Range expansion of the small spruce bark beetle *Ips amitinus*: a newcomer in northern Europe

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Abstract

1 *Ips amitinus* arrived in Northern Europe at the beginning of 1900s, although its recent expansions to the northernmost conifers have been rapid.

2 Analyses of recent records, MaxEnt models and regional population size estimates are used to discuss its peculiar range shifts and potential as a forest pest in Northern Europe.

3 *Ips amitinus* was probably absent in northern glacial refugia for Norway spruce in the Russian plain and northward expansions from its glacial refugia in the Central European mountains may have been slowed down by: (i) ecological barriers of post-glacial dry plains and bogs in Central Europe; (ii) heavy utilization of conifers; and (iii) Allee effects as a result of fragmented forests and an unfavourable climate for a cold-adapted species in the continental lowlands.

4 MaxEnt models predict that *I. amitinus* may become widespread in the Northern European forests, whereas its populations in the southernmost mountain ranges of Europe may decline in the future.

5 The population levels of *I. amitinus* in recently invaded northern areas are still lower than those in core areas of Central Europe, although the population development in Central Europe indicates that future bark beetle outbreak periods may boost the *I. amitinus* populations in Northern Europe as well.

Keywords climate change, Curculionidae, maximum entropy, *Picea*, *Pinus*, range shift, Scolytinae, species interaction.

Introduction

The range shifts of several forest insect pests in recent decades not only call for explanations, but also raise concerns about the potential consequences of such range changes (Musolin & Saulich, 2012; Jepsen *et al.*, 2013; Burke & Carroll, 2016). Range expansions may provide insect pests access to new pools of forest resources, and it may be a challenge to predict the outcome when such invaders have not co-evolved with their new forest environment (Erbilgin *et al.*, 2014; Cooke & Carroll, 2017; Rosenberger *et al.*, 2017). The concern is especially justified for pest species with significant impacts on ecosystems and communities, such as epidemic bark beetles that can affect large areas of boreal and temperate forests (Raffa *et al.*, 2008, Økland *et al.*, 2011). Understanding the mechanisms behind range shifts may be critical with respect to managing species invasions and their resulting impacts.

Each case of range shift appears to comprise a characteristic story depending on interactions between the features of the

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species' biology, climate and invaded environments. In North America, for example, two of the most serious bark beetle pests have undergone significant range shifts, although their stories are different. For the cold-intolerant southern pine beetle (*Dendroctonus frontalis* Zimmermann), northward expansions in the Northeastern U.S.A. have often been explained by warmer winters rather than lack of suitable hosts, even though the susceptibility of the northern forest stands vary with stand structure and forest type (Aoki *et al.*, 2018). Climate is also involved in the expansions of the mountain pine beetle in North America (*Dendroctonus ponderosae* Hopkins) (Raffa *et al.*, 2015) but, for this species, the traits and responses of naïve host pine species during its eastward expansions have also been a major topic of investigation (Erbilgin *et al.*, 2014; Burke & Carroll, 2016).

The most damaging bark beetle in Europe, the spruce bark beetle *Ips typographus* (L.), has been present in the whole distribution range of its main host Norway spruce *Picea abies* (L.) for millenia (see Discussion), although a high population density and epidemic outbreaks have been reported increasingly towards north during the recent decades (Aakala *et al.*, 2011; Økland *et al.*, 2011). Among other European *Ips* species (Stauffer *et al.*, 1997), the larch bark beetle *Ips cembrae* (Heer) is native to Europe and is recognized mainly as a pest of larch (*Larix* spp.) and occasionally of pine (*Pinus* spp.) and spruce (*Picea* spp.) (EFSA PLH, 2017a). It has been expanding its geographical range in western and Northern Europe during the second half of the 20th Century, including its first observations in Britain in 1955, the Netherlands in 1974, Belgium in 2005 and Sweden in 2011 (Lindelöw *et al.*, 2015; EFSA PLH, 2017a). The double-spined bark beetle *Ips duplicatus* (Sahlberg) is mainly associated with spruce species, although it can also infest species of pine and larch (CABI, 2018). This bark beetle is retracting its wide range in the north of European and Siberian taiga, whereas it is extending southwards from its natural range (Lekander *et al.*, 1977; Grodzki, 2003; Vakula *et al.*, 2007; Holuša *et al.*, 2010; Olenici *et al.*, 2010). It is considered to be a newcomer in some parts of Central Europe, where spreading and outbreaks have been observed from the 1990s onward (Vakula *et al.*, 2015; CABI, 2018). *Ips mannsfeldi* (Wachtl, 1879) is distributed on black pine (*Pinus nigra* J.F Arnold) and Scots pine (*Pinus sylvestris* L.) in Central and South Europe, and this species is expanding its range in Turkey (Sarikaya *et al.*, 2018). Furthermore, outbreaks of *Ips acuminatus* (Gyllenhal) have been recently observed both in Swiss and Italian Alps and in southern Finland, comprising areas where outbreaks have not previously been recorded (Colombari *et al.*, 2013; Siitonen, 2014).

In the present study, we focus on the range shift of the small spruce bark beetle *Ips amitinus* (Eichhoff, 1871) in Europe. This bark beetle is mostly a secondary species, although it co-occurs with other bark beetle species (*e.g. I. typographus*) and participates in bark beetle outbreaks in the mountain ranges of Central (Stolina, 1969; Postner, 1974; Stauffer & Zuber, 1998; Zach *et al.*, 2010), Southeast and Southern Europe (Jurc & Bojović, 2004; Ribič, 2007). The peculiar story of this species is that it arrived in Northern Europe much later than its close relative *I. typographus*, which is a native species throughout the distribution area of Norway spruce in Northern Europe. Subsequently, it has exhibited a fast expansion all the way to the northernmost conifer forests in Europe during the few last decades.

We describe and analyze the recent expansion of *I. amitinus* in Northern Europe and, by comparison with its biology and forest environment, we suggest hypotheses to explain the pattern of its northward expansions. We use the current range and population records of *I. amitinus* to predict its potential distribution and severity as a forest pest in Northern Europe under both current and future climates.

Materials and methods

The focal species

Ips amitinus is one of seven *Ips* species in Europe (Stauffer *et al.*, 1997). In a genetic re-examination, it was concluded that *I. amitinus* var. *montana* (Coleoptera, Scolytidae) is synonymous to *I. amitinus* (Stauffer & Zuber, 1998). *Ips amitinus* is mostly a secondary pest species associated with dying coniferous trees, such as *Picea abies* and Serbian spruce *Picea omorica* (Panz.) Purk., although it can also develop in Swiss pine *Pinus cembra* L., dwarf mountain pine *Pinus mugo* Turra, Macedonian pine *Pinus peuce* Grieseb., Scots pine *Pinus sylvestris* L. and other pine species (Pfeffer, 1995). Some of the northern records of *I. amitinus* by M. Yu. Mandelshtam during the last decades in Arkhangelsk Oblast and the Republic of Karelia were from Scots pine only, even when Norway spruce were found nearby. In Central Europe, it is clustered within the *I. typographus* group as a result of its positive interspecific association with *I. typographus* and *Pityogenes chalcographus* (L) under endemic conditions (Jakuš, 1995; Stauffer *et al.*, 1997) and the activity of these three species together can result in decline of whole stands (Witrylak, 2008). The larval gallery has three to seven mother tunnels and is clearly distinguished from that of *I. typographus* (Postner, 1974) and, similar to *I. typographus*, it transfers pathogens, as well as intestinal nematodes and endoparasitoids, and transports phoretic mites (Lukášová *et al.*, 2013; Zach *et al.*, 2016). *Ips amitinus* usually colonizes the upper parts of spruce trunks, with snapped trees being attacked in the first year, and then uprooted trees in the second year after wind disturbance (Jakuš, 1998). In younger stands (21–40 years), it can attack the entire length of the trunk and may be more abundant than *I. typographus* (Witrylak, 2008). Roubal (1937–1941) describes *I. amitinus* as an abundant mountain species, where it can be dominant locally and even without the co-occurrence of *I. typographus*. According to Pfeffer (1955), *I. amitinus* is relatively more abundant towards higher elevations up to the tree line. It has one generation in the mountain forests of the West Carpathians (Pfeffer, 1954, 1955; Witrylak, 2008), whereas two generations occur at altitudes below 600 m a.s.l. (Holuša *et al.*, 2012). In Finland, the adults of *I. amitinus* appear to overwinter in soil and not under bark of logs and standing trees (Annila & Nuorteva, 1976). The biology of *I. amitinus* is sometimes considered as similar to *I. typographus* (Pfeffer, 1955; Zumr, 1982), although there are many gaps in the knowledge regarding its biology and ecology (Witrylak, 2008).

