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Implications for the distributional range of the European bark beetles under future climate change

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The European continent is rich in forest resources, with bark beetles being the most significant biological disturbance impacting European forest ecosystems. Over the past few decades, many trees have died due to bark beetle infestations, causing considerable economic damage to forestry. It is estimated that climate change will affect the distributional range of bark beetles, increasing the risk of outbreaks. However, the ability of different beetle populations to respond to climate change remains unknown. For this purpose, we selected nine species of bark beetles commonly found in Europe and constructed the MaxEnt model to simulate the distribution pattern of bark beetles under climatic conditions based on 21 environmental variables. Modeling projected changes in the distribution of different species of bark beetles under four climate scenarios for 2081–2100 using future climate variables and testing the hypothesis that narrow-ranged species are more vulnerable to climate change than wide-ranged species. The results show that the distribution of most bark beetles is influenced by temperature-related variables. With climate change, the suitable distribution areas for most species will expand and gradually shift to higher latitudes. Furthermore, most of northern Europe will be invaded by multiple bark beetle species in the future. These findings contribute to understanding the distributional dynamics of bark beetles in Europe under climate change, thereby facilitating the development of early-intervention strategies to reduce the risk and impact of species outbreaks.

Keywords MaxEnt, Climate change, Bark beetle, Potential effect, Range changes

Biotic and abiotic factors, including fires, droughts, storms, herbivores, pathogens, and insect outbreaks are key factors affecting global temperate forest systems[1]. However, in recent decades, the disturbance regime for forests has changed significantly, and disturbances have become more frequent and severe[2,3]. Among other things, climate change contributes significantly to forest system disturbances, and is likely to contribute to bark beetle outbreaks. Bark beetles, which frequently infest trees, are the most important biological disturbance affecting forest systems[4,5].

Bark beetles, belonging to the subfamily Scolytinae within the family Curculionidae in the order Coleoptera, are a group of beetles that primarily damage trees. They are widely distributed and highly diverse, with over 6,000 species identified to date. It is known that only a small fraction of bark beetle species severely harm trees, while most species have little impact on tree health[6,7]. Bark beetles can be categorized into primary and secondary species. Primary bark beetles are capable of successfully invading and killing healthy trees, while secondary bark beetles settle only on dead or dying trees[8,9]. Temperature and drought are the two most important factors influencing bark beetle outbreaks in Europe. The development and generational cycles of bark beetles are directly related to temperature; under suitable temperatures, they exhibit high reproductive capacity, with some regions experiencing two or even three generations per year[2,10]. Additionally, water stress increases the intensity of bark beetle attacks on trees[11].

Climate is a major factor influencing species' distributions and abundance[12]. The Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (AR6) indicates that human activities, such as fossil fuel combustion and land use changes, have led to global warming over the past century, raising the current global average temperature by 1.1 °C above pre-industrial levels. It is anticipated that the distributional ranges of many species will change under future climate conditions, and species that are not sufficiently adaptable to climate change may face extinction[13,14]. Ecological niches describe the range of environmental conditions within

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which a population survives in an ecosystem[15]. Many studies have concluded that there is a positive correlation between the breadth of a species' niche and its distributional range[16–18]. Species with narrower niches are more susceptible to the impacts of climate change and are at a higher risk of extinction.

Ecological niches are one of the most important foundations for the study of ecology, revealing the relationships between species distribution changes and environmental variables under climate change[15,19]. Currently, Species Distribution Models (SDMs) are widely used in various research fields, including the spatiotemporal distribution patterns of species, species invasions, and the impacts of climate change on species distribution or diversity patterns[20,21]. SDMs use species occurrence records and environmental variables to simulate the fundamental niche of species and predict their potential distribution[22]. With advancements in ecological research, Several SDM algorithms have been developed, such as Generalized Linear Models (GLM), Random Forests (RF), and the Maximum Entropy Model (MaxEnt). The MaxEnt model, with its high prediction accuracy and simplicity of operation, is currently one of the most widely used models[23–25]. For instance, in the Congo, Cokola et al.[26] predicted the suitable habitat areas for the major maize pest *Spodoptera frugiperda* using MaxEnt. Li et al.[27] used the MaxEnt model to simulate the ecological niches of suitable habitats for 15 species of *Rhododendron* and their eight pollinators, and found that the range of suitable habitats for species of the *Rhododendron* genus will be reduced under future climate change. Similarly, Sun et al.[22] used MaxEnt and six General Circulation Models (GCMs) to simulate the potential abundance distribution of oak species in China, discovering that oak species would migrate to higher altitudes or latitudes under climate change.

In recent decades, the frequency and scale of bark beetle outbreaks in Europe have increased significantly, resulting in the death of a large number of trees annually[28]. Recurring infestations have gradually changed the structure of forests across Europe, resulting in large areas of dead trees and greater damage to the forestry economy[29]. For example, the European spruce bark beetle (*Ips typographus*) has caused the death of more than 150 million m^3 of forest in the last fifty years[30]. In the Czech Republic, just 3 million m^3 of trees were damaged by insects prior to 2015, and this has steadily increased to 22 million m^3 by 2019[31]. Climate change has induced shifts in the ecological niches of bark beetles. Some studies have shown that climate change will affect the ranges of certain beetles. For instance, Hansen et al.[32] predicted that under global warming, the populations and spread of *Dendroctonus rufipennis* and *Dendroctonus ponderosae* would increase in western USA and Canada; Also in Europe, Marini et al.[33] found that temperature is the primary climatic driver facilitating *Ips typographus* outbreaks in eight European countries. However, it remains unclear whether all bark beetle species will be similarly affected by climate change and whether they will expand their range in the future. Meanwhile, current research usually focuses on *Ips typographus* while our study goes a step further by considering different bark beetle species and comparing their distributional changes. To better understand the dynamics of bark beetles and to identify potential outbreaks exacerbated by climate change, it is crucial to consider various factors so that we can fully understand the suitability of different populations of beetles to climate change, to prevent large-scale outbreaks and reduce future economic losses.

We investigated the distributional dynamics of different bark beetle species in Europe under climate change to test the hypothesis that insects with relatively narrow distribution are more susceptible to climate change[34]. In this paper, we used the MaxEnt model in combination with six Global Circulation Models (GCMs), known species distribution records and different environmental variables to simulate and predict the distributional dynamics of European bark beetles for the current period and under four future scenarios. The study aims to identify the potential suitable distribution and distribution changes for different bark beetle populations, analyze the dominant environmental factors influencing their distribution, and predict their primary shift directions under the four scenarios. Furthermore, we aim to validate whether narrowly distributed bark beetle species are more susceptible to the impacts of climate change compared to widely distributed species.

Materials and methods

Species distribution data

We extracted distribution data for nine bark beetle species widely present in Europe, including eight primary bark beetles and one secondary bark beetle[9]. These species comprise three from the genus *Ips*, three from *Pityogenes*, one from *Polygraphus*, one from *Pityophthorus*, and one *Tomicus*. The occurrence records were mostly gathered from the Global Biodiversity Information Facility (GBIF: https://www.gbif.org/) (Fig. 1). Through screening, we removed erroneous, duplicate, and geographically incomplete records, as well as records located in non-terrestrial areas. To reduce spatial autocorrelation and data redundancy that could impair prediction results, we used the spatial rare occurrence data function of the SDM Toolbox (v2.5) in ArcGIS 10.2 the SDMtoolbox (v2.5) in ArcGIS 10.2[35,36]. Each occurrence point was assigned a 1 km radius buffer, in cases of overlap, we randomly retained one occurrence point and deleted the others. After processing, we acquired distribution records for the nine target species (Table 1; Fig. 1).

