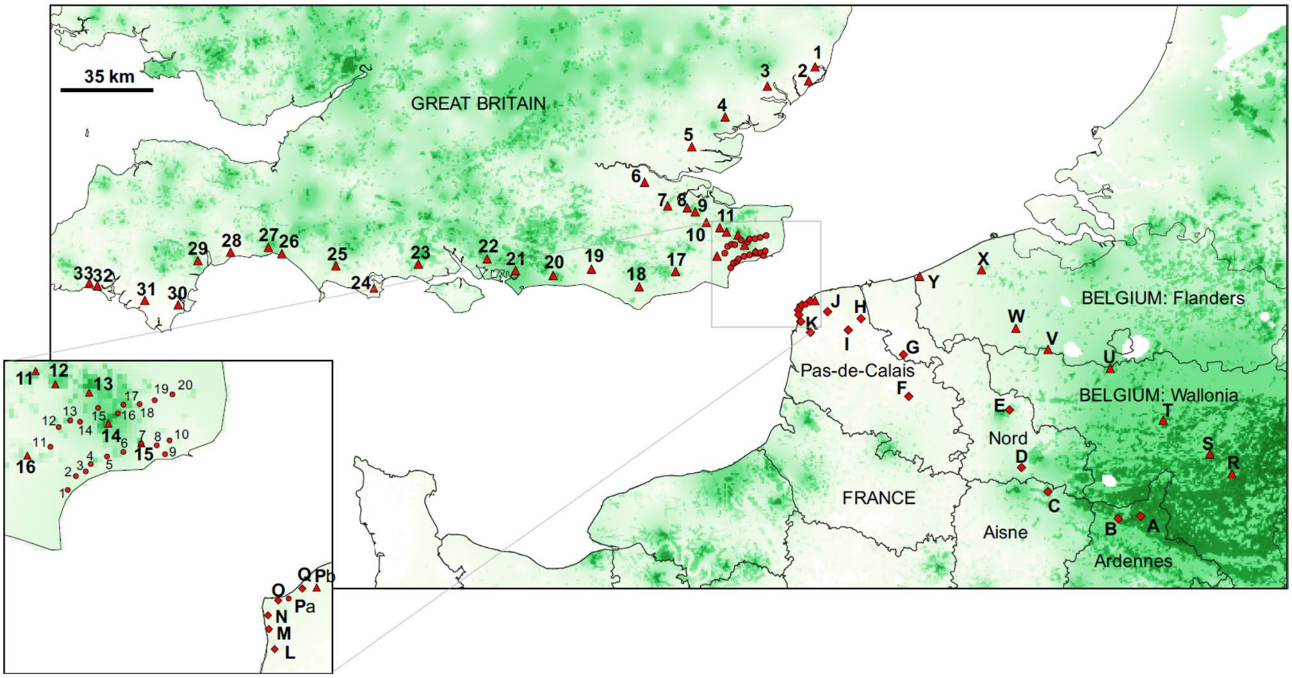


**Fig. 1** Location of *Ips typographus* trapping sites across France, Belgium and England in 2021 and 2022. Transect details: red filled circles = sites active in 2021 only (England; France site *Pa*); red filled diamonds = sites active in 2021 and 2022 (France); red filled triangles = sites active in 2022 only (Belgium, France site *Pb*). The inset map provides detail of the 'coastal' trapping sites on either side of the channel. The approximate local density of *Picea* spp. is illustrated by the shading (Brus et al. 2011), but as spruce coverage density was not included in our model, no density scale is provided

Each site along the French part of the network was selected to be as near as possible (c. 10—100 m) to a spruce or conifer woodland using the French national forest inventory, IGN *(*https://inventaire-forestier.ign.fr/*)*, and descriptions from the Museum National d'Histoire Naturelle *(*https://inpn.mnhn.fr/accueil/index*)*. No conifer stands could be found beyond site K in the area of the coastal French sites (L-Q), so all traps at these locations were placed in open countryside. The 2021 English sites were all selected to be in open countryside (agricultural fields with scattered broadleaf woods and hedgerows), specifically avoiding any association with conifer forest and any potentially undetected *Ips* populations. However, the presence of a mixed conifer forest containing *Picea abies* within the locality of the English transects (representing the nearest spruce woodland to the coast) was used as an opportunity to investigate how trap catches might be influenced by placement in a spruce woodland (2021 site #16).

The 2022 trap network was revised as follows:

1. An additional transect of 8 sites (R-Y, Fig. 1) was erected in Belgium to confirm the French trapping gradient detected in 2021. The 2022 Belgian transect began at Wyompont in the Belgian Ardenne region and proceeded parallel to the French transect, to the coast at De Panne. The 2022 French transects (17 sites, A-Q) remained the same as in 2021, though site P was relocated slightly due to technical issues (indicated as site Pa / Pb in Fig. 1).
2. The English coastal transect was modified to extend more widely along the south coast (Fig. 1), to detect any dispersing beetles over a greater area. The east-coast section extended over 90 km of (straight-line) distance from Suffolk to south-eastern Essex (2022 sites 1–5), and the south-coast section extended over 400 km from Kent to eastern Cornwall (2022 sites 15–33). The 2022 English coastal trapping sites were located on average 8.3 km from the sea.
3. The English inland transect was modified to assess how far inland any incoming beetles could travel. The 2022 'inland' transect extended north-west from the Kent coast towards London (2022 sites 6–15), continuing the direction of the French transect, and connecting the two parts of the coastal transect. Based on findings from 2021, all 2022 English trapping sites were chosen to be located adjacent to conifer forest (360 m on average), to increase the likelihood of detecting dispersing beetles.

## Traps

Each trap was made from a PET 2-L commercial transparent (soft drinks) bottle, cut longitudinally and turned upside-down to form a 21 × 13 cm interception pane, the inverted bottleneck serving as a collecting funnel connected to a 50-ml clear plastic sample container half-filled with propylene glycol (at 60% concentration) as a preservative. The lures consisted of an 8 × 6 cm polyethylene Ziplock bag (50 µm thick), containing a cellulose wick impregnated with 80 mg of (S)-*cis*-verbenol (Merck, 95% purity) diluted in 2 ml of 2-methyl-3-buten-2-ol (Merck, 98% purity), mimicking the *I. typographus* aggregation pheromone. In a calibration experiment, a batch of ten lures exposed to a 0.05 m/s airflow at 20 °C ± 2 °C in a wind tunnel showed a steady diffusion rate of 50–60 mg/day, over 29 days (Supplementary Material 1). Traps were fixed at a height of around 2–2.5 m to telegraph/electrical poles or non-coniferous trees, typically located along quiet lanes to provide accessibility while limiting any interference. Five bottle traps were deployed at each trapping site, preferably at least 10–20 m from each other, and facing random directions.

In 2021, the traps operated from late April in England/mid-May in France to late September. In 2022, the revised transect operated from early April to mid-October in England and mid-April to mid-September in France and Belgium. All traps were emptied every 2–4 weeks in England and every 4 weeks in France and Belgium, and all lures were changed every 4 weeks. Collected beetles were counted individually when there were only a few individuals present in the traps, or their number was assessed by measuring the total volume of each trap collection in a graduated glass, after a careful calibration of this process.

## Statistical analyses: Linear modelling of beetle trap captures

All statistical analyses were carried out in R (R Core Team 2022).

To determine whether the coasts of England are within reach of dispersing individuals during outbreak periods, linear modelling was carried out to characterise the reduction of *Ips typographus* captures at increasing distances from the core outbreak area. For all models, the response was trap captures. Because the French/Belgian and English data were collected across different periods (Table 1), and because of differences in the site selection process between years, the data were analysed separately by region and year. The trap captures were visualised and examined in order to exclude apparently anomalous data that would unreasonably influence the models. Data from the French traps directly adjacent to the coast (Fig. 1, sites L-Q) were excluded because of a localised increase in captures, which may have been caused by low-flying beetles "touching down" to avoid flying over the sea. (No conifer woodlands are present in this area).