Plotting of expansion

The expansions of *I. amitinus* in Estonia, Finland, Russia and Sweden were plotted for each decade in the period 1970–2017
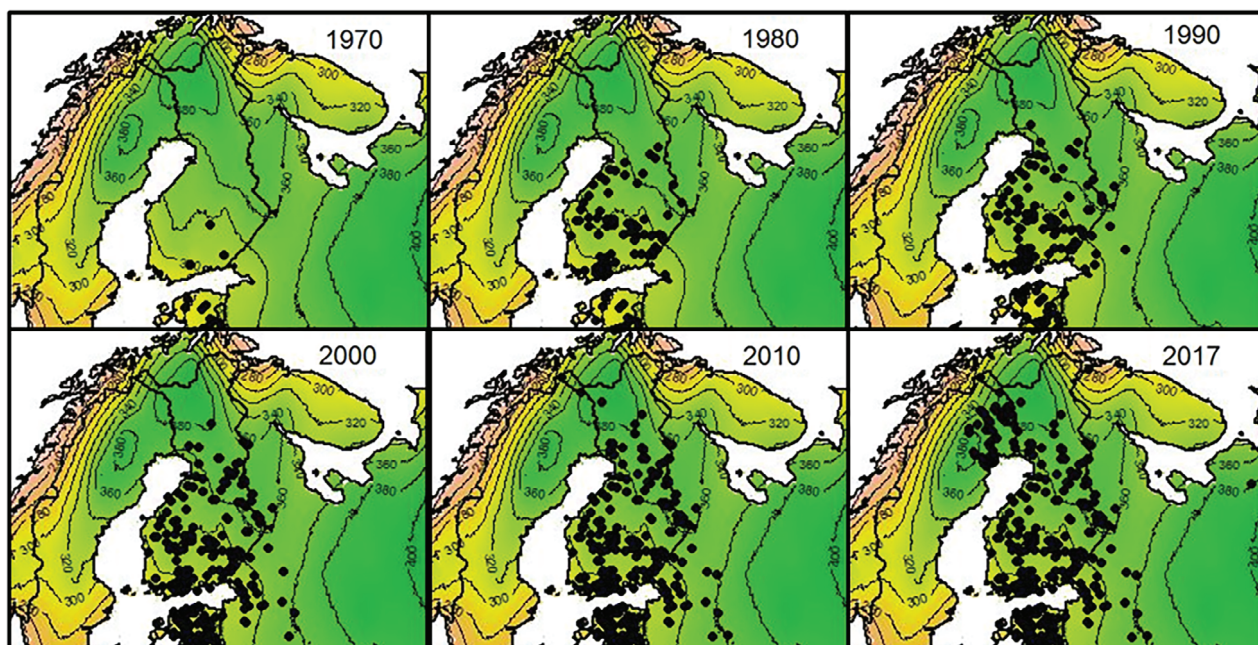
Figure 1 Distribution of *Ips amitinus* records in the Nordic countries in each of the last decades from 1970 onward, based on the data from Estonia, Finland, Russia and Sweden. Isoclines show the degree of climatic continentality (i.e. annual range of temperature derived from the temperature of the coldest and warmest months; BIO7: www.worldclim.org/bioclim).

(Fig. 1). Data for these plots were compiled from databases (Finnish Expert Group on Coleoptera), the literature and unpublished records, which were identified and checked by experts (see Supporting information, Appendix S1). Data for these sources mostly derive from the reported findings of collectors and are only exceptionally based on systematic search, such as an inventory organized by the Swedish University of Agricultural Sciences in northern Sweden in 2017 (see Supporting information, Appendix S1). The plots were made as accumulated plots of records up to indicated periods to illustrate the total expansion of the species (Fig. 1). Plots of only records for individual years and periods were not used because the data based on unsystematic sampling would not be sufficient to reveal the real spread or retractions for each year or period. Furthermore, we expect that retractions from newly expanded localities in the north as a result of winter mortality are rare because *I. amitinus* appears to be a cold-adapted species (see Discussion), and its overwintering adults are probably protected from low winter temperatures in soil under insulating snow (Annila & Nuorteva, 1976). We included isoclines for the degree of climatic continentality (i.e. annual range of temperature derived from the temperature of the coldest and warmest month) using the package Contour in R (R Core Team, 2017) and temperature data downloaded from Worldclim (2018).

We plotted the yearly maximum distance (*Maxdist*) from entry point to the farthest *I. amitinus* record in Finland (Fig. 2A) and these plots were also made as accumulated plots for the same reasons as described above. We used nonparametric statistics (Spearman's ρ) to determine how *Maxdist* was correlated with the yearly number of sites of bark beetle records in Finland in the database of the Finnish Expert Group on Coleoptera (*bbsiteF*), which is considered to be a proxy for sampling intensity in each

of the years of the study period. Spearman's ρ was also used for the correlation between *Maxdist* and yearly summer temperature of Finland [*tempFt* = mean temperatures (°C) of the months May to August].

We also plotted statistics of coniferous forest for the surrounding 100×100 km of the farthest records plotted in each year. The statistics comprised percentage cover of coniferous forest and the volumes (m^3) of pine and spruce per 100×100 km and the latitudes used in the plots were based on epsg projection 2393 (Fig. 2C,D). All forests statistics were downloaded in GeoTIFF file format from the Luke file service for publicly available data (http://kartta.metla.fi/index-en.html) and gridded to a cell size of 100×100 km. All plots were made in R (R Core Team, 2017) and each plot included either a linear trend line (Fig. 2A) or a trend line based on a cubic smoothing spline using the function smooth.spline in R (Fig. 2C,D).

Species distribution modelling

The maximum-entropy approach (MaxEnt) was chosen to model the potential distribution (Phillips *et al.*, 2004, 2006; Phillips *et al.*, 2018) of *I. amitinus* because it has been shown to outperform other species distribution modelling methods and can handle presence only data (Elith *et al.*, 2006). MAXENT, version 3.4.1, was run in R (R Core Team, 2017) using the dismo package (Hijmans *et al.*, 2017). Background samples were drawn from the whole extent of the environmental space of Europe because the whole area is within dispersal distance of *I. amitinus* and contains environmental conditions that could be distinguished. We ran MAXENT with only linear, quadratic and threshold features because this is recommended with respect to producing a more interpretable model. Manual forward selection
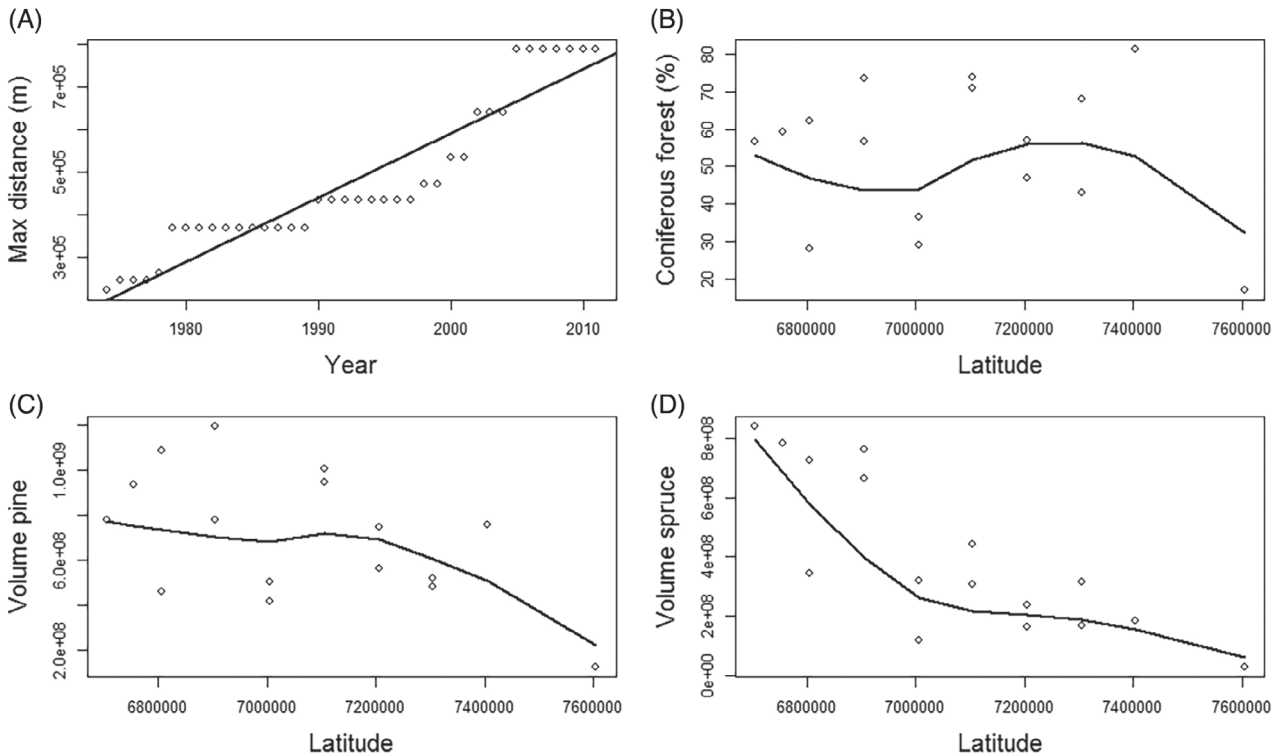
Figure 2 The yearly maximum distance from entry point to the farthest *Ips amitinus* record in Finland (A), as well as percentage cover of coniferous forest (B), volume (m³) of pine (C) and spruce (D) in the surrounding 100 km × 100 km of the farthest records in each year plotted by latitude (epsg:2393).

of explanatory variables was performed and the area under the receiver operating characteristic curve was used to evaluate the performance of the individual models. Ten-fold cross-validation was chosen as replicate runs, because it utilizes the data more efficiently.

Ips amitinus presence data in the MaxEnt analyses were compiled from databases (Finnish Expert Group on Coleoptera and Global Biodiversity Information Facility), the literature and unpublished records (see Supporting information, Appendix S1) and prepared for the model runs in R using the dismo package. Presence data were finally corrected for sampling bias by random subsampling.