Environmental variables

The 19 climatic variables used in this study were obtained from the WorldClim v2.1 database (https://www.worldclim.org/) (Table 2), with a spatial resolution of 30 arc-seconds (approximately 1 km²). These variables cover both the current period (1970–2000) and the future period (2081–2100). To account for the impact of climate change scenarios on model accuracy, we used data from the Coupled Model Intercomparison Project (CMIP). In the 1970 s, under the auspices of the World Climate Research Program (WCRP), the first CMIP was organized to coordinate and compare simulation results from different climate models around the world. Currently, CMIP6 is the latest Coupled Model Intercomparison Project proposed by the WCRP. It represents the most extensive effort in over 20 years in terms of the number of participating models, the completeness of scientific experimental design, and the volume of simulation data. CMIP6 adopts a new framework that combines Shared Socioeconomic Pathways (SSPs) with Representative Concentration Pathways (RCPs), and

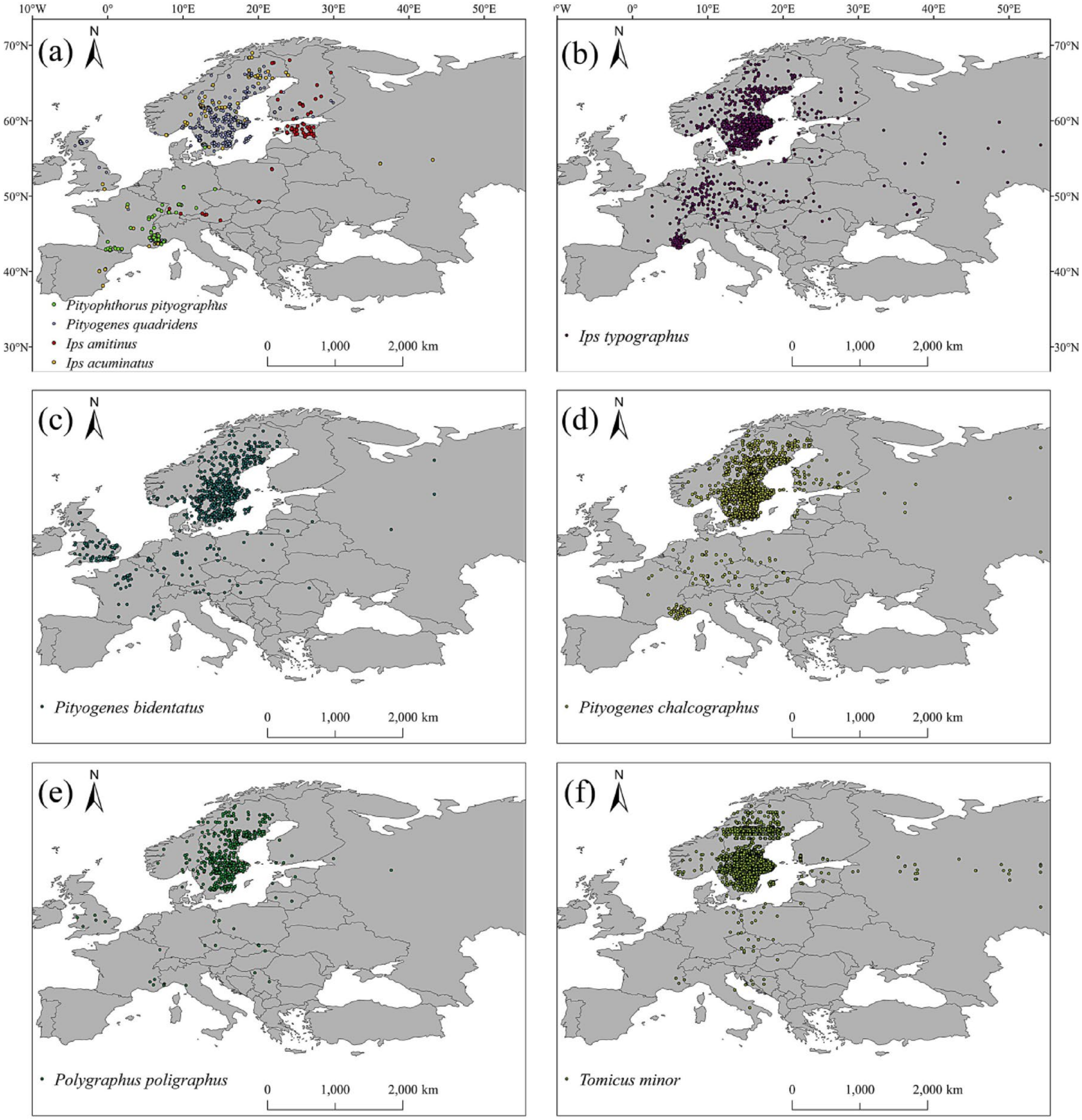


Fig. 1. Distribution records of 9 species of bark beetles. **a**, *Ips acuminatus, Ips amitinus*, *Pityogenes quadridens, Pityophthorus pityographus*; **b**, *Ips typographus*; **c**, *Pityogenes bidentatus*; **d**, *Pityogenes chalcographus*; **e**, *Polygraphus poligraphus*; **f**, *Tomicus minor.* The maps were created by ArcGIS 10.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

it has been demonstrated to be superior to CMIP5 in terms of its applicability across multiple regions. We deployed six CMIP6 future climate models to obtain multimodel ensemble (MME) climate data[37]The six climate models are: CMCC-ESM2 (Italy)[38] EC-Earth3-Veg (Europe)[39] INM-CM5-0 (Russia)[40] MPI-ESM1-2-HR (Germany)[41] MIROC6 (Japan)[42] and MRI-ESM2-0 (Japan)[43]. Each model includes four different Shared Socioeconomic Pathways (SSP): low-emission scenario SSP1-2.6 (SSP126), middle-of-the-road scenario SSP2-4.5 (SSP245), high-emission scenario SSP3-7.0 (SSP370), and extremely high-emission scenario SSP5-8.5 (SSP585). Additionally, we extracted three topographic variables—altitude (Alt), slope (Slp), and aspect (Asp)—from a digital elevation model (DEM) with a spatial resolution of 1 km. To avoid the negative impact of high spatial collinearity among climate variables on model efficiency, Pearson correlation tests were undertaken for each species in SPSS software. This helps in filtering out highly collinear variables that could contribute to model complexity and overfitting[44]. Among each set of significantly correlated variables ($|r|\geq 0.8$), only the variable with the clearest ecological relevance was retained for analysis. Following the correlation screening, jackknife tests by the MaxEnt model was used to further analyze the contribution and importance of environmental variables to the distribution of each species[45]. This approach allowed us to find the most suitable set of environmental variables for each species (Fig. 3).

Species	Number of records	The Area Under the Curve (AUC)	Maximum training sensitivity plus specificity Cloglog threshold
Ips acuminatus	116	0.983	0.3067
Ips typographus	802	0.924	0.3293
Pityogenes bidentatus	608	0.947	0.3111
Pityogenes chalcographus	828	0.939	0.2397
Pityogenes quadridens	191	0.982	0.2182
Polygraphus poligraphus	375	0.967	0.2521
Tomicus minor	931	0.941	0.2837
Ips amitinus	72	0.989	0.2095
Pityophthorus pityographus	64	0.976	0.1173

Table 1. Occurrence records, AUC values, and thresholds for suitable habitat classification for each species (The value is a threshold for suitable habitats).