For the English data, only the months where more than a few beetles were caught were analysed (May and June 2021; May, July and August 2022; Table 1). Trap data from the single (unreplicated) mixed conifer site in 2021 (#16) were much higher than the other sites and were not included in the model (Table 1). For all models, the explanatory variables were distance to the most southerly point of the transect (nearest to the Ardenne spruce-growing region), collection period and the interaction between these. In 2021, the most southerly point was site A; in 2022, distance was calculated from a midpoint between sites A and R (Fig. 1). In England, distance to the nearest conifer forest, and its interaction with distance to site A and collection period, were also included as explanatory variables in each model. Distance to the nearest conifer forest was not included as an explanatory variable because contrary to Britain where proximity to the stands might reinforce trap attractivity, the French/Belgian conifer forests could at the same time be sources of beetles and attractors, with an unequal weight of both effects along the transects. All continuous explanatory variables were scaled and centred using the scale function. To account for spatial autocorrelation, a random effect of trap nested within site was fitted. In 2022, country identity (Belgium or France) was also included as a main effect, and a random effect of trap, nested within site, nested within country was specified.

For all of the datasets, in the first instance, generalised linear mixed-effects models with a Poisson distribution specified were fitted. Overdispersion, zero-inflation and residual fits were checked in the DHARMa package (Hartig 2022). If the data were zero-inflated, generalised linear mixed models using template model builder were fitted in the glmmTMB package (Brooks et al. 2017). If the residual plots suggested between-quantile variation in the residual versus predicted data, negative binomial models were fitted either within the glmmTMB or lme4 packages (Bates et al. 2015). Final best-fit models were selected using Akaike's information criteria (AIC) and the fit as indicated by the DHARMa residual plots. The significance of the explanatory variables was assessed using the ANOVA function within the car package (Fox and Weisberg 2019). The models were simplified by progressively removing the highest-order non-significant interactions. Final best-fit models were selected using Akaike's information criteria (AIC) and the fit as indicated by the DHARMa residual plots. Model predictions of trap catch by distance to site A and collection period were made within emmeans (Lenth 2022); these were examined to determine the distance at which at least one beetle per trap was predicted (i.e. that dispersing beetles might be detected).

**Table 1** Collection periods and numbers of *Ips typographus* trapped by location

| Collection period and approximate month | Trapping dates | Location | Total catch per collection |
|---|---|---|---|
| 1. May 2021 | 1–12 May 21 | GB-ENG | 0 (+0 site 16) |
| | 12 May–3 Jun 21 | GB-ENG | 36 (+14 site 16) |
| 2. June 2021 | 1–21 Jun 21 | FRA (inland) | 19,062 |
| | | FRA (coastal) | 950 |
| | 3–16 Jun 21 | GB-ENG | 114 (+459 site 16) |
| | 16 Jun–15 Jul 21 | GB-ENG | 0 (+23 site 16) |
| 3. July 2021 | 22 Jun–22 Jul 21 | FRA (inland) | 6164 |
| | | FRA (coastal) | 0 |
| | 15–28 Jul 21 | GB-ENG | 2 (+2 site 16) |
| 4. August 2021 | 23 Jul–23 Aug 21 | FRA (inland) | 1702 |
| | | FRA (coastal) | 1 |
| | 28 Jul–19 Aug 21 | GB-ENG | 2 (+1 site 16) |
| 5. September 2021 | 24 Aug–20 Sep 21 | FRA (inland) | 454 |
| | | FRA (coastal) | 1 |
| | 19 Aug–8 Sep 21 | GB-ENG | 0 (+0 site 16) |
| | 8–22 Sep 21 | GB-ENG | 1 (+1 site 16) |
| 6. April 2022 | 8 Apr–4 May 22 | GB-ENG | 0 |
| 7. May 2022 | 19 Apr–20 May 22 | FRA (inland) | 9340 |
| | | FRA (coastal) | 18 |
| | | BEL | 4294 |
| | 4–25 May 22 | GB-ENG | 10 |
| 8. June 2022 | 20 May–20 Jun 22 | FRA (inland) | 3435 |
| | | FRA (coastal) | 0 |
| | | BEL | 2707 |
| | 25 May–8 Jun 22 | GB-ENG | 0 |
| | 8–22 Jun 22 | GB-ENG | 2 |
| 9. July 2022 | 20 Jun–20 Jul 22 | FRA (inland) | 2840 |
| | | FRA (coastal) | 2 |
| | | BEL | 5944 |
| | 22 Jun–14 Jul 22 | GB-ENG | 11 |
| | 14 Jul–3 Aug 22 | GB-ENG | 50 |
| 10. August 2022 | 20 Jul–23 Aug 22 | FRA (inland) | 2032 |
| | | FRA (coastal) | 8 |
| | | BEL | 3318 |
| | 3 Aug–1 Sep 22 | GB-ENG | 36 |
| 11. September 2022 | 23 Aug–21 Sep 22 | FRA (inland) | 461 |
| | | FRA (coastal) | 0 |
| | | BEL | 407 |
| | 1 Sep–9 Oct 22 | GB-ENG | 0 |

England 2021 catches from the spruce woodland (site #16, not included in model) are provided in brackets. The English transects were modified for 2022, and beetles were trapped over a wider area (2022 sites #6–22; Fig. 1). French coastal trap catches are presented separately from the inland trap catches

FRA = France, BEL = Belgium, GB-ENG = England

## Suitability of meteorological conditions for dispersal across the channel

To determine how many days were apparently suitable for beetle dispersal across the channel, meteorological data were inspected and systematically assessed. Daytime hourly temperature and wind speed/direction data were obtained from paired inland and coastal weather stations in England (East Malling, north Kent and Langdon Bay, Dover) and France (Cambrai and Cap-Griz-Nez, Pas-de-Calais). Wind direction was plotted using the 'Arrowhead' function in the shape package of R (Soetaert 2021). The suitability of prevailing wind conditions for cross-channel dispersal from the continent to the Kent coast was also assessed visually using average wind data from the Meteociel website (Fig. 2, Meteociel 2023). For each date, wind direction at 10:00, 13:00 and 16:00 were examined, with each timepoint assessed as 'suitable' or 'not suitable' for assistance of cross-channel dispersal. Wind blowing from within the SE quadrant (between the east and south cardinal points) was deemed suitable to potentially assist dispersal across the channel. If two of the three timepoints were assessed as 'suitable', the date was assessed as 'suitable'.

## Results

### 2021 Dispersal: linear modelling of beetle trap captures

Dispersing *Ips typographus* were collected all along the 2021 trapping transect, from the Ardenne region to the English coast. In both France and England, analyses showed more beetles were caught closer to Ardenne Site A (sites A and B collected over 16,000 beetles in 2021; Fig. 1), with abundance declining with increasing distance from this area (Table 2, Fig. 3). Both French and English beetle catches also varied by collection period, with a notable peak in June

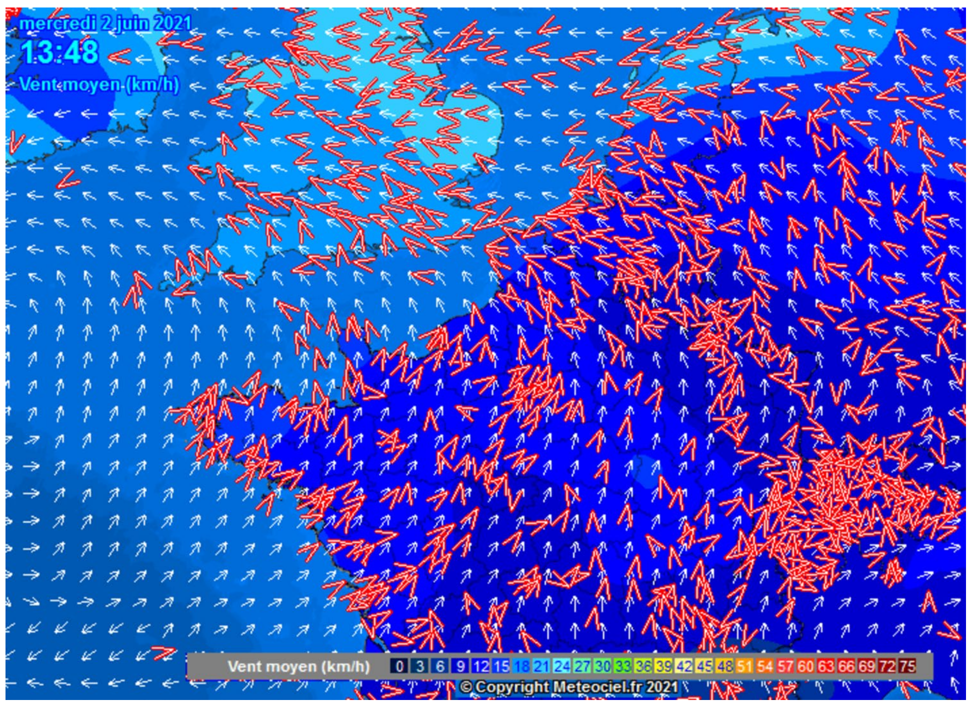


**Fig. 2** Example wind chart showing prevailing wind conditions assessed as suitable to assist dispersal of *I. typographus* across the English channel (Meteociel 2023)