Twelve environmental covariates were chosen in accordance with our knowledge of bark beetle biology and, based on downloaded climate data sets of both current and future climates, these were considered in the MaxEnt model runs: Precipitation of warmest quarter (the total precipitation during the warmest 3 months of the year in mm); precipitation for the individual months of May, June, July and August (total monthly precipitation for each month, mm); minimum temperature of coldest month (January, °C); mean temperature of the warmest quarter (3 months, °C); temperature for the individual months of May, June, July and August (maximum temperature of each month, °C); and continentality (maximum temperature of the warmest month minus minimum temperature of the coldest month, °C). All data sets were based on a spatial resolution of approximately 1 km² and were downloaded from the Worldclim database (WorldClim, 2018), including Global climate data (Hijmans *et al.*, 2005) of current conditions (average for

1961–1990) and projected future climate according to the Max Planck Institute Earth System Model (MPI-ESM-LR) (http://worldclim.org/CMIP5_30s) and greenhouse gas concentration pathways RCP85 for the year 2050 (average for 2041–2060). We do not have access to datasets of windfelling storm events; however, this factor is probably most relevant for the abundances of *I. amitinus* and might be less important for predicting the presence/absence by MaxEnt and the long-term distribution of *I. amitinus* at a large scale.

Population sizes in northern Europe versus core areas in Central Europe

The MaxEnt predictions were used to localize the current optimal areas for *I. amitinus* in Europe. Using available data from databases (see Supporting information, Appendix S1), we compared captures of *I. amitinus* during the last 2–3 decades in unbaited window traps between the optimal area of Finland and the Western Carpathians Mountains, which is the optimal area of Central Europe closest to the northern expansion. We included only captures in transparent unbaited window trap from coniferous forests containing Norway spruce and/or Scots pine within these optimal areas. There is no commercially available efficient pheromone bait for *I. amitinus*, and unbaited traps enabled us to calculate the relative abundance of *I. amitinus* compared with other bark beetle species. The trapping area in Finland was limited to the mainland to the south and west of Kuopio (longitude 27.679338, latitude 62.893335), which, in the MaxEnt model, appeared as the current optimal area for *I. amitinus* in Finland,

and the trap data were obtained from the period 1991–2016 in the database of the Finnish Expert Group on Coleoptera. In Western Carpathians Mountains, the captures included unbaited transparent window traps from Velická dolina (1460 m a.s.l.), Tichá dolina, Tomanová dolina and Bielovodská dolina in the period 2004–2017, which was divided into a non-epidemic period (2004) and an epidemic period (2005–2017). More details of the datasets are provided in the Supporting information (Appendix S1). The captures of *I. amitinus* were compared between these areas either as abundance (i.e. number of *I. amitinus* individuals per window trap) or relative abundance (i.e. number of *I. amitinus* divided by number of all bark beetles individuals per window trap). We consider the present captures of *I. amitinus* in window traps as rough indicators of population size because type of window trap and length of trapping season may vary among the many trapping localities in the data. To visualize the spatio-temporal development of abundances after wind disturbances, the yearly captures by window traps from Western Carpathians Mountains were also compared between wind-disturbed areas, partly wind-disturbed forest stands and surrounding undisturbed forest stands. All plots of yearly values and boxplots across the periods were performed in R (R Core Team, 2017).

Results

Expansion of I. amitinus in northern Europe

Ips amitinus has shown a fast northward expansion in Northern Europe during recent decades (Fig. 1). Although *I. amitinus* was recorded from Estonia at the beginning of 1900s (Mikutowicz, 1905; Leius, 1939), it was not recorded in southern Finland until the beginning of the 1950s (Nuorteva, 1956). In subsequent decades, *I. amitinus* has expanded quickly northward in Finland, Karelia and Murmansk Province of Russia (Fig. 1). In 2011, it was found at latitude 69.38523 in the Murmansk Province near Melkefoss on the border to Norway in Pasvik Nature Reserve, which is close to the northern treeline of spruce and pine in Fennoscandia (Shcherbakov *et al.*, 2013).

Ips amitinus has also been expanding eastward and westward. Eastward, it was found for the first time in St Petersburg Province (Zelenogorsk) in 1978 at approximately longitude 29.673902 (M. Yu. Mandelshtam *leg.*). In subsequent years, several new records were made towards east and into areas in Russia of an increasing degree of climatic continentality (i.e. ranging between the maximum summer and the minimum winter temperatures; Bonacina, 1923), including the Leningrad Region, the Republic of Karelia, Novgorod and the Arkhangelsk Provinces (Fig. 1; see also Supporting information, Appendix S1). Here, we report the record of *I. amitinus* at approximately latitude 64.6948 and longitude 43.3985 in Pinega in Arkhangelsk Province from 2013 (M. Yu. Mandelshtam *leg.*), which is the easternmost record of this species within Europe so far. Scots pine was reported as the host in many of the Russian records, including the easternmost record in Pinega and the northernmost record from Melkefoss.

Westward, the first record of *I. amitinus* from Sweden came in 2012 close to the border to Finland (Lindelöw, 2013). Later surveys show a southward expansion in the eastern part of northern Sweden, whereas the western part of northern Sweden was not surveyed. The latest records of *I. amitinus* in Sweden from 2017 are from approximately the same latitude as Luleå (latitude 65.584819, longitude 22.1567026), whereas it was not found during inspections of localities to the south of these records in 2017 (Fig. 1).

Regarding the range expansion in Finland, the maximum distance from the first record of *I. amitinus* in Finland to the farthest point of each year (*Maxdist*) followed approximately a linear trend line of $y = 15.2x - 298.9$ ($r^2 = 0.89$), which corresponds to an average distance of yearly expansion of 15.2 km (Fig. 2). Some years represented a leap in expansion above the trend, whereas, in other years, the maximum distance to the farthest point was below the trend. It is noted that the northernmost records are not independent of sampling intensity in each year. *Maxdist* was positively correlated (Spearman's $\rho = 0.67$) with the yearly number of sites of bark beetle records in Finland in the database of the Finnish Expert Group on Coleoptera (*bbsiteF*), which is considered to be a proxy for sampling intensity in each of the years of the study period. The northward leaps were also associated with especially warm summers in Finland because *Maxdist* was positively correlated (Spearman's $\rho = 0.58$) with the summer temperature of Finland in the current year *tempFt* [mean temperatures (°C) of the months May to August]. However, a positive correlation between *bbsiteF* and *tempFt* (Spearman's $\rho = 0.48$) may indicate that increases of *Maxdist* in the warm years could also be indirectly connected with a higher sampling intensity in the warm summers.

The yearly maximum distance from entry point did not appear to be significantly influenced by the density of coniferous forest or the relative content of Scots pine or Norway spruce in the expansion route of *I. amitinus* through Finland. We could not identify any marked change in the yearly maximum distances in the plot where *I. amitinus* entered landscapes with a different percentage cover of coniferous forest or with different proportions of pine- versus spruce-dominated forest (Fig. 2). The average volume of both spruce and pine declined towards north (Fig. 2C,D), whereas the trend of the maximum distances per year for the expansion of *I. amitinus* remained fairly constant all the way up to the northernmost localities in the last year of the time series (Fig. 2A).

Potential distribution of I. amitinus in Europe

MaxEnt models were used to predict the potential distribution of *I. amitinus* under the current climatic conditions and future climatic projections (Fig. 3). For Europe as a whole, the highest probability of distribution was found in the mountain ranges of Central, Southeast and Southern Europe, which is the native distribution area of *I. amitinus*. The Western Carpathians appear as an optimal area for *I. amitinus* in the MaxEnt predictions, which corresponds well with the strong populations found in this region (Pfeffer, 1932; Zumr, 1984). In addition, the areas around the Baltic Sea where *I. amitinus* has invaded in recent times also appear to be highly suitable for *I. amitinus*, including the Baltic states and the southern and western parts of Finland (Fig. 3A).

MaxEnt models based on the current climate showed that a large part of Scandinavia might be suitable for further expansion
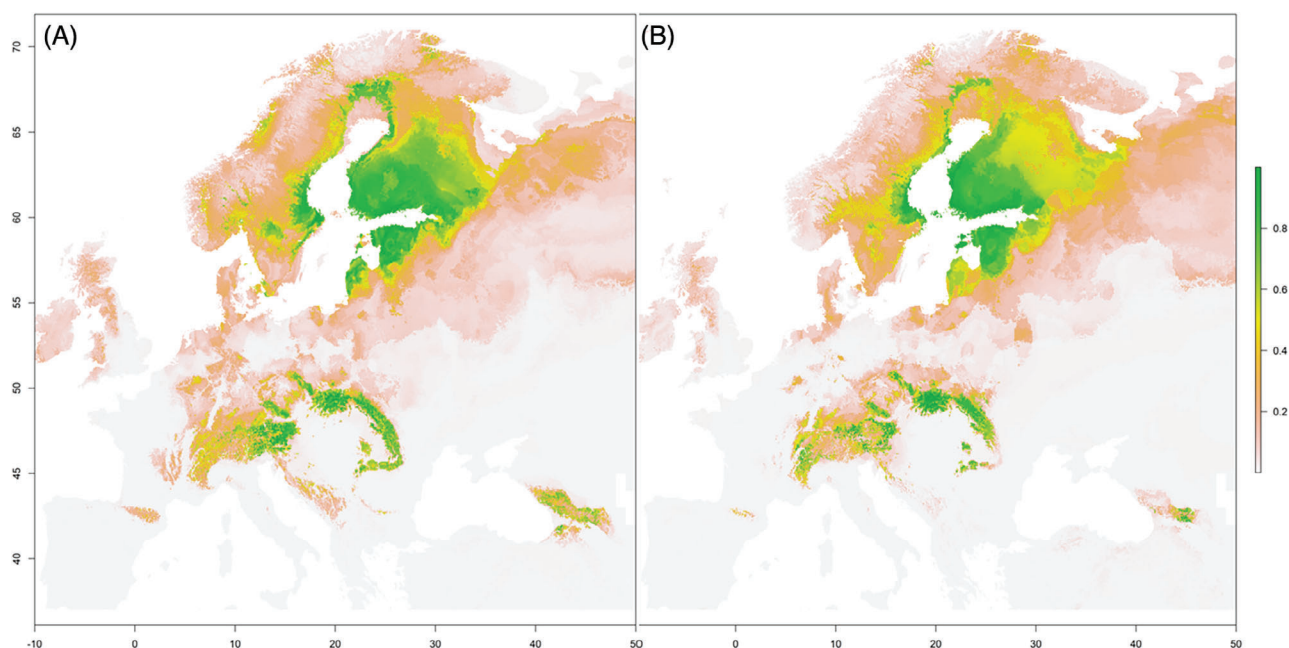
Figure 3 Potential distribution of *Ips amitinus* in Europe predicted by Maximum entropy modelling (MaxEnt). (A) Prediction based on the current climatic conditions (1961–1990). (B) Prediction based on the IPPC5 climate projections for a future climate (2081–2100) (WorldClim, 2018). The colour gradient ranging from white to dark green (scale at the right side) indicates an increasing probability of *Ips amitinus* occurrence.

of *I. amitinus* (Fig. 3A). The recent areas of expansions in northern Sweden fit well in the areas of northern Sweden with a high probability of distribution in the MaxEnt model. The predicted pattern of *I. amitinus* by MaxEnt resembles the distribution of high-density conifer forests in Northern Europe, and the conifer forests in the southern and western parts of Scandinavia also appear to be suitable for the further spread of this species in the future. The most influential set of climatic variables explaining 70.8% of the MaxEnt prediction included the mean temperatures of the three warmest months of the year, maximum temperature of July, total monthly precipitation of August and minimum temperature of January.