Environmental variable	Variable description	Unit
Bio1	Annual Mean Temperature	℃
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	℃
Bio3	Isothermality	-
Bio4	Temperature Seasonality	-
Bio5	Max Temperature of Warmest Month	℃
Bio6	Min Temperature of Coldest Month	℃
Bio7	Temperature Annual Range	℃
Bio8	Mean Temperature of Wettest Quarter	℃
Bio9	Mean Temperature of Driest Quarter	℃
Bio10	Mean Temperature of Warmest Quarter	℃
Bio11	Mean Temperature of Coldest Quarter	℃
Bio12	Annual Precipitation	mm
Bio13	Precipitation of Wettest Month	mm
Bio14	Precipitation of Driest Month	mm
Bio15	Precipitation Seasonality (Coefficient of Variation)	mm
Bio16	Precipitation of Wettest Quarter	mm
Bio17	Precipitation of Driest Quarter	mm
Bio18	Precipitation of Warmest Quarter	mm
Bio19	Precipitation of Coldest Quarter	mm
Slp	Slope	-
Asp	Aspect	-
Alt	Altitude	m

Table 2. Description of environmental variables.

Construction and validation of maxent

MaxEnt (V3.4.4) was used to construct and analyze the suitability models for nine species of bark beetles under different climate change conditions. The filtered species distribution points and corresponding environmental variables were imported into the model. From the bark beetle distribution points, 75% were randomly selected as the training set, while the remaining 25% were used as the test set. The options for "Create response curves" and "Jackknife test" were selected. To reduce model error, the model was run 10 times using the bootstrap method. The final model results were based on the average values from these ten replicates. The output format was set to ASCII.

The model's predictive performance was evaluated using the Receiver Operating Characteristic (ROC) curve, with the Area Under the Curve (AUC) serving as the metric for model prediction accuracy[46]. The AUC is a threshold-independent rank test for the occurrence-background point prediction results, assessing the probability that the occurrence points are ranked higher than the background points. The AUC values range from 0 to 1, with values closer to 1 indicating greater model performance[23]. The AUC evaluation criteria are as follows: Fail: 0.5–0.6; Poor: 0.6–0.7; Fair: 0.7–0.8; Good: 0.8–0.9; Excellent: 0.9-1.0[47]. Response curves were used to investigate the relationships between various environmental variables and the predicted probability of bark beetle presence.

To identify suitable and unsuitable habitats for the species, the commonly applied "Maximum training sensitivity plus specificity Cloglog threshold" was used. The model output was transformed into binary format maps using the raster reclassification tool in ArcGIS[48]. Areas above the threshold were defined as suitable habitats, while those below the threshold were classified as other areas.

Additionally, to classify different bark beetle into groups, a clustering analysis method was chosen to study the regional bark beetle populations. Clustering analysis directly compares the characteristics of different entities, grouping those with similar properties together while placing those with significant differences into separate categories. The main clustering analysis methods include K-means clustering, K-medoids clustering, and hierarchical clustering. Among them, K-means clustering is a method that calculates the degree of data aggregation based on distance. Due to its simplicity, strong interpretability, and effective clustering performance, it has been widely applied. The K-means clustering analysis method in SPSS software was applied for analyzing the habitat similarity of the nine bark beetle species based on the contribution of environmental variables from the model output. The methodology helps in classifying distinct bark beetle populations according to their habitat characteristics.

SDMtoolbox 2.0 was applied to analyze the changes in species habitat under four future climate scenarios, including contraction, expansion, no change, and other regions. Additionally, centroid analysis was conducted to determine the centroid coordinates of each species and their development directions from the current period to beyond 2100[49]. Furthermore, the correlation between the extent of change for each species and the current distribution area was analyzed to assess whether species with broad and narrow distributions respond differently to climate change[36]. A positive correlation between future species distribution change and current distribution area size indicates that species with broader distributions will gain more (or lose less) suitable habitat, while a negative correlation suggests the opposite scenario[34].

Results

Model accuracy evaluation and dominant environmental variables

According to the results of the MaxEnt model, AUC values were obtained for each species (Table 1). All AUC values were above 0.92, showing a good model performance and high accuracy. Based on cluster analysis of environmental variable contributions from the MaxEnt model results for each species, the Bark beetle species were divided into two groups (Fig. 2). The first group includes species with temperature variables serving as the primary relevant factors, such as *Ips acuminatus*, *Ips typographus*, *Pityogenes bidentatus*, *Pityogenes chalcographus*, *Pityogenes quadridens*, *Polygraphus poligraphus*, and *Tomicus minor.* The second group comprises species with precipitation variables serving as the primary contributors, including *Ips amitinus* and *Pityophthorus pityographus*. In the first group, temperature-related environmental variables were the strong driver factors of current and future distribution (Fig. 3). Isothermality (bio3) was the most important environmental factor for *P. bidentatus* and *T. minor*, while Temperature Seasonality (bio4) had the greatest impact on *I. typographus*. The distribution of *I. acuminatus* was mainly determined by Mean Temperature of Wettest Quarter (bio8), while Mean Temperature of Warmest Quarter (bio10) was the most important environmental factor for *P. chalcographus*, *P. quadridens*, and *P. poligraphus*. The potential distribution of species in the second group was driven primarily by precipitation-related environmental variables, with Precipitation of Warmest Quarter (bio18) having the most significant impact on *I. amitinus*, and Precipitation Seasonality (bio15) being the most important environmental variable affecting the distribution of *P. pityographus.*

Current potential distribution

Using the collected occurrence records, the potential distribution of nine species of bark beetles under current climate conditions was obtained (Fig. 4). The main distribution of the first group of species is in northern Europe, including nations such as Sweden, Finland, and Norway. Some species, such as *I. typographus* and *P. bidentatus*, were also found throughout central Europe. Overall, the countries with the largest distributional area include Norway, Sweden, Finland, Latvia, Poland, Slovakia, Germany, and France. The general potential distribution pattern shows a north-south difference, with the distributional area of bark beetles increasing with latitude. *I. typographus* has the broadest distributional range, including Norway, Sweden, Finland, Latvia, Poland, Lithuania, and Germany, covering an area of approximately 192,427 km² (Table 3). The next most widely distributed species is *P. chalcographus*, which has a similar distributional range to *I. typographus* and is mainly found in Norway, Sweden, Finland, Denmark, Slovakia, Romania, and Ukraine, with a distribution area of approximately 147,462 km².

The distribution of the second group of species (Fig. 4h, i) differs from the first group. *P. pityographus* has its main distribution in southern Europe, with occurrences in France, Germany, Italy, Switzerland, Bosnia and Herzegovina, covering an area of approximately 937,753 km². *Ips amitinus*, by contrast, has its main distribution in northern Europe, with occurrences in Finland, Estonia, Latvia, Lithuania.

Range changes of bark beetle under future climate change

By 2100, the primary trend in suitable habitat changes for most species under different climate scenarios is expansion (Figs. 5 and 6). Under the low-forcing SSP126 scenario, six species exhibit significant range expansion. The largest expansion is observed in *I. typographus*, with an increase of approximately 309.719×10^3 km², primarily in northern Sweden and Norway, as well as central European countries such as France and Poland. The smallest expansion occurs in *P. pityographus*, with an increase of approximately 73.166×10^3 km², mainly concentrated in Sweden, Finland, Estonia, the Czech Republic, and Germany. Conversely, the suitable habitat of *P. bidentatus*, *P. chalcographus*, and *P. pityographus* exhibited contraction under this scenario. The largest contraction is observed in *P. chalcographus*, with a reduction of approximately 286.022×10^3 km², mainly in Germany, France, Italy, Serbia, Bulgaria, and Belarus. The smallest contraction occurs in *P. quadridens*, with a reduction of approximately 61.604×10^3 km², primarily in France, Belarus, Latvia, Lithuania, and northern Sweden.