**Table 2** Significant explanatory variables in the minimal linear modelling of beetle trap catches

| Model | Explanatory variable | $X^2$ | Df | *p* |
|---|---|---|---|---|
| France 2021 | Scale (distance to site A) | 17.3 | 1 | < 0.0001 |
| | Collection date | 1090.0 | 3 | < 0.0001 |
| | Scale (distance to site A): collection date | 36.6 | 3 | < 0.0001 |
| England 2021 | Scale (distance to site A) | 10.8 | 1 | 0.001 |
| | Collection date | 32.7 | 1 | < 0.0001 |
| | Scale (distance to nearest conifer forest) | 17.7 | 1 | < 0.0001 |
| | Scale (distance to site A): collection date | 5.2 | 1 | 0.022 |
| France/Belgium 2022 | Scale (distance to Ardenne midpoint) | 33.9 | 1 | < 0.0001 |
| | Collection date | 364.5 | 4 | < 0.0001 |
| | Distance to A: collection date | 48.1 | 4 | < 0.0001 |
| England 2022 | scale (distance to Ardenne midpoint) | 5.7 | 1 | 0.017 |
| | Collection date | 21.7 | 2 | < 0.0001 |

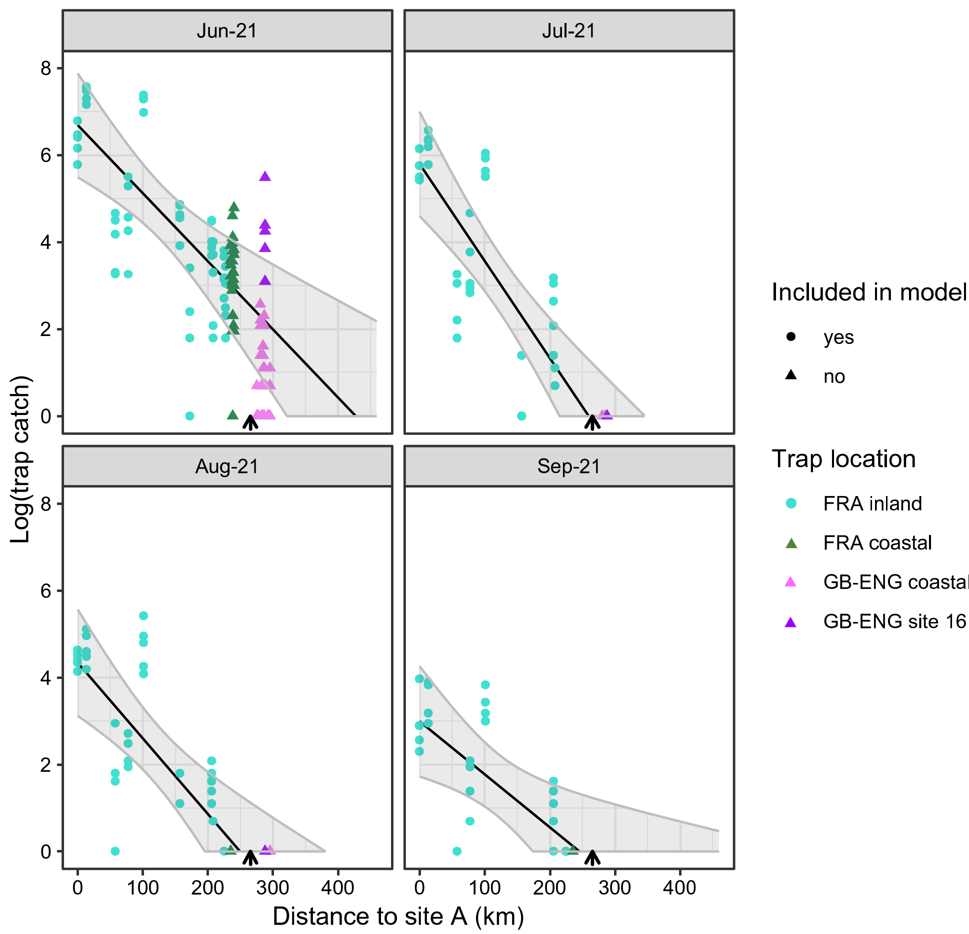


**Fig. 3** Predictions of trap catches with distance from transect origin, based on the France 2021 model. (transect origin = Site A, Ardenne forest; see Table 2 for model details). Solid line = mean model predictions; grey ribbon = 95% confidence intervals; arrow (↑) = shortest distance to English coastline from site A (265 km). Model includes French data only; points denote both French (FRA) and English (GB-ENG) raw trap catch data from the collection periods specified, where at least one beetle was trapped. The *x*-intercept is the distance at which the model-predicted trap catch = 1

2021 followed by considerably lower abundance (Table 1); the slope of the fitted model also varied by collection period (Table 2, Fig. 3). The French data were best described by a negative binomial distribution which allowed for zero inflation (more zeroes than would be expected within the fitted distribution), varying by collection period; the English data were best described by a Poisson distribution. Proximity to conifer woodland strongly increased beetle numbers collected in England (Table 2). This was most apparent at the 2021 spruce woodland site #16, which collected 75% of the 665 beetles trapped in England in that year (Table 1, site #16 data not included in the analysis), and further illustrated by 2021 site #7, located adjacent to a mixed woodland, which collected twice as many beetles (57 in total) as any other 'open-country' site.

In June 2021, the French model predicted that the mean distance from Site A at which a single trap would catch at least one beetle was 427 km (Table 3); the English coastline is ~265 km from site A, well within this predicted dispersal distance. For the other 2021 collection periods, the mean predicted distances for catching at least one beetle were slightly below 265 km, but with upper confidence limits suggesting that some beetles should still be caught in England, although in lesser numbers. The model predictions thus correlate well with the actual catches seen in England; many more beetles were caught in June, very few in July

**Table 3** Model-predicted distance from transect origin (2021: site A; 2022: midpoint of sites A and R) at which one beetle would be caught per trap, with 95% lower and upper confidence limits (LCL and UCL)

| Collection | Mean (km) | LCL | UCL |
|---|---|---|---|
| June-21* | 427 | 321 | 735 |
| July-21 | 259 | 215 | 315 |
| Aug-21 | 249 | 195 | 380 |
| Sep-21 | 245 | 174 | 591 |
| May-22* | 290 | 244 | 375 |
| Jun-22 | 213 | 188 | 252 |
| Jul-22* | 300 | 247 | 408 |
| Aug-22* | 303 | 244 | 439 |
| Sep-22 | 206 | 169 | 284 |

Collection periods for which the mean distances exceed 265 km in 2021, and 283 km in 2022 (the shortest distance from the source point of the transects to the English coastline), are indicated (*), suggesting a high likelihood of dispersing beetles reaching England

and August, and none at all in September when numbers collected in France were lowest (Table S1; Fig. 3).

## 2021 Dispersal: suitability of meteorological conditions for dispersal across the channel

Dispersing *Ips typographus* were first collected in traps in southern England in late May/early June 2021 (Table 1). This relatively late dispersal flight reflects a prolonged and cool spring that year, in which daytime temperatures only rose above the flight threshold temperature of *I. typographus* (16.5 °C; Wermelinger 2004) for the first time at the end of May (Fig. 4). Coincident with the rising temperatures, the prevailing wind direction shifted, so that from approximately 28 May through 2 June it blew from a direction suitable for cross-channel dispersal from the Continent (Fig. 4). *Ips typographus* adults were observed landing on English coastal traps during the 3 June collection, and the great majority of individuals were trapped during the following collection period (to 16 June) including at every French site and at 18 of the 20 English sites (Table 1, Fig. 3).

