

Threats to North American forests from southern pine beetle with warming winters

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In coming decades, warmer winters are likely to ease range constraints on many cold-limited forest insects^{1–5}. Recent unprecedented expansion of the southern pine beetle (SPB, *Dendroctonus frontalis*) into New Jersey, New York and Connecticut in concert with warming annual temperature minima highlights the risk that this insect pest poses to the pine forests of the northern United States and Canada under continued climate change⁶. Here we present projections of northward expansion in SPB-suitable climates using a statistical bioclimatic range modelling approach and current-generation general circulation model output under Representative Concentration Pathways 4.5 and 8.5. Results show that by the middle of the twenty-first century, the climate is likely to be suitable for SPB expansion into vast areas of previously unaffected forests throughout the northeastern United States and into southeastern Canada. This scenario would pose a significant economic and ecological risk to the affected regions, including disruption of local ecosystem services⁷, shifts in forest structure⁸, and threats to native biodiversity⁹.

SPB is a major forest pest in the southeastern United States responsible for 14 million m³ of timber losses worth an estimated US\$1.7 billion over 1990–2004¹⁰. SPB has historically been most damaging in southeastern states, with limited activity in the northern portion of its range including Ohio, Pennsylvania and Maryland. However, SPB outbreaks have become increasingly problematic and extensive in southern New Jersey since 2001, and populations have been detected for the first time on Long Island, New York, in 2014 and in Connecticut in 2015^{6,11}.

A link between SPB outbreaks and winter cold extremes has long been recognized¹², and minimum air temperatures between -14 and -20 °C have been observed to cause critical overwintering mortality in SPB^{4,13,14}. The recent northward expansion of SPB has occurred amidst regionally warming winters and decreasing incidences of cold extremes¹⁵. Since mean annual temperatures in the northeastern United States are projected to rise by 2–6 °C by 2100¹⁵, with possibly larger increases in winter cold extremes^{16,17}, the climatic constraints limiting SPB incursion further into northern pine forests will probably recede dramatically in the coming decades. Here we present a projected timeline for the expansion of SPB-suitable climates in eastern North America under continued climate change through 2090.

Previous modelling experiments of SPB range expansion under climate change have used statistical and physiological relationships between SPB outbreaks and weather established within the historic range, assuming that these relationships hold at the expansion

frontier, and have applied uniform climatic perturbations that overlook the temporal complexity and spatial heterogeneity of projected warming^{4,5}. In this study, we address these shortcomings by developing a statistical model linking recent SPB range expansion to changing incidence of cold extremes, and by using spatially explicit current-generation general circulation model (GCM) projections.

We also robustly analyse the sources and magnitudes of uncertainty in this timeline of expansion. In climate prediction, there are generally three components of total uncertainty: internal variability (natural stochastic climate variability), inter-GCM variability (resulting from differences in construction between GCMs), and scenario uncertainty (due to variation between plausible future emissions scenarios). Our phloem temperature model, which simulates thermal inertia of tree stems, introduces an additional source of uncertainty related to the thermal buffering coefficient, the K value, which depends on tree diameter (see Methods). Uncertainty estimation in past projections of insect range expansion under climate change has examined only variable emissions scenarios, ignoring other sources of uncertainty^{1–3}. While inter-model variability and scenario uncertainty are technically reducible, internal variability is fundamentally irreducible and therefore defines the theoretical minimum uncertainty in estimated timelines of SPB-suitable climate expansion (see Supplementary Information). In this study, we estimate the proportion of total uncertainty in our projections arising from various sources to understand its potential reducibility and role in informing adaptive management decisions (for example, prescribed fire, forest harvesting¹⁸).

SPB's spread across southern New Jersey has occurred amid a warming trend: for example, the -10 °C winter minimum phloem temperature isotherm has migrated northwards by 0.6° latitude (~ 65 km) per decade since 1980 ($P < 0.01$) (Fig. 1a). Meanwhile, the latitude of the northernmost SPB sighting has drifted north by 0.8° latitude (~ 85 km) per decade since 2002 ($P = 0.01$). Inter-annual north–south variation in SPB's northern range frontier only weakly corresponds to extreme temperature minima (Fig. 1a) and probably depends on ecological factors of less consequence to longer-term changes including forest conditions, host-tree vigour and predator dynamics¹⁹. SPB is absent in all New Jersey grid cells experiencing phloem temperatures less than -16 °C (corresponding to air temperatures of -18 to -20 °C) (Fig. 1b), substantiating a lethal minimum temperature constraint on SPB. Our estimate of this limiting temperature concurs with past estimates within SPB's historical range⁴, suggesting that recent range expansion is because of warming and not plasticity in the cold tolerance of northern SPB populations¹³.