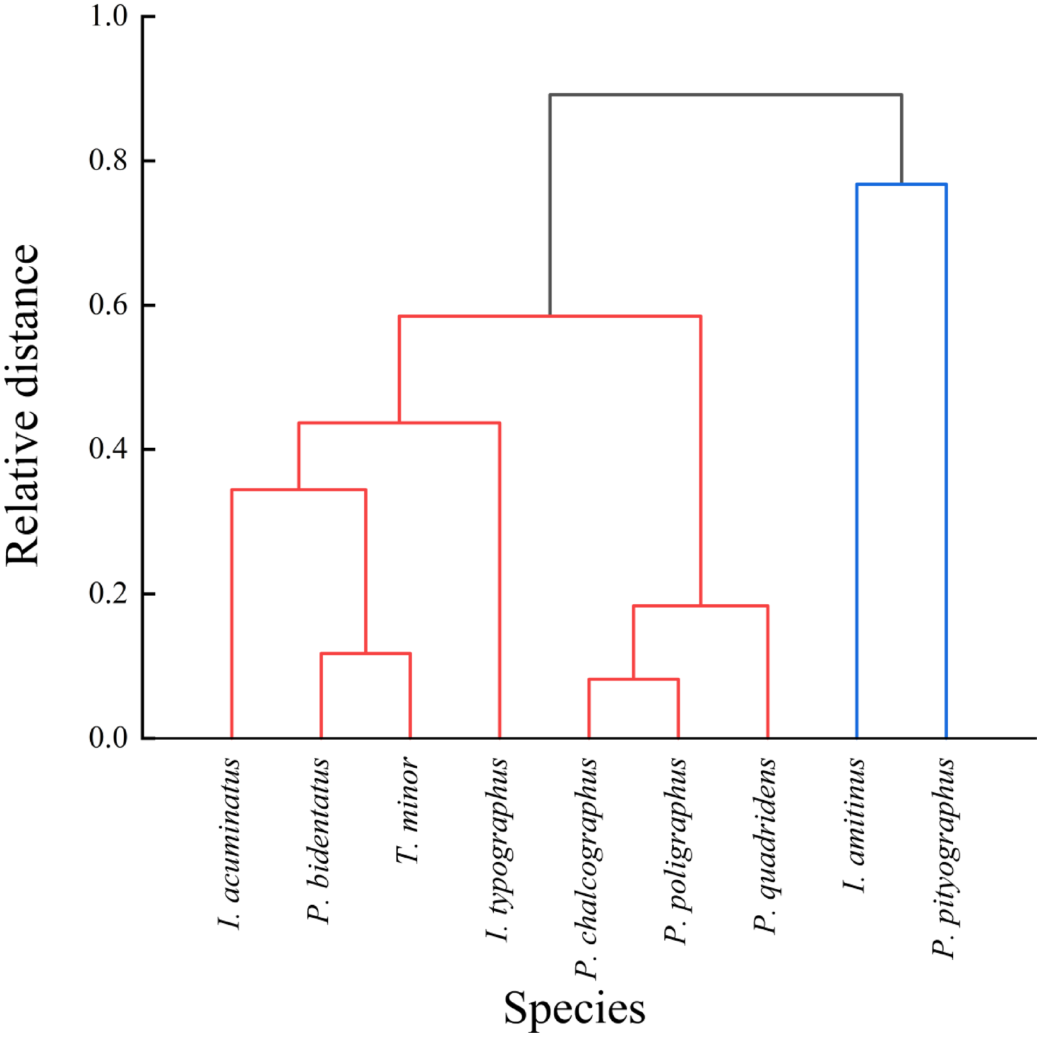


Fig. 2. Cluster analysis of environmental variables based on 9 Bark Beetle.

Under the moderate-forcing SSP245 scenario, the suitable habitat of five species contracted significantly. The largest reduction is observed in *I. typographus*, with a decrease of approximately 413.467 × 10^3 km^2, primarily in countries along the Baltic Sea coast and inland regions such as Belarus, the Czech Republic, and Hungary. By contrast, the remaining species exhibited significant range expansion. The most substantial expansion was observed in *I. amitinus*, with an increase of approximately 161.968 × 10^3 km^2, primarily in Norway, Finland, Sweden, Lithuania, and Latvia.

Under the high-forcing SSP370 scenario, only *I. typographus* exhibited a significant range contraction, with a reduction of approximately 413.467 × 10^3 km^2. In contrast, the suitable habitat of all other species expands. *P. bidentatus* shows the most extensive range expansion, increasing by approximately 295.382 × 10^3 km^2, with a broad distribution across France, Germany, Norway, Sweden, and Slovakia.

Under the extremely high-forcing SSP585 scenario, the suitable habitat of seven species is projected to expand significantly. *P. chalcographus* exhibited the largest expansion, increasing by approximately 242.152 × 10^3 km^2, with a widespread distribution across France, Germany, Norway, Finland, Sweden, Poland, and the Czech Republic. By contrast, *I. typographus* experienced the most substantial range contraction, with a reduction of approximately 516.783 × 10^3 km^2.

By the year 2100, the changes in species numbers under the four climate scenarios exhibit spatial specificity, with some areas having higher species numbers than the current period (Figs. 7 and 8). These areas were mainly located in countries such as Sweden, southern Norway, southern Finland, Latvia, and Estonia. This shows that most species are more likely to grow and reproduce in higher-latitude regions.

Under future climate conditions, most bark beetles will shift to higher latitudes (Fig. 9). Only *I. amitinus* (group 2) will migrate to lower latitudes. Additionally, under the SSP245 and SSP370 scenarios, *I. acuminatus* (group 1) will also gradually move towards lower latitude areas.

Under the four future climate scenarios, the current suitable area size of the nine bark beetle species shows a negative correlation with changes in their future suitable area (Fig. 10). Moreover, as radiation intensity increases,

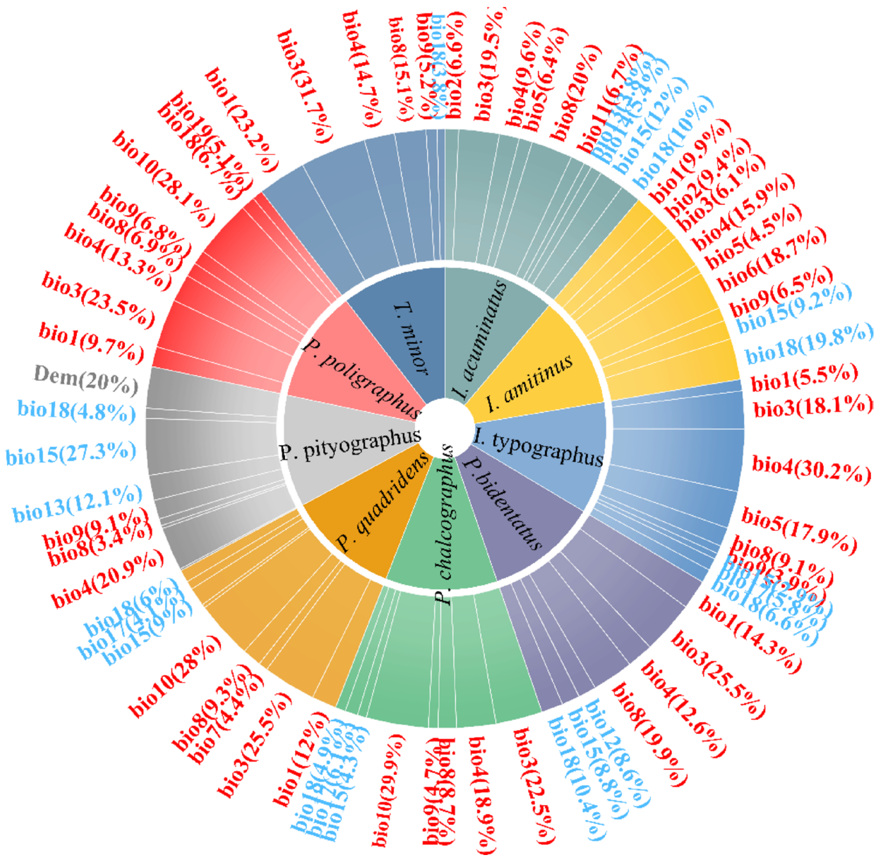


Fig. 3. Influence of environment related variables on the 9 species (Red font indicates temperature-related variables, blue font indicates precipitation-related variables, and gray font indicates terrain-related variables).

this correlation becomes stronger. In other words, among the nine bark beetle species in this study, those with a broader geographical distribution experienced smaller changes in their suitable area under climate change.