The MaxEnt predictions for a future climate did not deviate very strongly from the predictions for the current climate, although some differences were observed. The prediction includes a reduced potential in the western and southern parts of Europe, which might become too warm for this cold-preferring species under a warmer climate (Fig. 3). The most distinct difference was a reduction in the area of suitable habitat in the southernmost mountain ranges of Europe. The areas of colours indicating elevated distribution potential are smaller under a future climate for the mountain regions of the Pyrenees, the Dinaric Mountains, the Balkan Mountains, the Eastern and Southern Carpathians, and Caucasus (Fig. 3B). Similarly, the distribution potential appears to be reduced under a future climate in the westernmost and oceanic areas of Europe, such as Wales, Scotland, Denmark and the western coast of Scandinavia. In the northern part of Europe, there are only smaller changes with a warmer climate. The potential distribution in Estonia and in the western and southern part of Finland with the current climate remains equally high under a future climate, whereas the high potential in the western part of Latvia is slightly lower (Fig. 3B).

Population sizes in northern Europe versus core areas in Central Europe

We compared captures of *I. amitinus* in unbaited window traps between the optimal area within the Western Carpathians Mountains and the optimal area of Finland in accordance with the MaxEnt model (Fig. 3) (for details of trap data and area limitations, see Materials and methods). The population levels of *I. amitinus* in Northern Europe are generally lower than those in the core areas of Central Europe, although less involvement in bark beetle epidemics in these recently invaded areas appears to be important with respect to this difference.

The abundance of *I. amitinus* was relatively low in both areas under non-epidemic conditions (Fig. 4A). The mean and median values of abundance were clearly higher in the Western Carpathians Mountains (median = 1; mean = 4.67) compared with Finland (median = 0; mean = 1.35) and the difference was significant (Exact Wilcoxon–Mann–Whitney test, $Z = -1.85$, $P = 0.04$).

Also, the relative abundance of *I. amitinus* (the abundance of *I. amitinus* divided by the abundance of all bark beetles captured per trap) in the same non-epidemic conditions was significantly higher in the Western Carpathians Mountains (median = 0.0075; mean = 0.007) compared with Finland (median = 0; mean = 0.0016) (Exact Wilcoxon–Mann–Whitney test, $Z = -2.564$, $P = 0.0085$) (Fig. 4B).

The relative population levels of *I. amitinus* vary greatly over time in both areas (Fig. 4C,D). The levels observed by window traps during non-epidemic conditions in Finland (Fig. 4C) were generally much lower than those observed during a period of epidemic population development in the Western Carpathians Mountains (Fig. 4D). The time series from Finland is remarkably
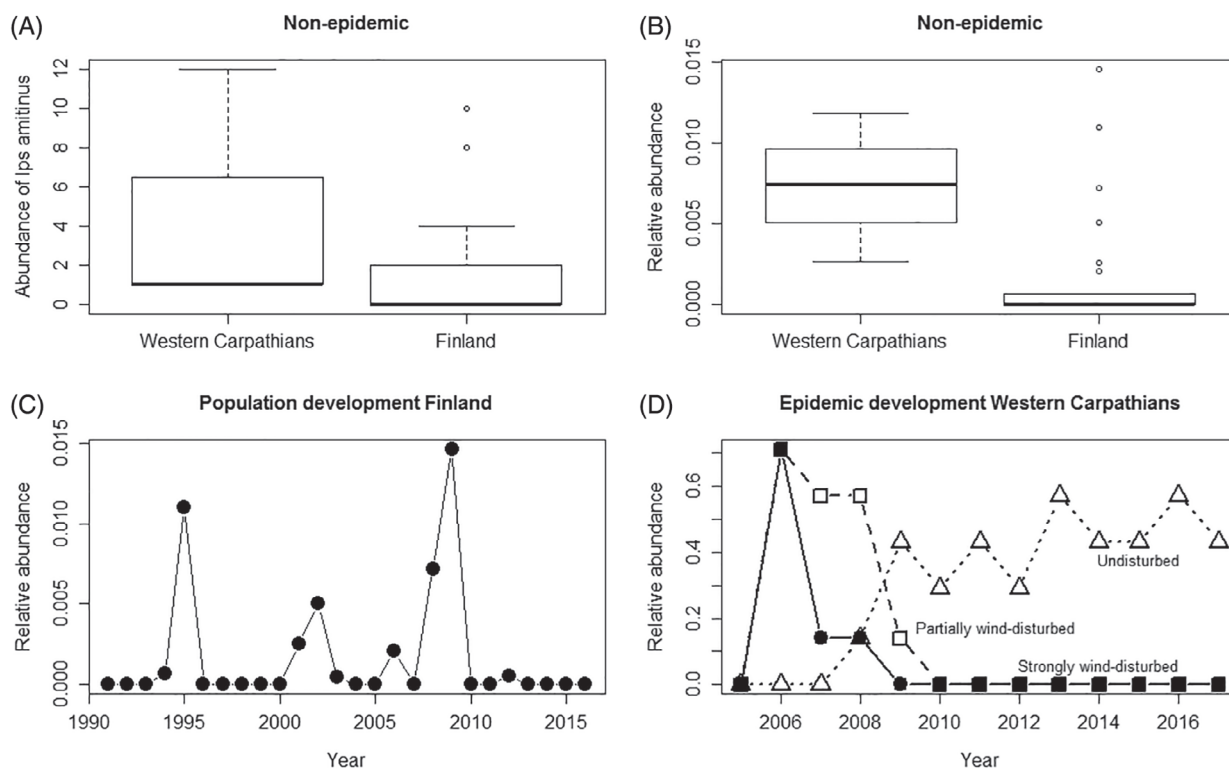
Figure 4 Comparison of *Ips amitinus* population levels between optimal areas in Finland and optimal areas in the Western Carpathian Mountains in Slovakia under non-epidemic conditions (A, B) and time series of population development in the same areas (C, D). All estimated values were based on captures by unbaited window traps. (A) Comparison based on abundance (number of *I. amitinus* per window trap). (B) Comparison based on relative abundance (number of *I. amitinus* divided by number of all bark beetles individuals per window trap). (C) The relative abundance plotted per year in the period 1991–2016 in optimal areas of Finland. (D) The relative abundance plotted per year during an epidemic period (2005–2017) in optimal areas in the Western Carpathian Mountains. The relative abundance of *I. amitinus* per window trap increases first in the wind-disturbed (filled circles) and partly wind-disturbed forest stands (squares) and later in the surrounding undisturbed forest stands (triangles). The central lines of the box-and-whiskers plots (A, B) show the median, the box indicates lower and upper quartiles, and the whiskers show the largest and smallest observations that fall within a distance of 1.5 times the box size from the nearest quartile.

irregular, including some years with much higher relative abundances (Fig. 4C). However, it should be noted that many window traps contained zero *I. amitinus* individuals and that the population levels of this species may be under-estimated during non-epidemic periods. The relative occurrences (the fraction of traps including *I. amitinus*) in the total trap material from the Western Carpathians Mountains were strongly correlated with the abundances of *I. amitinus* (Spearman's $\rho = 0.997$), which implies that the likelihood of capturing *I. amitinus* in unbaited window traps (random catches) is very low in non-epidemic periods compared with epidemic periods.

The high captures in the Western Carpathians Mountains are found, however, where suitable breeding materials are spatially aggregated (Fig. 4D). With the characteristic dynamics of the epidemics in this region, the peak of the population abundances tends to move to the forest stands with the highest access to suitable breeding material available at a certain time. During the initial years after wind disturbance, the highest abundances and relative occurrences of *I. amitinus* (i.e. the proportion of traps where *I. amitinus* was found) were recorded in the strongly disturbed forest stands with a large amount of fallen spruce trees suitable for the breeding of *I. amitinus* (solid line and filled

circles in Fig. 4D). When these habitats became unsuitable for the breeding of bark beetles after few years as a result of a lack of food resources, *I. amitinus* adults colonized susceptible trees in the less disturbed forest stands in the surroundings of the windfall calamity. During this phase, the abundances and relative occurrences of *I. amitinus* increased in the partly disturbed (dashed line and squares) and undisturbed forest stands (dotted line and triangles in Fig. 4D).