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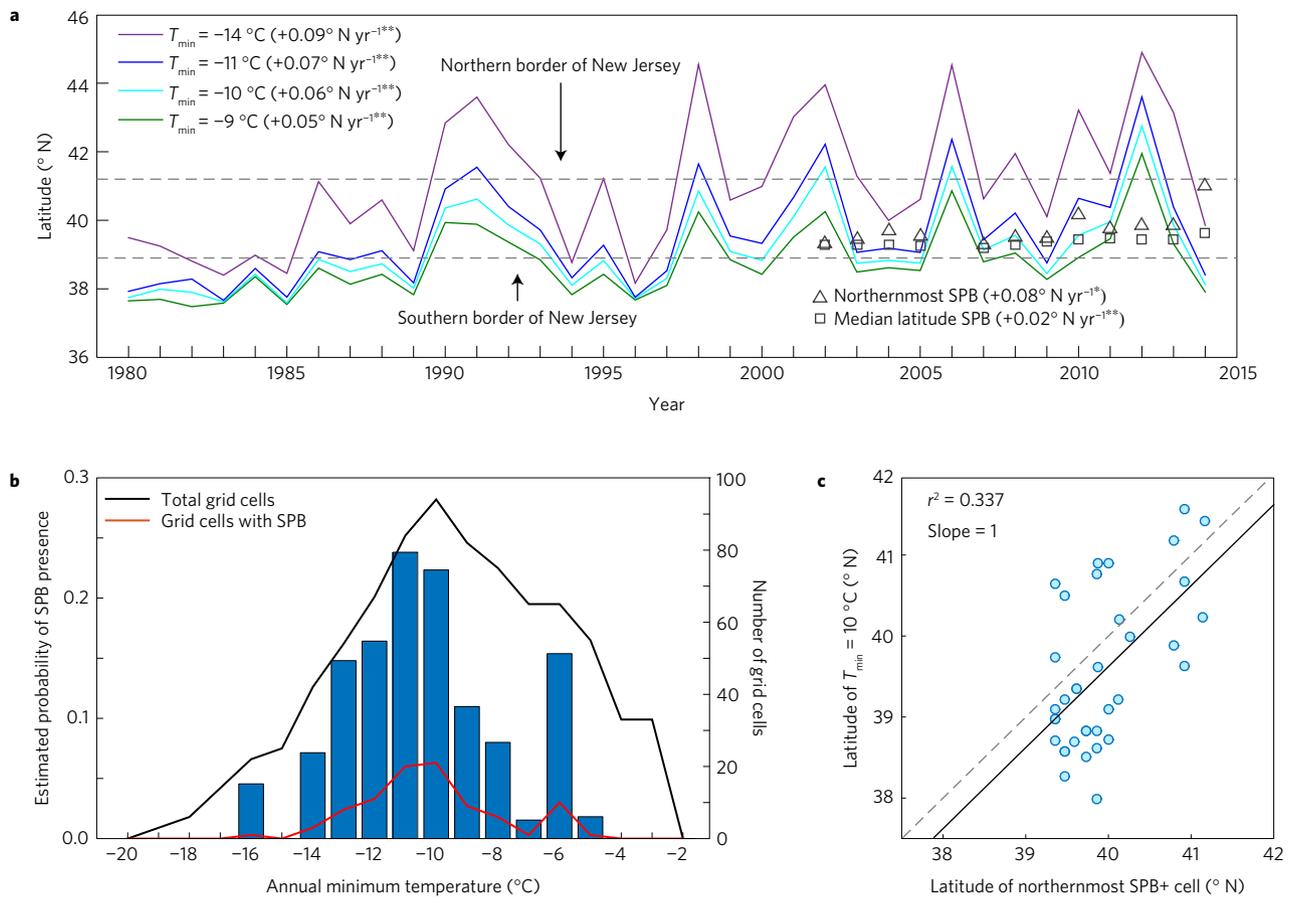