Discussion

Distributional range changes and key environmental variables

The geographical distribution range of most bark beetles is primarily driven by temperature-related variables, with only a small portion associated with precipitation-related variables (Fig. 2). This result is consistent with Smith's findings, which indicate that the developmental rates of some bark beetle species are primarily influenced by temperature, as it is typical for ectotherms[50]. Also Cao et al.[51] discovered that the key influencing factors for the potential range of *I. typographus* and *P. chalcographus* in Europe were mean temperature in the warmest season and mean temperature in the coldest season, respectively. González-Hernández et al.[52] through simulating the potential distributional range of *Dendroctonus* beetles in Mexican temperate forests, identified key bioclimatic variables affecting distribution, including annual temperature range, mean temperature of the wettest quarter, and mean temperature of the hottest quarter.

Under the influence of future temperature changes, by the year 2100, the suitable distribution areas for most of the study organisms will expand (Figs. 5 and 6). Previous research has showed that in warmer temperatures, the growth rate of bark beetles accelerates, leading to an increase in the number of generations per a year[53]. Concurrently, high temperatures may indirectly weaken the defense systems of host trees, considerably improving the efficiency of beetle infestation and gradually expanding the distribution area of their populations[54]. Different species are affected by environmental conditions differently. The Mean Temperature of Warmest Quarter and Isothermality were discovered as critical variables strongly correlated with the distribution of several species. The mean temperature of the warmest quarter generally represents the average temperature of the summer in European regions, and suitable temperatures during this period can enhance insect oviposition and larval growth. Meanwhile, isothermality, which refers to the annual temperature range, is also an important factor influencing insect generations and normal growth.

The distribution range of only two species were affected by precipitation. *I. amitinus* primarily parasitizes coniferous forests in northern Europe, while *P. pityographus* is more commonly found in coniferous forests in southern Europe. For these two insects, Precipitation in the Warmest Quarter is a crucial influencing factor. Water scarcity can significantly affect the resilience of trees, thereby compromising their health. Bark beetles take advantage of weakened trees due to water stress to facilitate rapid reproduction[55]. Under future climate change

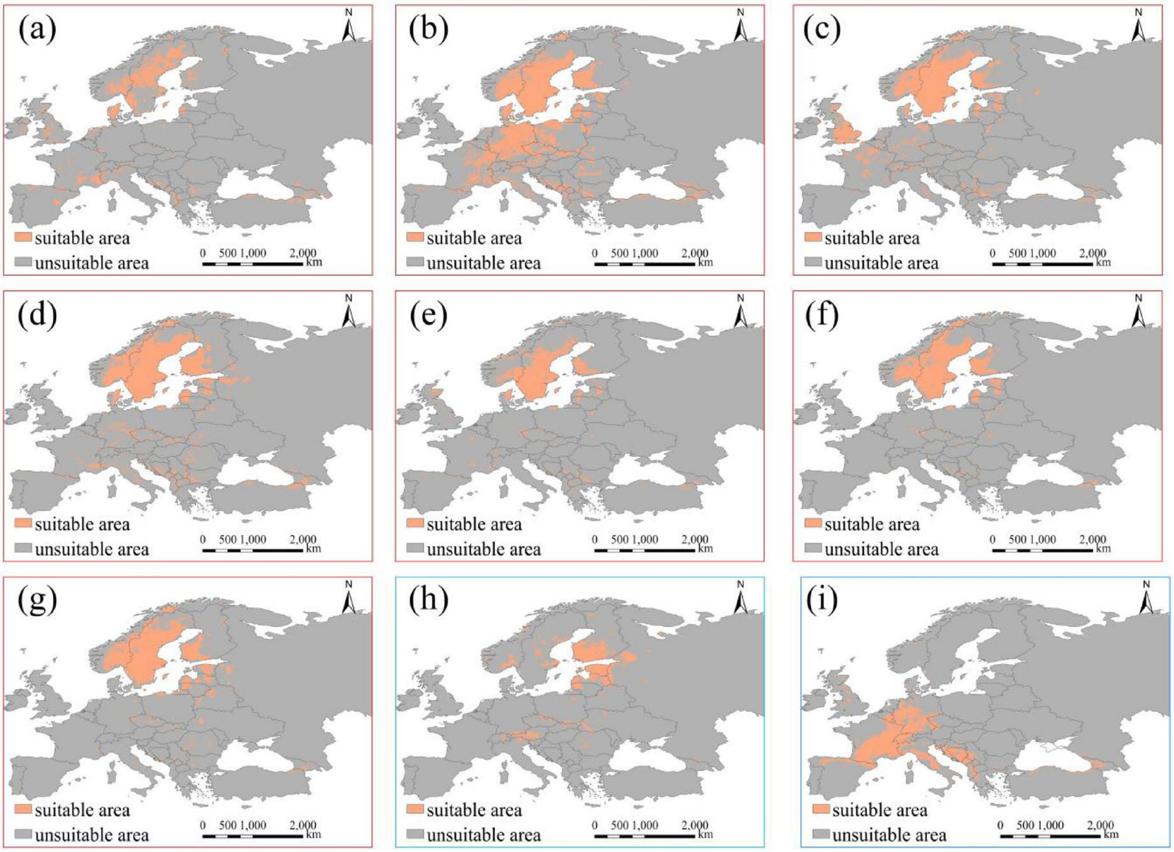


Fig. 4. The potential distribution of the nine bark beetle species under current climatic conditions. (**a**) *Ips acuminatus*, (**b**) *Ips typographus*, (**c**) *Pityogenes bidentatus*, (**d**) *Pityogenes chalcographus*, (**e**) *Pityogenes quadridens*, (**f**) *Polygraphus poligraphus*, (**g**) *Tomicus minor*, (**h**) *Ips amitinus*, and (**i**) *Pityophthorus pityographus* (Red frame indicates the potential area for the first group, while blue frame indicates the potential area for the second group). The maps were created by ArcGIS 10.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

	Historical	**SSP126**		**SSP245**		**SSP370**		**SSP585**	
Species	**×10^4 km^2**	**×10^4 km^2**	**%**	**×10^4 km^2**	**%**	**×10^4 km^2**	**%**	**×10^4 km^2**	**%**
I. acuminatus	67.5025	73.51	9	65.21	−3	71.99	7	76	13
I. typographus	192.427	199.13	3	169.23	−12	175.33	−9	162.29	−16
P. bidentatus	137.846	134.08	−3	126.26	−8	143.23	4	139.4	1
P. chalcographus	147.462	151.02	2	152.2	3	146.91	0	139.92	−5
P. quadridens	75.7113	91.7	21	89.21	18	90.1	19	85.76	13
P. poligraphus	97.2062	99.14	2	98.65	1	100.96	4	103.71	7
T. minor	112.279	113.99	2	112.66	0.3	110.97	−1	108.45	−3
I. amitinus	47.5704	68.18	43	60.30	27	53.64	13	63.05	33
P. pityographus	93.7753	89.66	−4	91.82	−2	96.83	3	104.44	11

Table 3. Bark beetle's distribution area changes in the future climate change scenarios.

scenarios, a reduction in precipitation during the warmest quarter could lead to extreme summer droughts, affecting tree health and providing favorable environmental conditions for bark beetle infestation of host trees.