Discussion

The analyses performed in the present study demonstrate that the distribution and range shift of *I. amitinus* differ from those of other *Ips* species in Europe. The biology and appearance of *I. amitinus* are in many ways very similar to those of its close relative *I. typographus*, except for some differences. For example, *I. amitinus* can utilize both dominant conifers in Northern Europe, Norway spruce and Scots pine, whereas *I. typographus* is mainly associated with Norway spruce and rarely attacks Scots pine. On this background, it may appear puzzling that *I. amitinus* is invading Northern Europe so late compared with *I. typographus*, which is native and widespread in

most European spruce forest regions. Records of *I. typographus* in Oslo date from 1025–1075 (Kenward, 1988) and extensive outbreaks of this species are reported from Northern Germany (Gmelin, 1787) and Scandinavia (Reventlow, 1811) in the 1700s. By contrast, *I. amitinus* was recorded in Finland for the first time in the 1950s (Nuorteva, 1956) and it has just recently started the invasion of Scandinavia and the northern part of European Russia. In Fennoscandia, *I. typographus* is considered to be a native spruce-associated species, whereas *I. amitinus* has been considered as an alien invasive species as a result of its late invasion. It is regulated in Greece and, in the U.K. and Ireland, both *I. amitinus* and *I. typographus* are regulated (EPPO, 2017; EFSA PLH, 2017b). A limited flight capability does not appear to be the reason for the late northward expansion of *I. amitinus* in Europe because this species is a stronger flier. In flight mill tests, on average, *I. amitinus* flew much longer than *I. typographus* or *Ips sexdentatus* (Börner, 1776) (Forsse, 1989), which are two species that are known to fly long distances (Piel *et al.*, 2005).

A difference in glacial refugia may have hindered an early expansion of *I. amitinus* in North Europe. It is unknown when *I. typographus* reinvaded Scandinavia after the last glaciation, although genetic studies by Mayer *et al.* (2015) indicate that it followed Norway spruce coming into Finland (6000–3000 BP) and later into Scandinavia (3000–2000 BP) along a northern route from glacial refugia of Norway spruce in the Russian plain (Tollefsrud *et al.*, 2008). *Ips amitinus* could not follow this invasion because it most probably was not present in these glacial refugia (as it invaded Russia only recently). The other glacial refugia for spruce were located in the Central European mountains (Tollefsrud *et al.*, 2008) where *I. amitinus* should have been present. However, the northward post-glacial expansion of spruce was hindered by the dry plains of Central and Southeast Europe, including the Hungarian Plain, and the bogs of Polesia (Latałowa & van der Knaap, 2006; Tollefsrud *et al.*, 2008), and this ecological barrier probably hindered *I. amitinus* from reaching Fennoscandia during post-glacial expansions of spruce from the glacial spruce refugia in the Central European mountains. Scots pine, the second host tree of *I. amitinus*, appears to have immigrated into northern Fennoscandia from refugia in Russia and southern Sweden from refugia in Central Europe (Naydenov *et al.*, 2007; Buchovska *et al.*, 2013). Because *I. amitinus* was not present in Russia, it could not follow the northern immigration of Scots pine to Fennoscandia. However, *I. amitinus* might have been present in the Central European refugia of Scots pine but, obviously, it did not follow the early immigration of Scots pine northwards for unknown reasons.

Because *I. amitinus* has been able to reach Northern Europe, the question arises as to why it did not happen earlier than in the 20th Century? Apparently, the northward expansion through the northern part of Central Europe has been relatively slow because the earliest records from Estonia are from the beginning of the 1900s (Mikutowics, 1905). One explanation for this may be that the coniferous forests in the northern part of Central Europe have been discontinuous and too scattered for the spread of *I. amitinus*. In Central Europe, deforestation as a result of agriculture was significant already by 300 BC, and the strong increase of the human population starting from the Middle Ages resulted in an increased pressure on forests and a very limited distribution of coniferous forests (Kaplan *et al.*, 2009).

As an example, Scots pine, which was widespread during the early to mid-Holocene, became extirpated in Ireland, Wales, England, Denmark, Belgium and The Netherlands (Huntley & Birks, 1983). From 1750 to 1850, deforestation reduced the forest area in Europe by 190 000 km^2 and, in addition, unmanaged forests were dominated by deciduous trees and managed by coppice forestry with deciduous trees (Naudts 2016). In the mid-19th Century, the increasing use of fossil fuels for energy and, subsequently, agricultural intensification halted net deforestation and even reverted the trend. Between 1750 and 2010, the forest area increased by 10% and, more importantly, the proportion of conifers increased from 30% to 57% (Naudts *et al.*, 2016). Furthermore, the proportion of the managed high stands increased from 36% to 72% of the forest area, unmanaged stands (often dominated by deciduous trees) decreased from 37% to 14% and coppice forestry decreased from 27% to 14% (Naudts *et al.*, 2016). All of these changes have strongly increased the habitat for *I. amitinus* and thus also the possibility of natural spread in Europe.

A low proportion of spruce in the landscapes may also have disfavoured the population development and the northward spread of *I. amitinus* in the Polish lowlands. In a comparative study of host preference from northern Sweden, *I. amitinus* was on average approximately twice as common on Norway spruce compared with Scots pine (D. Cocos, M. Schroeder and Å. Lindelöw, unpublished data) and several studies from Poland and neighbouring countries describe Norway spruce as the main host of *I. amitinus* (Witrylak, 2008). Furthermore, spruce is associated with outbreaks of *I. typographus* that enhance the populations of *I. amitinus* (Fig. 4D) (Økland *et al.*, 2009), whereas such associations are not known for pine. Large areas of forests in Poland, Germany and the Baltic states grow on sandy soil and are dominated by Scots pine. However, we still do not know how low the proportion of spruce should be before it would manifest by slowing the expansion rate of *I. amitinus*. In our studies from landscapes with a high coverage of coniferous forests in Finland, we did not find any indication that a lower density of Norway spruce versus Scots pine causes a slower rate of expansion (Fig. 2). Even though the density of spruce has a steeper decline than pine along the northern expansion route of *I. amitinus* in Finland (Fig. 2C,D), the trend of the maximum distances per year for the expansion of *I. amitinus* remained fairly constant all the way up to the northernmost records in Finland. However, the density of conifers in these northern landscapes might have been too high to reveal any effects on the expansion rate.

The late northern expansion of *I. amitinus* in Europe could also be associated with its preadaptation to a cold climate. Previous studies have shown that *I. amitinus* has optima in mountain areas of Central Europe, such as the Carpathian Mountains, Sumava Mountains and the Alps, whereas this species is less frequent and less abundant at lower elevation in the same region (Pfeffer, 1932; Stolina, 1969; Postner, 1974; Zumr, 1984). Adaptations to the cold climate of mountain forests are reflected by the fact that *I. amitinus* is associated with the uppermost conifers of the Western Carpathians, such as Norway spruce (Zach *et al.*, 2010), *Pinus cembra* L. and *Pinus mugo* Turra in the timber line of the High Tatra Mountains for 2007–2012 (P. Zach, unpublished data). In southern Bohemia, both the frequency

of occurrence (relative occurrence) and average density of *I. amitinus* galleries on spruce logs increase with elevation towards the highest altitudes (Zumr, 1984) and, at high altitude in Karkonoski National Park in Poland, *I. amitinus* showed a higher frequency of occurrences than *I. typographus* (Mazur & Kuźmiński, 2013). It has been observed that *I. amitinus* may survive winter temperatures down to at least −35 °C in the north of Slovakia (J. Vakula, unpublished data). Adaptations of *I. amitinus* to the cold climate are also indicated by the outputs of the present MaxEnt models (Fig. 3). Apart from in the newly expanded northern range, the highest probability of distribution was found in the mountain ranges of Central and South Europe, including an optimum in the Western Carpathians where *I. amitinus* has strong populations (Pfeffer, 1932; Stolina, 1969), whereas a low probability of distribution was observed in the lowlands to the north of the Carpathian Mountains (Fig. 3). Thus, as opposed to *I. typographus*, the temperate continental climate in the lowlands to the north of the mountain regions of Central Europe might comprise a less favourable environment that has contributed to slowing the northward expansion of *I. amitinus* in Europe. The expansion may have remained slow until *I. amitinus* reached southern Finland and Russian Karelia, where the cool continental climate is more comparable with the cold climate of its optimal area in the mountain regions of Central Europe.

Although there are several indications showing that *I. amitinus* is adapted to a cold climate, further research is needed to find the exact mechanisms that make this species cold-adapted. One possibility is that some part of its life cycle requires low temperature for termination of winter diapause, which is a phenomenon well known in many insect species (Tauber *et al.*, 1986). For example, many species require a certain number of days with temperature below a species-specific low temperature threshold for termination of winter diapause and successful further resumption of activity (Tauber & Tauber, 1976), whereas temperatures above this threshold during diapause might have detrimental effects on individuals and populations as a result of increased winter mortality, reduced size and/or compromised life cycle synchrony (Økland, 1989).

It is likely that some form of Allee effect (i.e. a positive correlation between population size and the per-capita population growth rate) as a result of poor performance has slowed the spread of *I. amitinus* in the continental lowlands between the mountain regions of Central Europe and the Boreal region in the north of Europe. It is known that Allee effects may slow down the rates of geographical range expansion and contribute to the formation of stable range boundaries (Lewis & Kareiva, 1993; Keitt *et al.*, 2001; Walter *et al.*, 2016). Because *I. amitinus* is present throughout these continental lowlands today (EPPO, 2017), the whole area has probably not been subject to very strong Allee effect simultaneously, which would bring all populations below the critical density and disable them to replace themselves (Lewis & Kareiva, 1993). It is more likely that widespread moderate Allee effects and/or local extinctions caused by environmental fluctuations and periods of strong Allee effects have resulted in a stagnation of spread and slow northward expansion (Walter *et al.*, 2016). Several factors might have contributed to Allee effects and a stagnation of northward expansion in the past; for example, a low coverage of suitable hosts,

unfavourable climate, natural enemies and community interactions might have been unfavourable for *I. amitinus* in the lowlands (Økland *et al.*, 2009).