## 2022 Dispersal: linear modelling of beetle trap catches

In 2022, more beetles were again caught closer to the Ardenne forests (midpoint between Sites A and R) on all transects (French, Belgian and English), and the number of beetles caught varied with collection date (Table 2, Fig. 5). The slope of the fitted model varied by collection date in Belgium and France, but not in England ($X^2 = 1.15$, df = 2, $p = 0.56$, maximal model (all explanatory factors included) for England, 2022) (Table 2). Country (Belgium or France) did not affect beetle catches ($X^2 = 0.04$, df = 1, $p = 0.84$, maximal model for Belgium and France, 2022), suggesting similar numbers were caught in both (sites A and B (France) collected > 13,000 beetles, and R and T (Belgium) collected > 9000). In England, proximity to conifer forest did not influence trap catches ($X^2 = 0.93$, df = 2, $p = 0.34$, maximal model for England, 2022); in 2022, all sites were selected to be close to coniferous woodland (Table 2). As in 2021, the continental data were best described by a negative binomial distribution, and the English data were best described by a Poisson distribution.

In 2022, the French/Belgian model predicted that the mean trap catch at the English coastline would be greater than one beetle in May, July and August (Table 3). As in 2021, these Continental model predictions correlate strongly with the catches seen in England, with more beetles caught in the English traps in these months (Table 1, Fig. 5). In 2022, beetles were collected in English sites 6–22 only, typically in small numbers (mean 3.5 beetles per 'positive' site), with 108 beetles collected in total.

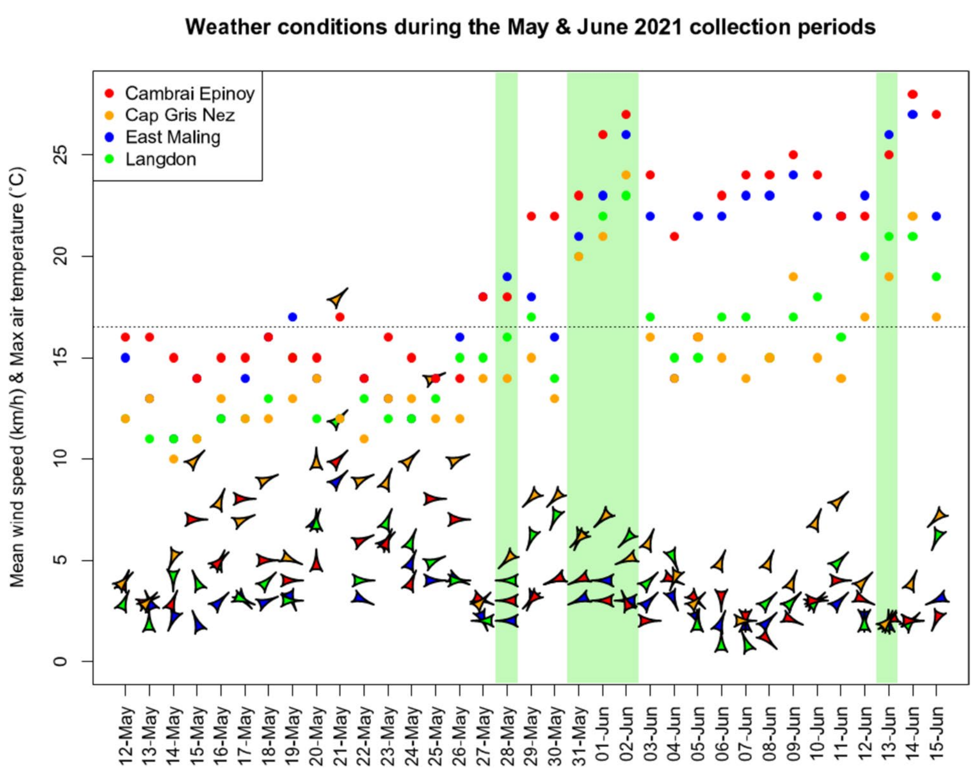


**Fig. 4** Daytime weather conditions (10.00—19.00) at coastal (Cap Gris Nez and Langdon) and inland (Cambrai Epinoy and East Malling) weather stations in England and France during the May–June 2021 collection periods. Daytime maximum temperatures are presented, and prevailing wind direction is displayed by directional arrows ('*north up*') with mean wind speed (km/hour). The dotted line indicates the minimum flight threshold temperature of *Ips typographus*. A green background indicates dates at which the prevailing wind direction and daytime temperature appeared suitable for cross-channel dispersal from northern France and Belgium to the Kent coast (Meteociel 2023)

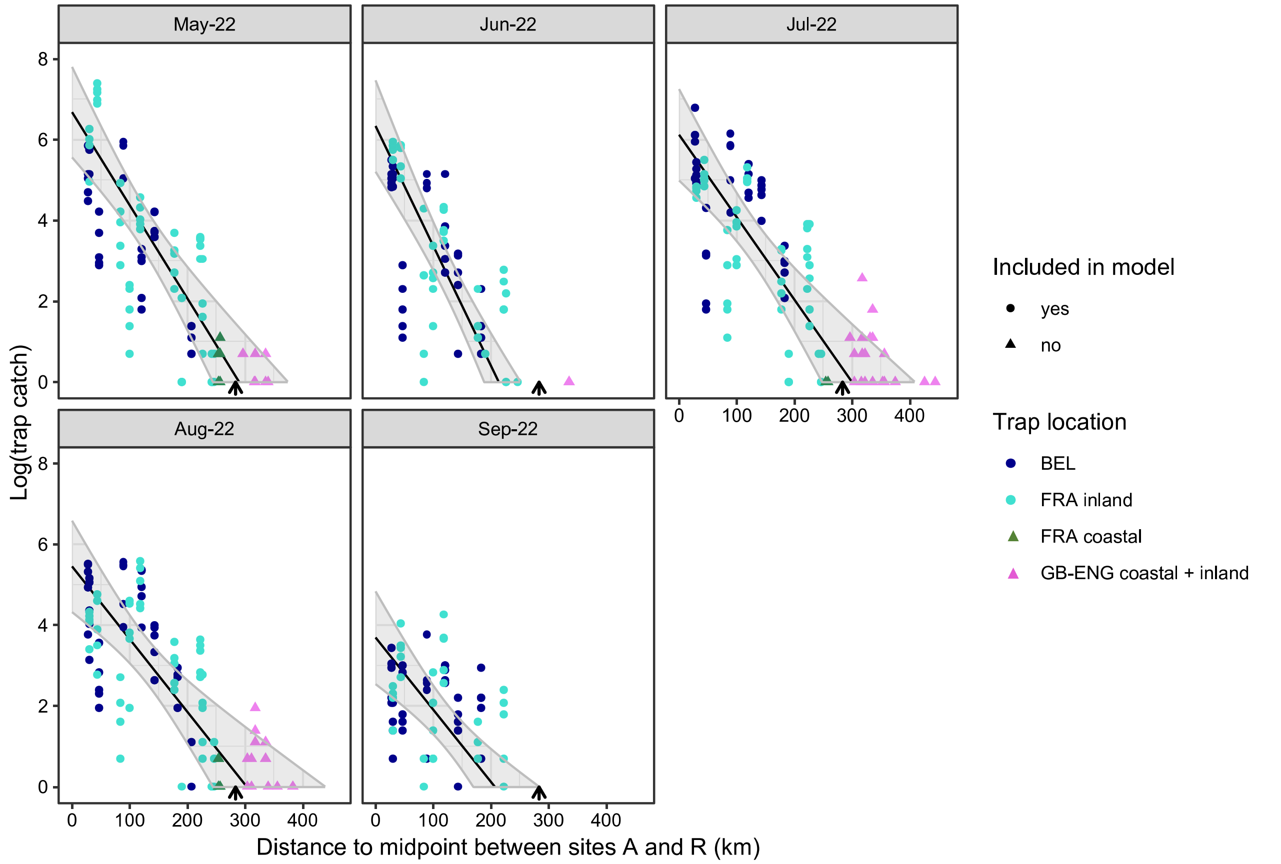


**Fig. 5** Predictions of trap catches with distance from transect origin, based on the France/Belgium 2022 model. (transect origin = midpoint of sites A and R, Ardenne forest; see Table 2 for model details). Solid line = mean model predictions; grey ribbon = 95% confidence intervals; arrow (↑) = shortest distance to English coastline from midpoint between site A and site R (283 km). Model includes French and Belgian data only; points denote French (FRA), Belgian (BEL) and English (GB-ENG) raw trap data from the collection periods specified, where at least one beetle was trapped. The *x*-intercept is the distance at which the model-predicted trap catch = 1

### 2022 Dispersal: suitability of meteorological conditions for dispersal across the channel

Weather conditions (wind and temperature) were assessed as suitable for cross-channel dispersal for several days in each of these three collection periods; wind direction appeared particularly suitable in August (Fig. 6).