The distributional range of bark beetles under future climate

Previous studies reported that climate change will expand the distributional range of bark beetles in Europe[51,56]. Our research further supports this viewpoint, showing that with continuous future climate changes, the major distribution areas for most of the species of bark beetles will increase (Fig. 5). Under the SSP126 scenario, the distribution area of *I. amitinus* is expected to expand the most, nearly 43% of its current distribution area. As many bark beetles typically have 1 to 2 generations per year with a short maturation time, adult activity in

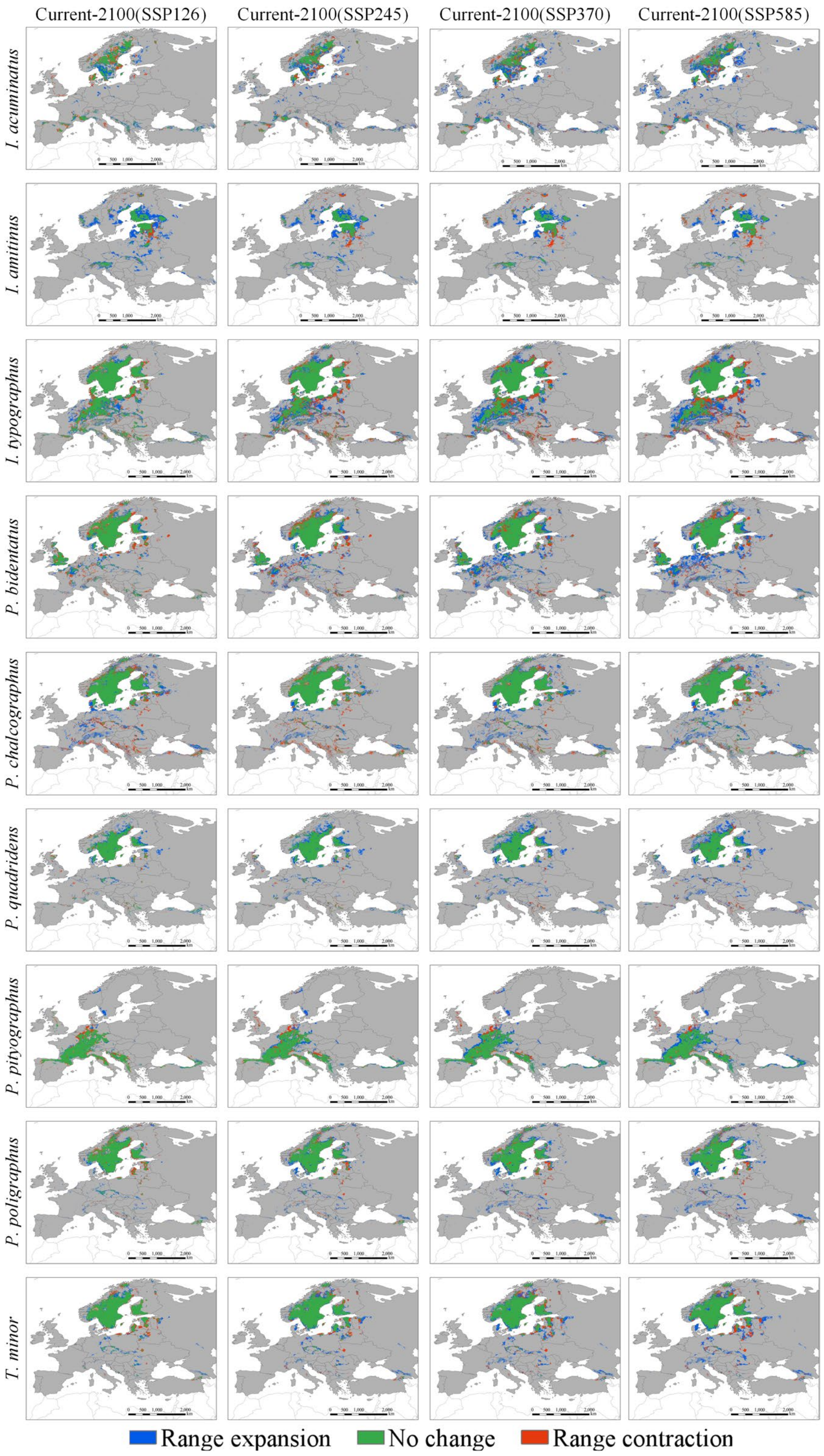


Fig. 5. Potential range changes for nine species of bark beetles under four future scenarios (blue areas indicate range expansion, green areas indicate no change in range, red areas indicate range contraction, and gray areas indicate other areas). The maps are created by ArcGIS 10.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

the forest varies, with some species exhibiting clear bursts of emergence throughout the growing season. This enables them to rapidly alter their distributional ranges. Therefore, bark beetles are likely to adapt to future climate changes and expand their distributional ranges[57,58]. However, despite the general trend of expansion for most bark beetles, certain species exhibit a reduction in their distributional range under the influence of

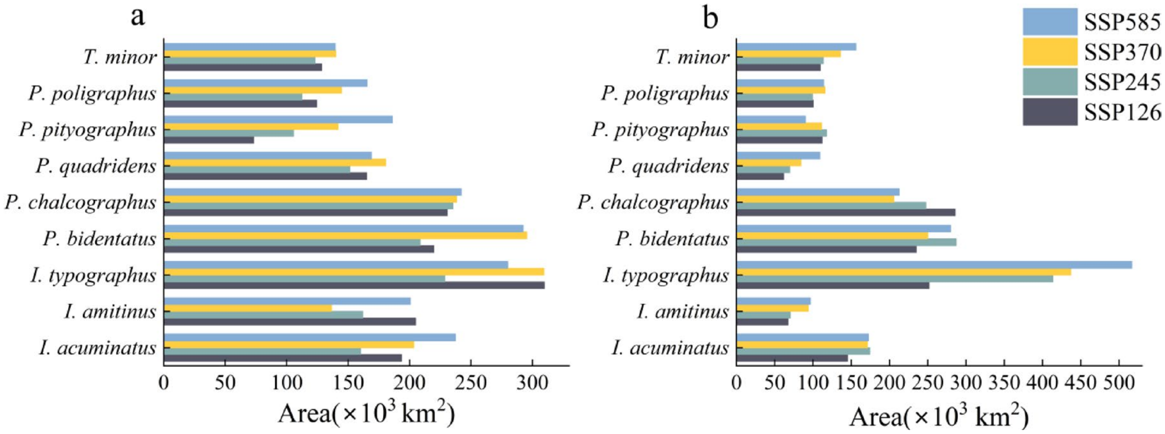


Fig. 6. Changes in potential range area (10^3 km^2 of nine bark beetle species under four future scenarios (a indicates the area of expansion of the nine species under the four future scenarios; b indicates the area of contraction of the nine species under the four future scenarios).