After entering into the region of cool continental climate (Peel *et al.*, 2016) and a high proportion of coniferous forests within Russia and Finland after the 1950s, the further northward expansion of *I. amitinus* was relatively fast, as demonstrated in the present study. In addition to the climate and forest types, the expansion was probably favoured by the intensification of forestry and a shift to large-scale clear-cutting, which started in the 1950s. The numerous open fresh clear-cuts with large amounts of logging waste and bolts of spruce and pine represented a favourable habitat for *I. amitinus* (Kacprzyk & Bednarz, 2015) and this was also the habitat where Koponen (1975, 1980) conducted his systematic sampling of this species during its expansions in Finland.

We found a fairly constant expansion rate of approximately 15.2 km/year, which is close to the estimate of 20 km/year based on the period before 1980 in Finland (Koponen, 1980). The expansion rate of *I. amitinus* is of the same magnitude as that found for another northward-expanding species in Finland, *Lymantria monacha* (L.), although, for this lymantrid species, the rate of spread is nonlinear, showing a marked increased expansion rate from the 1990s (Fält-Nardmann *et al.*, 2018). Because the winter minimum temperatures in southern Finland were significantly higher after 1990 than in the period before, this increased expansion rate is attributed to higher survival of the overwintering eggs of *L. monacha* that are laid in bark crevices (Fält-Nardmann *et al.*, 2018). However, the responses of various insect species to climate change are complex and vary depending on ecological peculiarities of species and regions (Musolin & Saulich, 2012). *Ips amitinus* appears to be less vulnerable to low winter temperatures because this species is probably protected from low winter air temperatures by overwintering in soil under insulating snow instead of under bark of logs and standing trees (Annila & Nuorteva, 1976). Thus, low winter temperatures were probably not a limiting factor for the northward expansion rate of *I. amitinus* either before or after 1990.

The results of the present study reveal a weak positive correlation between warm summers and the yearly expansion (Spearman's $\rho = 0.58$), although this would only explain the deviations from the fairly constant expansion rate of *I. amitinus*. Temperature influences different processes in the life cycle of the species and the responses of insects to the current climate change might be complex (Musolin, 2007; Musolin & Saulich, 2012) and, furthermore, high summer temperatures and low precipitation appear to have a general positive effect on the flight period and reproduction of most bark beetle species, including those adapted to cooler climate at high altitudes. However, the effect of summer temperatures on the expansion rate is uncertain because the sampling intensity was highly variable and correlated with both the variable of the yearly expansion and the yearly summer temperature.

Ips amitinus could potentially be spread by transportation of timber and wood products of conifers, although there are several indications that this is less likely compared with expansions on land. It has been speculated that *I. amitinus* could have been transported over the Gulf of Finland into Porkkala on the southern coast of Finland by timber transport after World War

II (Koponen, 1975). Alternatively, spreading on land around the Gulf of Finland is documented by spreading records along the route (Koponen, 1980; Mandelshtam, 1999; Voolma *et al.*, 2004). The interceptions of *I. amitinus* in ports of entry in Scandinavia confirm that this species could be moved by transportation of timber (Lundberg, 1995; Økland *et al.*, 2005), although none of these entries have led to establishment and a shortcut of the spreading route into Scandinavia. In general, ship transport does not appear to be an efficient way to spread bark beetles. Some bark beetle species have been frequently intercepted in ports of entry outside their native ranges without becoming established around the ports (Brockerhoff *et al.*, 2006; Haack, 2006) and this failure could be attributed to biological traits that require large numbers of individuals for the initiation of a new viable population (Liebhold & Tobin 2008). For range expansions on the continent, the relatively small deviations from constant speed of expansion in our data from Finland indicate that human-assisted spread has played a minor role compared with biological spread.

According to our MaxEnt models, a large part of Scandinavia is suitable for this species both under the present and future climates (Fig. 3). In the coming decades, we can expect that *I. amitinus* will expand southward in the eastern areas of Sweden with an especially high distribution potential according to the model predictions (Fig. 3). It may also expand into areas predicted as suitable in the south and west of Scandinavia. A north–south treeless mountain chain ranging along a long stretch of Scandinavia might influence the westward expansions of *I. amitinus*, whereas some valleys in the mountain chain containing pine forests may be the first entry points into the western side. Furthermore, *I. amitinus* was recorded in Pasvik nature reserve close to the Norwegian border on the Russian side in 2011 (Shcherbakov *et al.*, 2013) where there is no mountain chain to slow down the entry into pine forests in the north of Norway.

Ips amitinus may become an abundant and significant bark beetle species in the forests of Northern Europe in the future. The areas around the Baltic Sea are predicted to be equally suitable as one of its optimal areas in the Carpathian Mountains (Fig. 3). Our comparison based on window trap captures indicates that the population density levels of *I. amitinus* in these recently invaded areas are still lower than those in the core areas of Central Europe, although these populations may increase in future, especially in response to outbreak periods of *I. typographus*. The bark beetle outbreaks in European spruce forests occur periodically in response to major tree fellings by wind that occur irregularly in space and time (Økland & Bjørnstad, 2006; Marini *et al.*, 2017). During outbreak periods, these bark beetle species may have positive interactions that are facilitating both of the species involved in the interaction, and the strongest facilitation occurs for the relatively less aggressive species (Økland *et al.*, 2009). In the present case, *I. typographus* is the superior eruptive species in the outbreaks, whereas the co-occurring *I. amitinus* is an inferior species that strongly benefits from the interaction with *I. typographus* and sometimes reaches a level that kills trees. However, the proportion of *I. amitinus* versus *I. typographus* infestations may vary much in the field (Holuša *et al.*, 2012) and more research is needed to understand how the complex interaction dynamics of these species will manifest in different forest environments. In Fennoscandia, *I. amitinus* has still not reached the areas with a history of large *I. typographus* outbreaks (central and southern Sweden and southern Norway). When reaching those areas, future outbreak periods of *I. typographus* are likely to increase the *I. amitinus* populations in Fennoscandia step-by-step, where this species may also reach a level that kills trees in the optimal areas. In addition, an increase of abnormal weather events as a result of climate change, such as drought periods that weaken spruce defence, and possibly also more windfelling storms, may lead to more bark beetle outbreaks (Benestad, 2005; IPCC, 2012).

It should be noted that the present MaxEnt models do not account for changes in prediction that may occur after further range expansions of *I. amitinus*. As *I. amitinus* becomes more widespread, the MaxEnt models predictions may show a wider area than in the present model outcomes. More genetic work on this species could reveal the degree of plasticity as it enters into new bioclimatic zones. Some of the easternmost records of *I. amitinus* in Russia may imply that *I. amitinus* can tolerate a cold and highly continental climate and, in a worst-case scenario, further expansions might be limited by host tree availability rather than climatic restrictions. If so, this species might possibly expand to the east in accordance with the distribution of Norway spruce all the way to Russian Far East and China where there are new potential host species. At the other end of the climatic gradient, the results of the present study show that southern parts of Europe may become too warm for *I. amitinus*. Here, in a worst-case scenario, spruce forests might decline and *I. amitinus* and other boreomontane species might become rare or extinct.

Acknowledgements

Supporting information

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

Appendix S1. Sources of *Ips amitinus* records in the present study.

References

Aakala, T., Kuuluvainen, T., Wallenius, T. & Kauhanen, H. (2011) Tree mortality episodes in the intact *Picea abies*-dominated taiga in the Arkhangelsk region of northern European Russia. *Journal of Vegetation Science*, **22**, 322–333.

Annila, E. & Nuorteva, M. (1976) Dates of attack and emergence of *Ips amitinus* Eichh. (Col., Scolytidae) in Finland. *Annales Entomologici Fennici*, **42**, 28–30.

Aoki, C.F., Cook, M., Dunn, J., Finley, D., Fleming, L., Yoo, R. & Ayres, M.P. (2018) Old pests in new places: effects of stand structure and forest type on susceptibility to a bark beetle on the edge of its native range. *Forest Ecology and Management*, **419–420**, 206–219.

Benestad, R. (2005) Storm frequencies over Fennoscandia – relevance for bark beetle outbreak. RegClim results. *Met. Report No. 2005*, Norwegian Meteorological Institute, Oslo.

Bonacina, L.C.W. (1923) Climatic continentality and oceanity. *Nature*, **111**, 549.

Brockerhoff, E.G., Bain, J., Kimberley, M. & Knizek, M. (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research*, **36**, 289–298.

Buchovska, J., Danusevičius, D., Baniulis, D., Stanys, V., Šikšnianiene, J.B. & Kavaliauskas, D. (2013) The location of the northern glacial refugium of Scots pine based on mitochondrial DNA markers. *Baltic Forestry*, **19**, 2–12.

Burke, J.L. & Carroll, A.L. (2016) The influence of variation in host tree monoterpene composition on secondary attraction by an invasive bark beetle: Implications for range expansion and potential host shift by the mountain pine beetle. *Forest Ecology and Management*, **359**, 59–64.

CABI (2018) *Ips duplicatus* (double-spined bark beetle). Datasheet. Invasive species compendium. [WWW document]. URL https://www.cabi.org/isc/datasheet/28823 [accessed on 4 March 2019].

Colombari, F., Schroeder, M., Battisti, A. & Faccoli, M. (2013) Spatio-temporal dynamics of *Ips acuminatus* outbreak and implications for management. *Agricultural and Forest Entomology*, **15**, 34–42.