## Discussion

### Evidence of cross-channel dispersal

This study provides the first evidence that the highly damaging bark beetle *Ips typographus* can naturally disperse across the English channel from continental Europe and indicates that this is the likely pathway for numerous new incursions (localised breeding populations) of this pest recently detected in southern England. Adult *I. typographus* have been collected annually since 2019 in pheromone traps across Kent and neighbouring counties as part of a monitoring programme of spruce woodlands in England (Blake et al. 2024), but the origin of those individuals was initially uncertain, and only one population of the pest (undergoing eradication, Blake et al 2024) had been found prior to 2021. By trapping beetles simultaneously on both sides of the channel, coincident with suitable weather conditions and a large-scale dispersal event in June 2021 centred on the Ardenne region, we may be confident that dispersal has occurred across the channel. Simultaneous detections of *I. typographus* were also made at this time across southeast England by the monitoring programme (Blake et al. 2024). Since June 2021, at least 27 individual incursions of *I. typographus* have been detected in Kent, Sussex and Surrey (Defra 2023a) as small and isolated populations exhibiting one or more breeding galleries on Norway spruce trees (typically windthrown or snapped tops). Based on the extent and age of gallery formation, all incursions were concluded to have been initiated during the same June 2021 dispersal period. Eradication measures have been applied to each incursion detected,

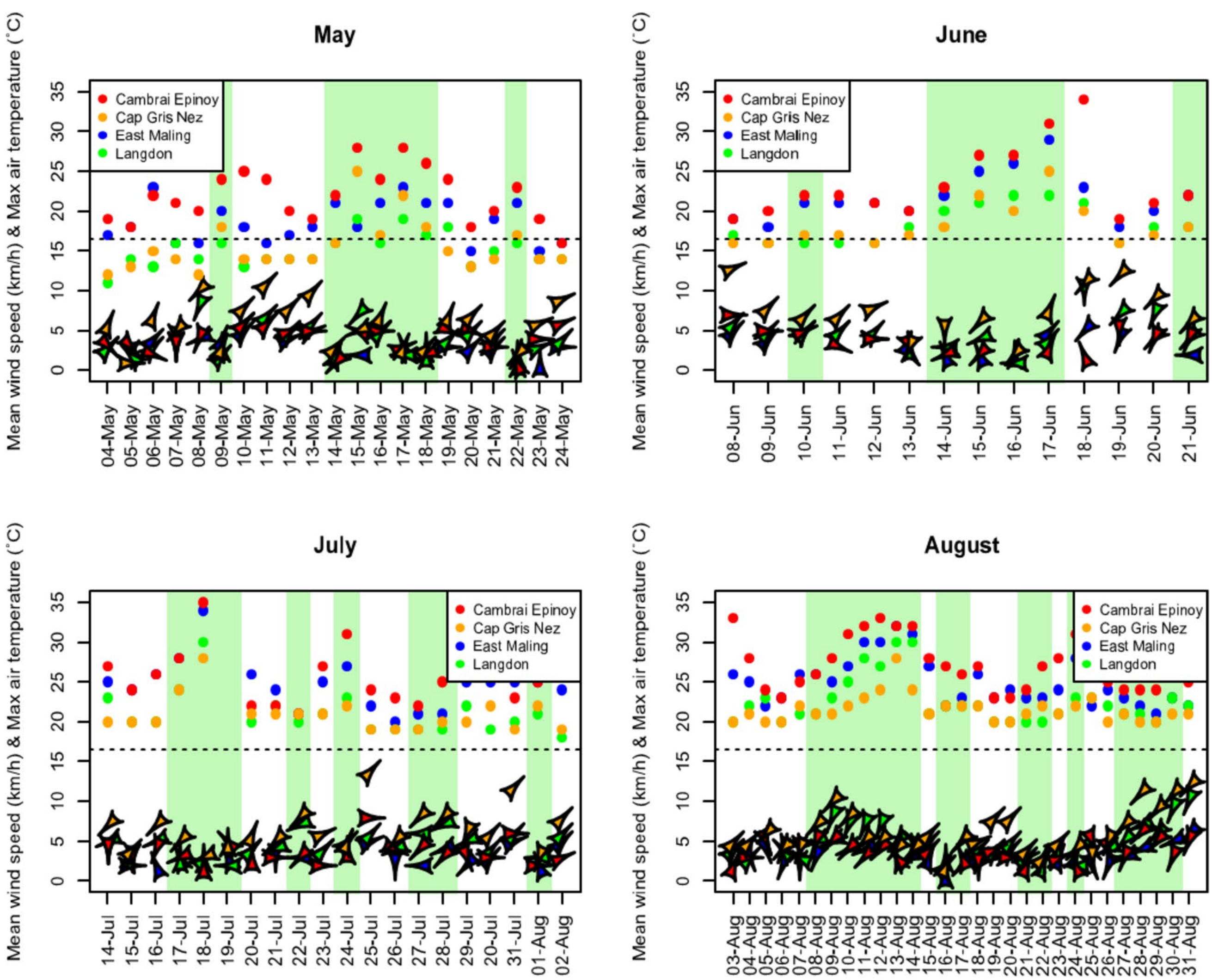


**Fig. 6** Daytime weather conditions (10.00–19.00) at coastal (Cap Gris Nez and Langdon) and inland (Cambrai Epinoy and East Malling) weather stations in France and England during the May–August 2022 collection periods. Daytime maximum temperatures are presented, and prevailing wind direction is displayed by directional arrows ('north up') with mean wind speed (km/hour). The dotted line indicates the minimum flight threshold temperature of *Ips typographus*. A green background indicates dates at which the prevailing wind direction and daytime temperature appeared suitable for cross-channel dispersal from northern France and Belgium to the Kent coast (Meteociel 2023)

requiring considerable resources. It is noteworthy that only 5 days were assessed as suitable for dispersal during that critical period (Fig. 4), and that a longer window of opportunity might have led to even more localised establishments.

The number of beetles dispersing into England in June 2021 appears to have been especially high, driven by a long cold spring resulting in a tight synchrony of beetle flight, exceptionally large populations in northern France and Belgium, and favourable wind conditions, and is evidenced by the observed gradient of abundance from the Ardenne to England. There is good agreement between the predictive modelling generated by the continental data and the observed trap catches in England, and it suggests additional cross-channel dispersal occurred later in 2021 and throughout summer 2022, albeit at a reduced scale. A small number of the beetles trapped in England in 2022 may however be offspring of individuals that established in 2021, although no incursions were detected within at least 5 km of the trapping sites.