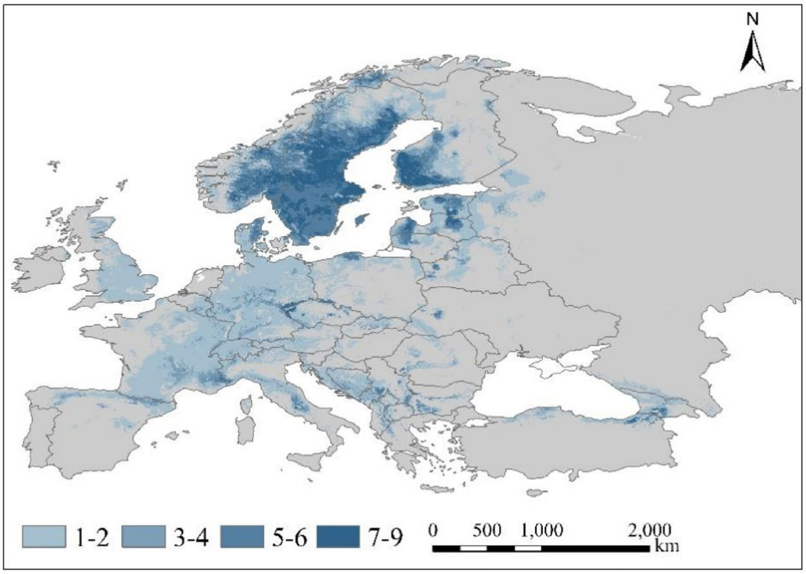
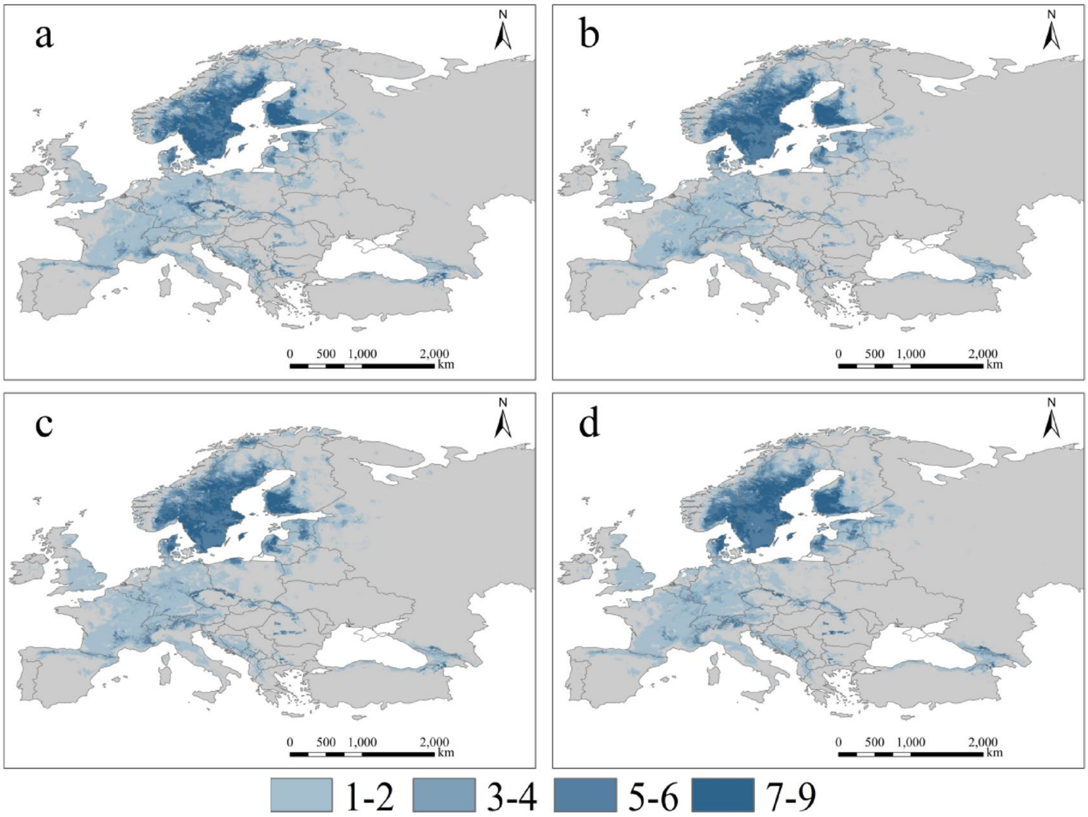


Fig. 7. Distribution of the number of species under the current period. The maps are created by ArcGIS 10.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

climate change. For example, *I. typographus* shows a contraction in SSP245, SSP370, and SSP585 scenarios. The trend of range contraction under high forcing scenarios may be related to the diapause restrictions of *I. typographus*. Jönsson's research indicates that changes in spring temperature and photoperiod can affect the spring diapause of *I. typographus*[59]. The climate scenario data used in Jönsson's study suggest that suitable spring temperature conditions will arrive earlier in the future, but *I. typographus* may not optimally respond to these earlier temperature conditions.

Range shifts are an important adaptive ability of species to future climate changes. Numerous research indicate that most species will migrate to higher latitude regions[35]. For instance, Bentz et al.[58] used phenological models to simulate the heat response of European *I. typographus*, indicating that *I. typographus* will shift northward under warming conditions. Similarly, Yang et al.[60] analyzed the distributional dynamics of invasive Asteraceae species in China under climate change, finding that most invasive Asteraceae species will move northward in the future. In our study, most temperature-affected bark beetles are predicted to shift to higher latitudes. However, *I. amitinus*, influenced by precipitation, is expected to move to lower latitudes in the future. This is probably because *I. amitinus* is also affected by changes in drought conditions than by temperature change[61]. The future dry conditions in southern regions are just what *I. amitinus* populations require for development.

Future outbreaks of bark beetles could lead to widespread invasions across much of the Scandinavian Peninsula (Figs. 7 and 8). Notably, the model predictions show that, in addition to the increasing species numbers in high-latitude regions, the Western Carpathians appear to be an ideal habitat for many species. This



The map was created using ArcGIS 10.2 (Esri, https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

Fig. 8. Changes in the distribution of species numbers of bark beetles under four future scenarios (a represents under SSP126 scenario, b under SSP245 scenario, c under SSP370 scenario, and d under SSP585 scenario). The maps are created by ArcGIS 10.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

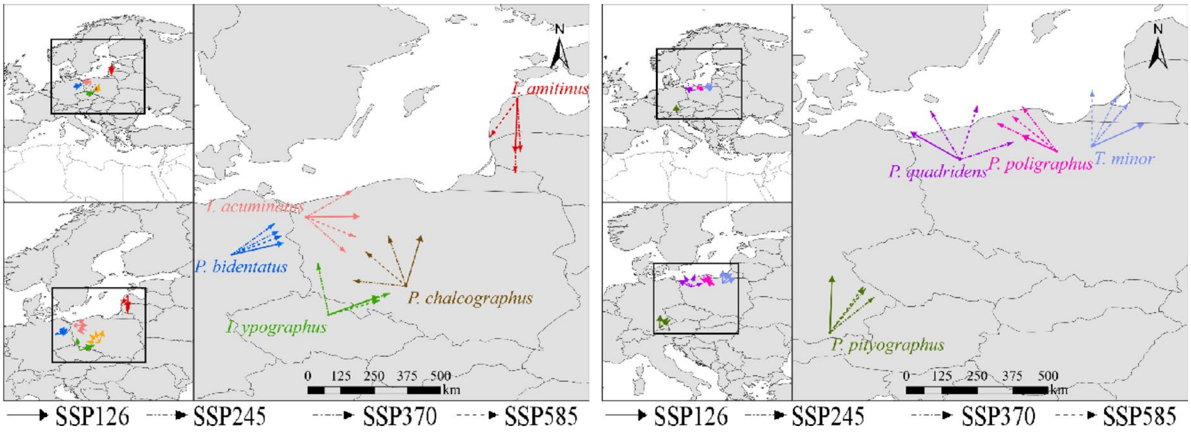


Fig. 9. Distribution centers and direction of change of nine bark beetle species under four future scenarios. The maps are created by ArcGIS 10.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview).

finding aligns with Zumr[62]who observed considerable numbers in this area. Insect numbers near the mountains are expected to increase significantly in the future, likely due to species shifting to higher latitudes or altitudes in response to global warming[63]. However, it must be recognized that bark beetles are not merely destructive pests, but also important natural disturbance agents. In some cases, they are even considered “keystone species,” as their activities can significantly enhance biodiversity, accelerate nutrient cycling, and create critical niches for subsequent forest regeneration. Therefore, when assessing the impacts of bark beetle range expansion under climate change, it is essential to fully consider their dual role in ecosystems, rather than viewing them solely as harmful pests.