Cooke, B.J. & Carroll, A.L. (2017) Predicting the risk of mountain pine beetle spread to eastern pine forests: considering uncertainty in uncertain times. *Forest Ecology and Management*, **396**, 11–25.

EFSA PLH (EFSA Panel on Plant Health) (2017a) Pest categorisation of *Ips cembrae*. Scientific Opinion. *EFSA Journal*, **15**, 5039.

EFSA PLH (EFSA Panel on Plant Health) (2017b) Pest categorisation of *Ips amitinus*. Scientific Opinion. *EFSA Journal*, **15**, 5038.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

EPPO (2017) *Ips amitinus*. EPPO global database. [WWW document]. URL https://gd.eppo.int/taxon/IPSXAM/distribution [accessed on 4 March 2019].

Erbilgin, N., Ma, C., Whitehouse, C., Shan, B., Najar, A. & Evenden, M. (2014) Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naive host ecosystem. *New Phytologist*, **201**, 940–950.

Fält-Nardmann, J., Tikkanen, O.-P., Ruohomäki, K. *et al.* (2018) The recent northward expansion of *Lymantria monacha* in relation to realised changes in temperatures of different seasons. *Forest Ecology and Management*, **427**, 96–105.

Forsse, E. (1989) *Migration in bark beetles with special reference to the spruce bark beetle Ips typographus*. Dissertation, Swedish University of Agricultural Sciences, Uppsala.

Gmelin, J.F. (1787) *Abhandlungen über die Wurmtrocknis*, p. 176. Crusius, Germany.

Grodzki, W. (2003) Distribution range of the double spined bark beetle *Ips duplicatus* C.R. Sahlb. (Col.: Scolytidae) in the mountain areas of southern Poland. *Sylwan*, **147**, 29–36.

Haack, R.A. (2006) Exotic bark- and wood- boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research*, **36**, 269–288.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hijmans, R.L., Phillips, S., Leathwick, J. & Elith, J. (2017) Dismo – species distribution modeling. [WWW document]. URL https://cran.r-project.org/web/packages/dismo/index.html [accessed on 4 March 2019].

Holuša, J., Lubojacký, J. & Knížek, M. (2010) Distribution of double-spined spruce bark beetle *Ips duplicatus* in The Czech Republic: spreading in 1997–2009. *Phytoparasitica*, **38**, 435–443.

Holuša, J., Lukášová, K., Grodzki, W., Kula, E. & Matoušek, P. (2012) Is *Ips amitinus* (Coleoptera: Curculionidae) abundant in Widerange of altitudes? *Acta Zoologica Bulgarica*, **64**, 219–228.

Huntley, B. & Birks, H.J.B. (1983) *Atlas of Past and Present Pollen Maps for Europe, 0–13,000 Years Ago*. Cambridge University Press, Cambridge, Massachusetts.

IPCC (2012) Managing the risks of extreme events and disasters to advance climate change adaptation. *A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change* (ed. by C. B. Field, V. Barros, T. F. Stocker *et al.*), p. 582. Cambridge University Press, U.K.

Jakuš, R. (1995) Bark beetle (Col., Scolytidae) communities and host and site factors on tree level in Norway spruce primeval natural forest. *Journal of Applied Entomology*, **119**, 643–651.

Jakuš, R. (1998) Patch level variation on bark beetle attack (Col., Scolytidae) on snapped and uprooted trees in Norway spruce primeval natural forest in endemic conditions: effects of host and insolation. *Journal of Applied Entomology*, **122**, 409–421.

Jepsen, J.U., Biuw, M., Ims, R.A., Kapari, L., Schott, T., Vindstad, O.P.L. & Hagen, S.B. (2013) Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone. *Ecosystems*, **16**, 561–575.

Jurc, M. & Bojović, S. (2004) Bark beetle outbreaks during the last decade with special regard to the eight-toothed bark beetle (*Ips amitinus* Eichh.) outbreak in the alpine region of Slovenia. *Biotic Damage in Forests. Proceedings of the IUFRO (WP7.03.10) Symposium held in Mátrafüred, Hungary, September 12–16, 2004* (ed. by G. Csóka, A. Hirka and A. Koltay), pp. 85–95. Hungarian Forest Research Institute, Hungary.

Kacprzyk, M. & Bednarz, B. (2015) The occurrence of bark beetles on cut Norway spruce branches left in managed stands relative to the foliage and bark area of the branch. *Journal of Forestry Research*, **20**, 143–150.

Kaplan, J.O., Krumhardt, K.M. & Zimmermann, N. (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, **28**, 3016–3034.

Kenward, H. (1988) Insect remains. *"Mindets tomt" - "Søndre felt": Animal Bones, Moss-, Plant-, Insect- and Parasite Remains*, De arkeologiske utgravninger i Gamlebyen, Oslo, Vol. **5** (ed. by E. Schia), pp. 115–140. Alvheim & Eide, Norway.

Keitt, T.H., Lewis, M.A. & Holt, R.D. (2001) Allee effects, invasion pinning, and species' borders. *The American Naturalist*, **157**, 203–216.

Koponen, M. (1975) Distribution of *Ips amitinus* (Eichhoff) (Coleoptera, Scolytidae) in Finland 1950–1973. *Annales Entomologici Fennici*, **41**, 65–69.

Koponen, M. (1980) Distribution of *Ips amitinus* (Eichhoff) (Coleoptera, Scolytidae) in Finland 1974–1979. *Notulae Entomologicae*, **60**, 223–225.

Latałowa, M. & van der Knaap, W.O. (2006) Late quaternary expansion of Norway spruce *Picea abies* (L.) karst. In Europe according to pollen data. *Quaternary Science Reviews*, **25**, 2780–2805.

Leius, K. (1939) Täiendavaid andmeid kodumaa ürasklaste (Ipidae) fauna kohta. Ergänzende Angaben über die Borkenkäfer-Fauna (Ipidae) in Estland (Zusammenfassung). *Eesti Metsanduse Aastaraamat (Estländisches Forstwirtschaftliches Jahrbuch, Tartu)*, **9**, 317–328.

Lekander, B., Bejer-Petersen, B., Kangas, E. & Bakke, A. (1977) The distribution of bark beetles in the Nordic countries. *Acta Entomologica Fennica*, **32**, 1–36.

Lewis, M.A. & Kareiva, P. (1993) Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, **43**, 141–158.

Lindelöw, Å. (2013) Väntad barkborre funnen i Sverige - fynd av *Ips amitinus* (Coleoptera, Scolytinae). [*Ips amitinus* (Coleoptera, Scolytinae) expected and found in Sweden]. *Entomologisk Tidskrift*, **134**, 203–206.

Lindelöw, Å., Isacsson, G., Ravn, H.P. & Schroeder, M. (2015) *Tetropium gabrieli* and *Ips cembrae* (Coleoptera; Cerambycidae and Curculionidae) – invasion of two potential pest species on larch in Sweden. *Entomologisk Tidskrift*, **136**, 103–112.

Lukášová, K., Holuša, J. & Turčáni, M. (2013) Pathogens of *Ips amitinus*: new species and comparison with *Ips typographus*. *Journal of Applied Entomology*, **137**, 188–196.

Lundberg, S. (1995) *Catalogus Coleopterorum Sueciae*. Naturhistoriska riksmuséet, Sweden.

Mandelshtam, M.Ju. (1999) Current status of *Ips amitinus* Eichh. (Coleoptera, Scolytidae) in north-West Russia. *Entomologica Fennica*, **10**, 29–34.

Marini, L., Økland, B., Jönsson, A.M. *et al.* (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography*, **40**, 1–010.

Mayer, F., Piel, F.B., Cassel-Lundhagen, A. *et al.* (2015) Comparative multilocus phylogeography of two Palaearctic spruce bark beetles: influence of contrasting ecological strategies on genetic variation. *Molecular Ecology*, **24**, 1292–1310.

Mazur, A. & Kuźmiński, R. (2013) Phenology of development and population characteristics of the small spruce bark beetle *Ips amitinus* (Eichh.) in the Karkonoski National Park. *Folia Forestalia Polonica*, **55**, 89–96.

Mikutowicz, J.M. (1905) Zur Koleopterenfauna der Ostseeprovinzen Russlands. *Korrespondenz-blatt des Naturforscher-Vereins zu Riga*, **48**, 73–92.

Musolin, D.L. (2007) Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Global Change Biology.*, **13**, 1565–1585.

Musolin, D.L. & Saulich, A.Kh. (2012) Responses of insects to the current climate change: from physiology and behaviour to range shifts. *Entomological Review*, **92**, 715–740.

Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J. & Luyssaert, S. (2016) Europe's forest management did not mitigate climate warming. *Science*, **351**, 597–600.

Naydenov, K., Senneville, S., Beaulieu, J., Tremblay, F. & Bousquet, J. (2007) Glacial vicariance in Eurasia: mitochondrial DNA evidence from Scots pine for a complex heritage involving genetically distinct refugia at mid- northern latitudes and in Asia minor. *BMC Evolutionary Biology*, **7**, 233.

Nuorteva, M. (1956) *Ips amitinus* Eichh. kaarnakuoriaisen esiintymisestä Suomessa. Ref.: Über das Auftreten des *Ips amitinus* Eichh. (Col., Scolytidae) in Finnland. *Annales Entomologici Fennici*, **22**, 168–170.

Økland, B. (1989) Laboratory studies of egg development and diapause in *Isoperla obscura* (Plecoptera) from a mountain stream in Norway. *Freshwater Biology*, **25**, 485–495.

Økland, B., Kvamme, T. & Wollebæk, G. (2005) Ny barkbilleart funnet overvintrende. *Skogeieren*, **10**, 30–31.