*Ips typographus* therefore seems able to disperse over considerably longer distances than have been previously recorded. Modelling suggests the beetle population could have dispersed over 400 km in June 2021, potentially allowing beetles to penetrate hundreds of km into central England (Table 3), although the channel could be expected to act as a filter, reducing numbers that ultimately arrived in England. This risk is reflected in the northward's expansion of the *Ips typographus* demarcated area, based on captures by wider environment traps (Defra 2023a). Movement over such distances would certainly require wind assistance, potentially by lofting insects to higher altitudes, or perhaps by a step-like progression of insects over a few days. The wind measurements used in this study are recorded at 10 m above ground level, but wind movements above the lowest atmospheric surface layer might display very different patterns. Dispersal by *I. typographus* has been considered to typically occur over short distances, with few individuals recorded flying more than around 500 m (e.g. Wichmann and Ravn 2001; Kautz et al. 2011). Long distance dispersal by bark beetles has proved difficult to quantify, though migration of around 43 km has been previously recorded (Nilssen 1984). Forsse and Solbreck (1985) calculated that some 10% of *I. typographus* individuals flew above the forest canopy and measured in a flight mill that some of them can fly for 2 h or more. Such individuals would be potentially available to be semi-passively carried by the wind over long distances.

The better fit of a negative binomial distribution, rather than a Poisson distribution, to the French and Belgian data is indicative of more variable trap catches there than in England. Local contributions to the pool of dispersing bark beetles from the eastern part of Belgium and France may be contributing to continental catches, as opposed to in England, where the individuals arriving from the continent would become more diluted at increasing distances.

## Mechanisms of long-distance dispersal

Robust evidence demonstrating the dispersal of insects across the barrier of the English channel remains limited, although the agricultural pest *Autographa gamma* (silver Y moth) undoubtedly utilises high-level airstreams to colonise the UK each spring (Chapman et al. 2012). Considering that trillions of insects are taken by the wind at high altitude (Hu et al. 2016), such rarely studied events are likely to be more common than suspected. Modelling of atmospheric conditions associated with the arrival of the invasive Harlequin ladybird, *Harmonia axyridis* (Siljamo et al. 2020) and the *Culicoides* midge vectors of Bluetongue animal disease virus (Burgin et al. 2017) indicates that air temperature, wind direction and wind speed were likely important in assisting their dispersal across the channel, as seems to be the case for *I. typographus*. Atmospheric trajectory analyses have been recently performed to demonstrate that *Spodoptera frugiperda* (fall armyworm) which arrived in Africa in 2016 could potentially use high-altitude air currents to move from North Africa to Europe (EFSA et al. 2018). This damaging crop pest has now been detected in Greece for the first time (EPPO 2023).

*Ips typographus* is readily moved in infested spruce material and is one of the most intercepted pests worldwide. Turner et al. (2021) record 727 interceptions of *I. typographus* between 1995 and 2019 at entry points across the world, making it the 8th most intercepted Scolytinae. Ward et al. (2022) report 505 interceptions between 1914 and 2008 at ports in 22 US states. It could be argued that the establishment of breeding populations in England validates the link proposed between 'propagule pressure' (as reflected by the frequency of such interceptions) and the successful establishment of a non-native pest (Brockerhoff et al. 2014). Propagule pressure is broadly defined as a measure of the number of non-native individuals introduced to a new area (e.g. via an infested shipment) and the number of such introduction events (Lockwood et al. 2005). Yet the extremely high interception rates of *I. typographus* contrast with a total absence of recorded establishments in all these areas, including until recently, Britain.

The failure of *I. typographus* to establish has been attributed to Allee effects, including a requirement for aggregation and a sufficiently large number of individuals to overcome the resistance of live host trees (Pureswaran et al. 2022; Ward et al. 2022). Yet field observations tell us that at low population densities, *I. typographus* would rather attack fallen trees than standing trees (Kausrud et al. 2011), and we also know that single females can establish a new brood on their own (Dacquin et al. 2023), a phenomenon which may be a factor in the recent incursions in England. Therefore, invoking propagule pressure and Allee thresholds necessary to overcome a living tree could be insufficient, and a closer look at these factors could provide useful insights. Rather than considering propagule size and number, beetle density or flow between the source and the recipient area might be a suitable metric to quantify propagule pressure for Britain. A similar example of wind-assisted long-distance dispersal was seen during a period of huge population expansion of mountain pine beetle *Dendroctonus ponderosae* (MPB), which successfully dispersed over the Rocky Mountains (de la Giroday et al. 2012) and was measured by Jackson et al. (2008) using an aerial drogue net. They calculated a mean density of 4,950 (18,600 maximum) beetles/ha, flying up to 800 m above the canopy and covering 30–110 km/day. The local density of *I. typographus* flying in a clearcut area has been estimated to be as high as 9000 individuals/ha in Sweden (Byers et al. 1989; Byers 1996), using passive sticky traps. The likely flow over the channel hypothesised here remains to be measured, however a 'rain' (sensu Simberloff 2009) of incoming beetles that could consolidate an attack on suitable host material appears to be the most likely scenario explaining how *I. typographus* established a breeding population in southern England. The very large dispersal distances recorded and modelled in this study must be intimately linked to the enormous source populations of the beetle (e.g. Hlásny et al. 2021). Outbreaks in southern Belgium and northeast France, the likely source region of the beetle, have killed over 23,600 ha of spruce forest between

2017 and 2022 (Gilles et al. 2023 preprint). Even a very small proportion of long-distance dispersers amongst such enormous *I. typographus* populations as are currently present in continental European forests would represent a large potential pool to take advantage of wind-assisted spread. Formal proof of *I. typographus* dispersal over the English channel might be provided by employing different methods with variable efficacy. The aerial capture technique used for MPB (Jackson et al. 2008) could be replicated, and though the dilution effect along the dispersal pathway would make this challenging, an understanding of the density and altitude reached by beetles above an outbreak area would be informative for modelling wind-assisted dispersal. Genetic analysis of the English incursions is underway (de Becquevort et al. in prep), but resolution may be limited by the weak population structure of *I. typographus* (even over several hundred km), due to its high dispersal capacity (Ellerstrand et al. 2022). This also proved a limiting factor for initial analyses of stable isotopes. A recent study on *I. typographus* using a Scheimpflug lidar offers new prospects for the long-distance detection of beetles flying at high altitude (Li et al. 2021). This could complement the use of the meteorological or entomological radars used so far (Jackson et al 2008; Chapman et al. 2012).

### Implications of cross-channel dispersal by a damaging pest

Critically, this study illustrates that the geographical isolation of the British Isles is unlikely to protect it from further establishments of *I. typographus*. This has important implications regarding Britain's Pest Free Area status and policy for managing both the pest and its spruce forests. A key objective is to prevent the permanent establishment and spread of *I. typographus*, particularly to major spruce-growing areas in Wales, northern England and Scotland. The scale of future incursions is likely to vary according to the size of the European source populations, the prevailing wind direction during the main periods of dispersal, and the presence and abundance of susceptible *Picea* in southern England. An early warning system for future large-scale dispersal events might be developed based on these factors, and this study demonstrates the advantages of coordinated trapping on either side of the channel. The surveillance programme in Britain would benefit from linking with monitoring work conducted on the Continent (e.g. DSF 2022). Wider knowledge of population size, flight activity, and prevailing weather conditions could be used to predict high risk periods for Britain and validated through the surveillance trapping. In addition, encouraging rapid removal of susceptible material (such as recent wind-throw and felled timber), and localised sanitation felling (with emphasis on poor-growing or water-stressed stands) are important elements of a longer-term strategy to manage *I. typographus* in Britain. The severity and scale of *I. typographus* outbreaks across central Europe provide a worrying backdrop to the detections of the beetle in Britain, so that a shift away from planting and growing spruce in southern England is now being considered.

Strikingly, most of the other non-native forest pests to have recently invaded Britain also first established in south-east England, presumably assisted by warmer summer temperatures prevalent there, and correlated with the large human population. Assumed pathways of introduction into this region include movement with imported plants for planting (e.g. eggs of oak processionary moth *Thaumetopoea processionea*; Townsend 2013), in wood products (e.g. Asian longhorn beetle *Anoplophora glabripennis* and the ambrosia beetles *Xylosandrus germanus* and *Gnathotrichus materiarius*; Straw et al. 2015, Inward 2020), and even transportation by vehicle (e.g. horse-chestnut leaf miner *Cameraria ohridella* either as free adults or pupae in leaves; Straw and Bellett-Travers 2004). However, the findings of this study suggest that aerial dispersal should also be considered as a pathway for insect pests. For example, recent detections including Oriental chestnut gall wasp *Dryocosmus kuriphilus* and Colorado potato beetle *Leptinotarsa decemlineata* (Defra 2023b) may both have resulted from the natural spread of European populations (e.g. Hurst 1970). The relatively cool British summer climate, rather than the barrier of the channel, may have precluded the establishment of many thermophilic insects in the past, but this protection may be eroding under the increasingly warm summers being observed in England (Met Office and climate series 2023). Horizon scanning for other plant pests which might aerially disperse across the channel would seem a valuable exercise to inform UK plant health policy and surveillance strategies.