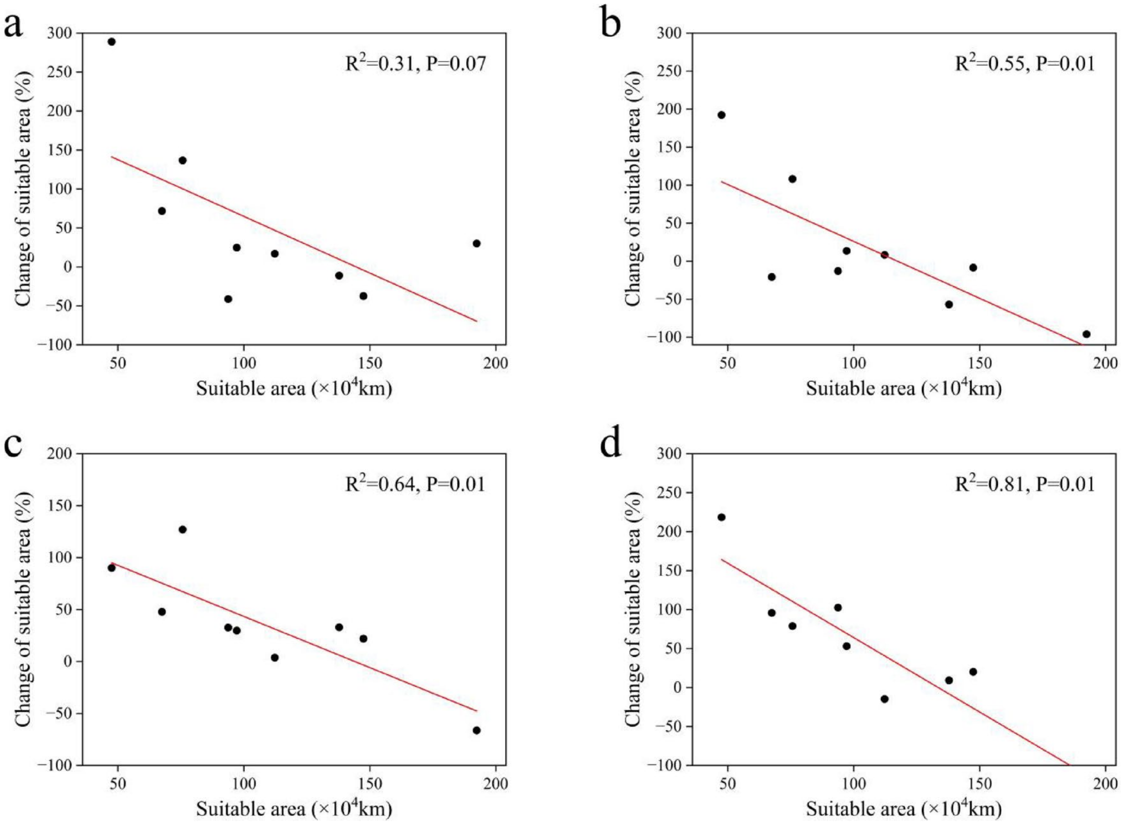


Fig. 10. Correlation of current period area of nine bark beetle species with changes in distribution area under four future scenarios (a shows under the SSP126 scenario, b under the SSP245 scenario, c under the SSP370 scenario, and d under the SSP585 scenario).

Relationship between current range size and magnitude of future range changes

The ecological niche and the geographical range of a species' population are closely related. Some studies indicate that species with narrower ranges are more vulnerable to climate change compared to those with wider ranges. For example, Wang et al.[18] found a negative correlation between the vulnerability of *Magnolia* species to future climate change and their distributional range. Similarly, Vincent et al.[64] studied 35 rare species and discovered that rarer species have weaker adaptive capacities to climate change. Our findings are in line with these studies, showing a negative correlation between the impact of climate change on bark beetles and their geographical distribution range (Fig. 10). Most species with a broad range exhibited smaller changes in distribution area under future climate change compared to those with a narrow range. For example, *I. amitinus*, which has a relatively small distribution range, shows a trend of rapid expansion in future environments with increased drought frequency. In contrast, *P. bidentatus* and *T. minor*, which have larger distribution ranges, exhibit the smallest changes in area among the nine bark beetle species studied, suggesting that they are relatively less affected by climate change. In other words, bark beetles with smaller distribution areas are more sensitive to future climate change. However, species with narrow distributions may also be more locally constrained by climate and more vulnerable to the negative impacts of localized stochastic events, potentially leading to a reduction in suitable habitat or even extinction[65]. For instance, the suitable area of *P. pityographus* is expected to decrease under low and medium forcing scenarios (SSP126 and SSP245), possibly due to local climatic constraints limiting its large-scale dispersal. Therefore, species with narrower distributions are more likely to exhibit strong responses to climate change. Though a relationship between distributional range and climate change susceptibility could be confirmed, this pattern should not be generalized. For instance, Qiu et al.[34] simulated the future distributional ranges of eight *Habenaria* and ten *Calanthe orchid* species and found no correlation between the current range size and future range changes.

Limitations of this study

The influence of environmental variables and topographic factors was considered without accounting for species dispersal abilities and biotic interactions. Considering only abiotic variables may lead to less accurate model predictions[66]. For instance, the analysis did not account for host tree availability, which is a crucial factor given that host trees will also shift their ranges under climate change and influence bark beetle dynamics—especially for those species that target stressed hosts. Additionally, the conclusions depended on the selected global circulation models (GCMs), thus, the uncertainty of GCMs can affect the accuracy of the results. A multi-model ensemble based on six different GCMs was used to minimize the impact of GCM uncertainty on the model.

The suitable distribution of bark beetle under future climates was predicted by using observed available records of the species. However, due to the possibility of incomplete records, the present distribution may not be fully reflected. Further research should consider the temporal aspect of occurrence records and incorporate biotic interactions for more accurate predictions.

Conclusions

MaxEnt model combined with bioclimatic variables from the CMIP6 multi-model ensemble (MME) was utilized to simulate and predict the potential impact of future climate on the distribution of narrowly and widely distributed bark beetles. Environmental factors influencing their distribution was also analyzed. For most species, temperature variables were the key factors influencing their distribution, with Mean Temperature of the Warmest Quarter and Isothermality being the most significant contributors. Under current climate conditions, Northern Europe is the primary potential distribution area. Under future climate scenarios, by 2100, eight bark beetle species are projected to expand northward, while only *I. amitinus* is expected to expand southward due to drought conditions. Furthermore, our findings suggest that the impact of climate change on bark beetles is negatively correlated with their distributional range. Consequently, the ability of both narrowly and widely distributed species to threaten forests under climate change requires further investigation and validation. The results of this study will contribute to a comprehensive and detailed understanding of the distribution patterns and dynamic changes of important bark beetles, and their future impact on European forests.

Data availability

The authors declare that the data that supports this research results can be found in the article. All data are available from the corresponding author upon request.

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Author contributions

Shengqi Jian and Yufei Han: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. Risto Kasanen: review & editing, Conceptualization. Juha Honkaniemi: review & editing. Samuli Junttila: review & editing. Fred O. Asiegbu: review and editing, Project administration, Funding acquisition, Supervision, Conceptualization. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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