Økland, B. & Bjørnstad, O.N. (2006) A resource depletion model of forest insect outbreaks. *Ecology*, **87**, 283–290.

Økland, B., Skarpaas, O. & Kausrud, K. (2009) Threshold facilitations of interacting species. *Population Ecology*, **51**, 513–523.

Økland, B., Erbilgin, N., Skarpaas, O., Christiansen, E. & Långström, B. (2011). Inter-species interactions and ecosystem effects of non-indigenous invasive and native tree-killing bark beetles. *Biological Invasions*, **13**, 1151–1164.

Økland, B., Netherer, S. & Marini, L. (2015) The Eurasian spruce bark beetle: the role of climate. *Climate Change and Insect Pests*, CABI Climate Change Series, Vol. **7** (ed. by C. Björkman and P. Niemelä), pp. 202–219. U.K.

Olenici, N., Duduman, M.-L., Olenici, V., Bouriaud, O., Tomescu, R. & Rotariu, C. (2010) The first outbreak of *Ips duplicatus* (Coleoptera, Curculionidae, Scolytinae) in Romania. *Methodology of Forest Insect and Disease Survey in Central Europe* (ed. by H. Delb and S. Pontuali). Proceedings of the 10th IUFRO Workshop of WP 7.03.10 September 20–23, 2010), pp. 135–140. Fakultät für Forst- und Umweltwissenschaften der Albert-Ludwigs-Universität and Forstliche Versuchs- und Forschungsanstalt (FVA), Freiburg, Germany. URL www.iufro.org.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2016) Updated world map of the Köppen-Geiger climate classification. [WWW document]. URL https://en.wikipedia.org/wiki/K%C3%B6ppen_climate_classification#/media/File:Europe_map_of_K%C3%B6ppen_climate_classification.svg.

Pfeffer, A. (1932) Kůrovci ve Vysokých Tatrách [Bark beetles in high Tatra Mountains]. *Les. Práce*, **11**, 1–23.

Pfeffer, A. (1954) *Lesnická Zoologie* [Forestry Zoology], Vol. **2**. SZN, Czechoslovakia.

Pfeffer, A. (1955) *Fauna ČSR. Svazek 6. Kůrovci − Scolytoidea. (Řád: Brouci − Coleoptera)*. Nakladatelství Československé Akademie Věd, Czechoslovakia.

Pfeffer, A. (1995) *Zentral- und westpaläärktische Borken- und Kernkäfer. Coleoptera, Scolytidae, Platypodidae*. Pro Entomologia, Naturhistoriches Museum, Switzerland.

Phillips S.J., Dudik M. & Schapire R.E. (2004) A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First International Conference on Machine Learning*, Banff, Canada, 2004, pp. 655-662. Princeton University, Canada. URL: https://www.cs.princeton.edu/~schapire/papers/maxent_icml.pdf.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Phillips, S.J., Dudík, M. & Schapire, R.E. (2018) *Maxent Software for Modeling Species Niches and Distributions*, Version 3.4.1. [WWW document]. URL http://biodiversityinformatics.amnh.org/open_source/maxent/

Piel, F., Gilbert, M., Franklin, A. & Grégoire, J.C. (2005) Occurrence of *Ips typographus* (Col., Scolytidae) along an urbanization gradient in Brussels, Belgium. *Agricultural and Forest Entomology*, **7**, 161–167.

Postner, M. (1974) Scolytidae (Ipidae), Borkenkäfer. *Die Forstschädlinge Europas*, Vol. **2** (ed. by W. Schwenke), pp. 334–482. Parey Verlag, Berlin, Germany.

R Core Team (2017) *R : A Language and Environment for Statistical Computing*. [WWW document]. URL https://www.r-project.org [accessed on 4 March 2019]

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G. & Romme, W.H. (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience*, **58**, 501–517.

Raffa, K.F., Aukema, B.H., Bentz, B., Carroll, A.L., Hicke, J.A. & Kolb, T.E. (2015) Responses of tree-killing bark beetles to a changing climate. *Climate Change and Insect Pests*, CABI Climate Change Series (ed. by C. Björkman and P. Niemelä), pp. 173–201. U.K.

Reventlow, C.D.F. (1811) *Min reise i Norge 1811* (ed. by J. Elgvin) in 1955. Gyldendal Norsk Forlag, Norway [in Norwegian].

Ribič, A. (2007) *Little eight-toothed spruce bark beetle (Ips amitinus, Col.: Scolytidae) in the regional unit Dravograd in 2005*. Graduation Thesis (Higher Professional Studies), University of Ljubljana, Slovenia.

Rosenberger, D.W., Venette, R.C., Maddox, M.P. & Aukema, B.H. (2017) Colonization behaviors of mountain pine beetle on novel hosts: implications for range expansion into northeastern North America. *PLoS ONE*, **12**, e0176269.

Roubal, J. (1937–1941) Katalog Coleopter (Brouku) Slovenska a Východních Karpat. *Katalog der Coleopteren Der Slowakei und der*

Ost-Karpathen. III, p. 363. Slovanský ústav, Nakladatelství Orbis, Czechoslovakia. Tiskárna Protektorátu Čechy a Morava v Praze.

Sarikaya, O., Karaceylan, I.B. & Sen, I. (2018) Maximum entropy modeling (maxent) of current and future distributions of *Ips mannsfeldi* (Wachtl, 1879) (Curculionidae: Scolytinae) in Turkey. *Applied Ecology and Environmental Research*, **16**, 2527–2535.

Shcherbakov, A.N., Nikitsky, N.B., Polevoj, A.V. & Humala, A.E. (2013) To Coleoptera fauna of insects in Pasvik nature reserve (Insecta, Coleoptera). *Forest Bulletin of Moscow State Forest University*, **6**, 16–21 (in Russian).

Siitonen, J. (2014) *Ips acuminatus* kills pines in southern Finland. *Silva Fennica*, **48**, 1145. https://doi.org/10.14214/sf.1145.

Stauffer, C., Lakatos, F. & Hewitt, G.M. (1997) The phylogenetic relationships of seven European *Ips* (Scolytidae, Ipinae) species. *Insect Molecular Biology*, **6**, 233–240.

Stauffer, C. & Zuber, M. (1998) *Ips amitinus* var. *montana* (Coleoptera, Scolytidae) is synonymous to *Ips amitinus*: a morphological, behavioural and genetic re-examination. *Biochemical Systematics and Ecology*, **26**, 171–183.

Stolina, M. (1969) Der Einfluss der Ipidenfauna auf die Entwicklung der Struktur von Naturwäldern in den Westkarpathen. *Schweizerische Zeitschrift für Forstwesen*, **11**, 610–627.

Tauber, M.J. & Tauber, C.A. (1976) Insect seasonality: diapause maintenance, termination, and postdiapause development. *Annual Review of Entomology*, **21**, 81–107.

Tauber, M.J., Tauber, C.A. & Masaki, S. (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York, New York.

Tollefsrud, M.M., Kissling, R., Gugerli, F. *et al.* (2008) Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. *Molecular Ecology*, **17**, 4134–4150.

Vakula, J., Kunca, A., Zúbrik, M., Leontovyč, R., Longauerová, V. & Gubka, A. (2007) Distribution of two invasive pests in Slovakia since 1996. *Alien, Invasive Species and International Trade (Proceedings, IUFRO Unit 7.03.12, Jedlnia)* (ed. by H. Evans and T. Oszako), pp. 105–113. Forest Research Institute, Poland.

Vakula, J., Zúbrik, M., Galko, J., Gubka, A., Kunca, A., Nikolov, C. & Bošeľa, M. (2015) Influence of selected factors on bark beetle outbreak dynamics in the Western Carpathians. *Forestry Journal*, **61**, 149–156.

Voolma, K., Mandelshtam, M.J., Shcherbakov, A.N. *et al.* (2004) Distribution and spread of bark beetles (Coleoptera: Scolytidae) around the Gulf of Finland: a comparative study with notes on rare species of Estonia, Finland and North-Western Russia. *Entomologica Fennica*, **15**, 198–210.

Walter, J.A., Johnson, D.M. & Haynes, K.J. (2016) Spatial variation in Allee effects influences patterns of range expansion. *Ecography*, **40**, 179–188.

Witrylak, M. (2008) Studies of the biology, ecology, phenology, and economic importance of *Ips amitinus* (Eichh.) (Col., Scolytidae) in experimental forests of Krynica (Beskid Sadecki, southern Poland). *Acta Scientiarum Polonorum Silvarum Colendarum Ratio et Industria Lignaria*, **7**, 75–92.

WorldClim 2018. Global Climate Data [WWW document]. URL www.worldclim.org [accessed on 4 March 2019].

Zach, P., Kršiak, B., Kulfan, J. & Holecová, M. (2010) Attraction of bark beetles (Coleoptera: Scolytidae) to Norway spruce in timberline forest in Tatra Mountains, West Carpathians. *Lesnícky Časopis [Forestry Journal]*, **56**, 285–293.

Zach, P., Kršiak, B., Kulfan, J., Parák, M. & Kontschán, J. (2016) Mites Trichouropoda and Uroobovella spp. (Uropodoidea) phoretic on bark beetles (Scolytinae): a comparison from a declining mountain spruce forest in Central Europe. *International Journal of Acarology*, **42**, 212–217.

Zumr, V. (1982) The data for the prognosis of spring swarming of main species of bark beetles (Coleoptera, Scolytidae) on spruce (*Picea excelsea* L.). *Zeitschrift für Angewandte Entomologie*, **93**, 305–320.

Zumr, V. (1984) Spatial distribution of bark beetles (Coleoptera, Scolytidae) in Norway spruce and their indifference in relation to forest belts. *Lesnictví*, **30**, 509–522.