## Author contributions

JCG, DI and EC conceived and designed the study. EC, DI, JCG, KB and SH Conducted the fieldwork, and EC and KB made identifications. KR analysed the data. DI, JCG and KR wrote the manuscript, and all authors read and approved it. Daegan J.G. Inward, Emilio Caiti are joint lead authors.

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**Data availability** The datasets generated during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to declare.

**Ethical approval** This article does not contain any studies with human participants or vertebrates performed by any of the authors.



## References

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bevan D, King CJ (1983) *Dendroctonus micans* Kug. - a new pest of spruce in the UK. Commonw for Rev 62:41–51

Blake M, Straw N, Kendall T, Whitham T, Manea A, Inward D, Jones B, Hazlitt N, Ockenden A, Deol A, Brown A, Ransom E, Smith L, Facey S (2024) Recent outbreaks of the spruce bark beetle Ips typographus in the UK: discovery, management, and implications. Trees for People. https://doi.org/10.1016/j.tfp.2024.100508

Brockerhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. Ecol 95:594–601. https://doi.org/10.1890/13-0465.1

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. https://doi.org/10.32614/RJ-2017-066

Brus DJ, Hengeveld GM, Walvoort DJ, Goedhart PW, Heidema AH, Nabuurs GJ, Gunia K (2011) Statistical mapping of tree species over Europe. Eur J Res 131:145–157. https://doi.org/10.1007/s10342-011-0513-5

Burgin L, Ekström M, Dessai S (2017) Combining dispersion modelling with synoptic patterns to understand the wind-borne transport into the UK of the bluetongue disease vector. Int J Biometeorol 61:1233–1245. https://doi.org/10.1007/s00484-016-1301-1

Byers JA (1996) An encounter rate model of bark beetle populations searching at random for susceptible host trees. Ecol Model 91:57–66. https://doi.org/10.1016/0304-3800(95)00166-2

Byers JA, Anderbrant O, Löqvist J (1989) Effective attraction radius: a method for comparing species attractants and determining densities of flying insects. J Chem Ecol 15:749–765. https://doi.org/10.1007/BF01014716

Caudullo G, Tinner W, de Rigo D (2016) *Picea abies* in Europe: distribution, habitat, usage and threats. In: de Rigo D, Caudullo G, Houston Durrant T, Mauri A, San-Miguel-Ayanz J (eds) European atlas of forest tree species. Publications Office of the European Union, Luxembourg, pp 114–116

Chapman JW, Bell JR, Burgin LE, Reynolds DR, Pettersson LB, Hill JK, Bonsall MB, Thomas JA (2012) Seasonal migration to high latitudes results in major reproductive benefits in an insect. Proc Natl Acad Sci 109:14924–14929. https://doi.org/10.1073/pnas.1207255109

Dacquin P, Caiti E, Grégoire JC, Aron S (2023) Preemergence mating, inbreeding, and their consequences in the bark beetle *Ips typographus*. J Pest Sci. https://doi.org/10.1007/s10340-023-01650-4

de la Giroday HMC, Carroll AL, Aukema BH (2012) Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. J Biogeogr 39:1112–1123. https://doi.org/10.1111/j.1365-2699.2011.02673.x

Defra (2023a) Pest risk analysis for *Ips typographus*. https://planthealthportal.defra.gov.uk/data/pests/16019/data Accessed 24 Jan 2024

Defra (2023b) Colorado potato beetle larvae confirmed in Kent. https://www.gov.uk/government/news/colorado-potato-beetle-larvae-confirmed-in-kent Accessed 24 Jan 2024

Dourojeanni MJ (1971) Catalogue des Coléoptères de Belgique , fasc. V, 100-101: catalogue raisonné des Scolytidae et Platypodidae. Société Royale d'Entomologie de Belgique, Bruxelles (BE)

DSF (2022) Département de la Santé des Forêts (France). Crise scolytes sur épicéas. Quel est le bilan, fin 2021? https://agriculture.gouv.fr/crise-scolytes-sur-epiceas-quel-est-le-bilan-fin-2021 Accessed 24 Jan 2024

EFSA (2018) EFSA PLH Panel (EFSA Panel on Plant Health), Jeger M, Bragard C, Caffier D, Candresse T, Chatzivassiliou E, Dehnen-Schmutz K, Gilioli G, Gregoire J-C, Jaques Miret JA, Navarro MN, Niere B, Parnell S, Potting R, Rafoss T, Rossi V, Urek G, Van Bruggen A, Van der Werf W, West J, Winter S, Day R, Early R, Hruska A, Nagoshi R, Gardi C, Mosbach-Schultz O, MacLeod A (2018) Scientific Opinion on the pest risk assessment of *Spodoptera frugiperda* for the European Union. EFSA J 16(8):5351

Ellerstrand SJ, Choudhury S, Svensson K, Andersson MN, Kirkeby C, Powell D, Schlyter F, Jönsson AM, Brydegaard M, Hansson B, Runemark A (2022) Weak population genetic structure in Eurasian spruce bark beetle over large regional scales in Sweden. Ecol Evol 12(7):e9078. https://doi.org/10.1002/ece3.9078

EPPO (2023) EPPO reporting service no. 10 Paris, 2023–10

Fielding N, Evans B, Burgess R, Evans H (1994) Protected Zone surveys in Great Britain for *Ips typographus, I. amitinus, I. duplicatus* and *Dendroctonus micans*. Research Information Note 253, Forestry Commission

Fielding NJ, Evans HF (1997) Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain. Biocontrol News Inf 18:51–60

Forest Research (2023) Forestry statistics 2023. https://www.forestresearch.gov.uk/tools-and-resources/statistics/forestry-statistics/ Accessed 24 Jan 2024

Forestry Commission (2018) Importing wood, wood products and bark. Forestry Commission Plant Health Guide. Forestry Commission, Edinburgh

Forsse E, Solbreck CH (1985) Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. J Appl Entomol 100:47–57. https://doi.org/10.1111/j.1439-0418.1985.tb02756.x

Fox J, Weisberg S (2019) An {R} Companion to Applied Regression, 3rd edn. https://socialsciences.mcmaster.ca/jfox/Books/Companion/ Accessed 24 Jan 2024

Franklin A, Grégoire JC (1999) Flight behaviour of *Ips typographus* L. (Col., Scolytidae) in an environment without pheromones. Ann Sci for 56:591–598. https://doi.org/10.1051/forest:19990706

Franklin A, Debruyne C, Grégoire JC (2000) Recapture of *Ips typographus* (Col., Scolytidae) with attractants of low release rates:

localized dispersion and environmental influences. Agric for Entomol 2:259–270. https://doi.org/10.1046/j.1461-9563.2000.00075.x

Gilles A, Lisein J, Cansell J, Latte N, Piedallu C, Claessens, H (2023) Evolution of the bark beetle crisis in spruce (Picea abies) forests: a spatial and temporal remote sensing analysis in Belgium and North-eastern France. Preprint: https://doi.org/10.21203/rs.3.rs-3051830/v1 Accessed 24 Jan 2024

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6, https://CRAN.R-project.org/package=DHARMa Accessed 24 Jan 2024

Hlásny T, König L, Krokene P, Lindner M, Montagné-Huck C, Müller J, Qin H, Raffa KF, Schelhaas MJ, Svoboda M, Viiri H (2021) Bark beetle outbreaks in Europe: State of knowledge and ways forward for management. Curr for Rep 7:138–165. https://doi.org/10.1007/s40725-021-00142-x

Hu G, Lim KS, Horvitz N, Clark SJ, Reynolds DR, Sapir N, Chapman JW (2016) Mass seasonal bioflows of high-flying insect migrants. Science 354(6319):1584–1587. https://doi.org/10.1126/science.aah4379

Hurst GW (1970) Can the Colorado potato beetle fly from France to England? Entomol Mon Mag 105:1265–1267

Inward DJ (2020) Three new species of ambrosia beetles established in Great Britain illustrate unresolved risks from imported wood. J Pest Sci 93:117–126. https://doi.org/10.1007/s10340-019-01137-1

Jackson PL, Straussfogel D, Lindgren BS, Mitchell S, Murphy B (2008) Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. Can J for Res 38:2313–2327. https://doi.org/10.1139/X08-066

Kausrud KL, Grégoire JC, Skarpaas O, Erbilgin N, Gilbert M, Økland B, Stenseth NC (2011) Trees wanted—dead or alive! Host selection and population dynamics in tree-killing bark beetles. PLoS ONE 6(5):e18274. https://doi.org/10.1371/journal.pone.0018274

Kausrud K, Økland B, Skarpaas O, Grégoire JC, Erbilgin N, Stenseth NC (2012) Population dynamics in changing environments: the case of an eruptive forest pest species. Bio Rev 87:34–51. https://doi.org/10.1111/j.1469-185X.2011.00183.x

Kautz M, Dworschak K, Gruppe A, Schopf R (2011) Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. For Ecol Manag 262:598–608. https://doi.org/10.1016/j.foreco.2011.04.023

Komonen A, Schroeder LM, Weslien J (2011) *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. J Appl Entomol 135:132–141. https://doi.org/10.1111/j.1439-0418.2010.01520.x

Lenth R (2022) Emmeans: estimated marginal means, aka least-squares means. R package version 1.8.3, https://CRAN.R-project.org/package=emmeans Accessed 24 Jan 2024

Li M, Jansson S, Runemark A, Peterson J, Kirkeby CT, Jönsson AM, Brydegaard M (2021) Bark beetles as lidar targets and prospects of photonic surveillance. J Biophotonics 14:e202000420. https://doi.org/10.1002/jbio.202000420

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228. https://doi.org/10.1016/j.tree.2005.02.004

Mayer F, Piel FB, Cassel-Lundhagen A, Kirichenko N, Grumiau L, Økland B, Bertheau C, Grégoire J-C, Mardulyn P (2015) Comparative multilocus phylogeography of two Palaearctic spruce bark beetles: influence of contrasting ecological strategies on genetic variation. Mol Ecol 24:1292–1310. https://doi.org/10.1111/mec.13104

Met Office UK climate series (2023) Hadley Centre Central England Temperature (HadCET) dataset. https://www.metoffice.gov.uk/hadobs/hadcet/ Accessed 24 Jan 2024

Meteociel (2023) Historic data for average wind conditions recorded at weather stations in France and neighbouring countries, www.meteociel.fr

Meurisse N, Couillien D, Grégoire JC (2008) Kairomones traps: a tool for monitoring the invasive spruce bark beetle, Dendroctonus micans (Coleoptera: Scolytinae) and its specific predator, *Rhizophagus grandis* (Coleoptera: Monotomidae. J Appl Ecol 45:537–548. https://doi.org/10.1111/j.1365-2664.2007.01423.x

Mezei P, Jakuš R, Pennerstorfer J, Havašová M, Škvarenina J, Ferenčík J, Slivinský J, Bičárová S, Bilčík D, Blaženec M, Netherer S (2017) Storms, temperature maxima and the Eurasian spruce bark beetle *Ips typographus*—An infernal trio in Norway spruce forests of the Central European High Tatra Mountains. Agric for Meteorol 242:85–95. https://doi.org/10.1016/j.agrformet.2017.04.004

Netherer S, Hammerbacher A (2022) The Eurasian spruce bark beetle in a warming climate: Phenology, behavior, and biotic interactions. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier Academic Press, London, pp 89–131. https://doi.org/10.1016/B978-0-12-822145-7.00011-8

Netherer S, Panassiti B, Pennerstorfer J, Matthews B (2019) Acute drought is an important driver of bark beetle infestation in Austrian Norway spruce stands. Front for Glob Change 2:39. https://doi.org/10.3389/ffgc.2019.00039

Nilssen AC (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Ann Ento Fenn 50:37–42

Piel F, Gilbert M, Franklin A, Grégoire JC (2005) Occurrence of *Ips typographus* (Col., Scolytidae) along an urbanization gradient in Brussels. Belgium Agric for Entomol 7:161–167. https://doi.org/10.1111/j.1461-9555.2005.00262.x

Plant Health England (2019) The Plant Health (*Ips typographus*) (England) Order 2019. https://www.legislation.gov.uk/uksi/2019/40/pdfs/uksi_20190040_en.pdf Accessed 24 Jan 2024

Pureswaran DS, Meurisse N, Rassati D, Liebhold AM, Faccoli M (2022) Climate change and invasions by non-native bark and ambrosia beetles. In: Gandhi KJK, Hofsetter RW (eds) Bark Beetle Management, Ecology, and Climate Change. Academic Press, Elsevier, London, pp 3–30. https://doi.org/10.1016/B978-0-12-822145-7.00002-7

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Scheepers D, Eloy MC, Briquet M (1997) Use of RAPD patterns for clone verification and in studying provenance relationships in Norway spruce (*Picea abies*). Theor Appl Genet 94:480–485

Siljamo P, Ashbrook K, Comont RF, Skjøth CA (2020) Do atmospheric events explain the arrival of an invasive ladybird (*Harmonia axyridis*) in the UK? PLoS ONE 15:e0219335. https://doi.org/10.1371/journal.pone.0219335

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Soetaert K (2021) Shape: functions for plotting graphical shapes, colors. R package version 1.4.6, https://CRAN.R-project.org/package=shape Accessed 24 Jan 2024

Straw NA, Bellett-Travers M (2004) Impact and management of the horse chestnut leaf-miner (*Cameraria ohridella*). Arboric J 28:67–83. https://doi.org/10.1080/03071375.2004.9747402

Straw NA, Fielding NJ, Tilbury C, Williams DT, Inward D (2015) Host plant selection and resource utilisation by Asian longhorn beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in southern England. Forestry 88:84–95. https://doi.org/10.1093/forestry/cpu037

Taberlet P, Fumagalli L, Wust-Saucy AG, Cosson JF (1998) Comparative phylogeography and postglacial colonization routes in

Europe. Mol Ecol 7:453–464. https://doi.org/10.1046/j.1365-294x.1998.00289.x

Taylor CM, Hastings A (2005) Allee effects in biological invasions. Ecol Lett 8:895–908. https://doi.org/10.1111/j.1461-0248.2005.00787.x

Townsend M (2013) Oak processionary moth in the United Kingdom. Outlooks Pest Manag 24:32–38. https://doi.org/10.1564/v24_feb_10

Trubin A, Mezei P, Zabihi K, Surový P, Jakuš R (2022) Northernmost European spruce bark beetle *Ips typographus* outbreak: modelling tree mortality using remote sensing and climate data. For Ecol Manag 505:119829. https://doi.org/10.1016/j.foreco.2021.119829

Turner RM, Brockerhoff EG, Bertelsmeier C, Blake RE, Caton B, James A, MacLeod A, Nahrung HF, Pawson SM, Plank MJ, Pureswaran DS, Seebens H, Yamanaka T, Liebhold AM (2021) Worldwide border interceptions provide a window into human-mediated global insect movement. Ecol Appl 31:e02412. https://doi.org/10.1002/eap.2412

Ward SF, Brockerhoff EG, Turner RM, Yamanaka T, Marini L, Fei S, Liebhold AM (2022) Prevalence and drivers of a tree-killing bark beetle, *Ips typographus* (Coleoptera, Scolytinae), in international invasion pathways into the USA. J Pest Sci 96:845–856. https://doi.org/10.1007/s10340-022-01559-4

Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. For Ecol Manag 202:67–82. https://doi.org/10.1016/j.foreco.2004.07.018

Wichmann L, Ravn HP (2001) The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. For Ecol Manag 148:31–39. https://doi.org/10.1016/S0378-1127(00)00477-1

Winter TG (1985) Is *Ips typographus* (Linnaeus) (Coleoptera:Scolytidae) a British insect? Entomol Gaz 36:153–160