Figure 1 | Spatial correspondence between recent SPB expansion and warming annual minimum phloem temperatures. a, Southernmost latitudes of occurrence for various minimum winter phloem temperatures over 1980–2014 (solid lines), maximum (triangles) and median (squares) latitude of SPB presence across New Jersey over 2002–2014 (no data for 2006). Linear trends in latitudes are shown in legends (double asterisks denote $P < 0.01$, single asterisks denote $P < 0.05$). **b**, Total cells (black line), cells with SPB presence (red line), and estimated probability of SPB presence (bars) over 1°C annual minimum phloem temperature bins. Data are aggregated across New Jersey over 2002–2014. **c**, Latitude of northernmost SPB-positive grid cell versus southernmost latitude of critical phloem temperature at corresponding longitudes over 2002–2014 for the range-predicting temperature of -10°C ($n = 36$). The one-to-one relationship is shown in dashes.

Q.3

1 Among a series of candidate range-predicting minimum phloem
 2 temperatures, we found that the latitude of the -10°C isotherm best
 3 correlated with the latitude of the northernmost SPB occurrence
 4 across six longitudinal bins ($r^2 = 0.34$, Fig. 1c, Supplementary
 5 Fig. 2 and Supplementary Table 3). This temperature exceeded
 6 the lethal limit of -16°C , probably because low beetle survival
 7 at or below -16°C reduced the likelihood of a sighting. We
 8 therefore designated the year after which winter minimum phloem
 9 temperatures remain above -10°C for ten consecutive years as the
 10 year of emergence of a SPB-suitable climate. This ten-year window
 11 can be applied consistently to each annual time step over 2006–2080
 12 (see Supplementary Information).

13 On the basis of the 27-GCM mean (Supplementary Table 1), we
 14 project increases in annual minimum air temperature of 3.5 – 7.5°C
 15 for Representative Concentration Pathway (RCP) 4.5 and 8.5
 16 across the northeastern United States and southeastern Canada
 17 by 2050–2070, with annual minimum phloem temperatures rising
 18 by a slightly smaller 3.0 – 7.0°C (Supplementary Fig. 3). These
 19 projections are consistent with other studies using Coupled Model
 20 Intercomparison Project Phase 5 (CMIP5; ref. 16) and other model
 21 suites¹⁷. Given this warming trend and our criteria for SPB-suitable
 22 climates, vast areas across the northeastern United States and
 23 southern Ontario and Quebec are projected to become climatically
 24 hospitable to SPB populations before 2080 (Fig. 2a), according to
 25 multi-run mean projections. We project sufficient warming for the

Q.4

26 establishment of SPB along the Atlantic coast to Nova Scotia before
 27 2020, and from southern New England through Wisconsin between
 28 2040 and 2060 (Fig. 2a). The projected years of emergence for areas
 29 already affected by SPB in New Jersey and New York agree with
 30 observations. These results are relatively robust to alternative range-
 31 predicting temperatures (Fig. 3, see Methods).

32 There is considerable uncertainty in the above multi-run mean
 33 results. Among 162 model runs using differing GCMs, emissions
 34 scenarios and K values (see Methods), the earliest projected year
 35 of emergence differs from the latest by 43 years (Fig. 2b,c).
 36 To understand the origin of this uncertainty, we estimated the
 37 proportion of total uncertainty arising from the four sources
 38 (Fig. 4a): internal variability (12%), emissions scenario (13%), inter-
 39 GCM (58%) and K value (17%). While uncertainty from internal
 40 variability is theoretically fully irreducible and comprises a plurality
 41 of total uncertainty in some areas (Fig. 4b), the emissions scenario
 42 and inter-GCM portions are effectively irreducible in the near term
 43 (see Supplementary Information). This finding suggests that forest
 44 managers should consider the range of plausible years of emergence
 45 in setting adaptation priorities and strategies.

46 In addition to sufficiently mild winters, SPB requires suitable
 47 host-tree species with sufficient areal density to survive in a given
 48 location. To identify where and when SPB-suitable climates coincide
 49 with SPB-susceptible forests, we mapped the ranges of forest types
 50 defined by dominant pine species alongside isolines representing

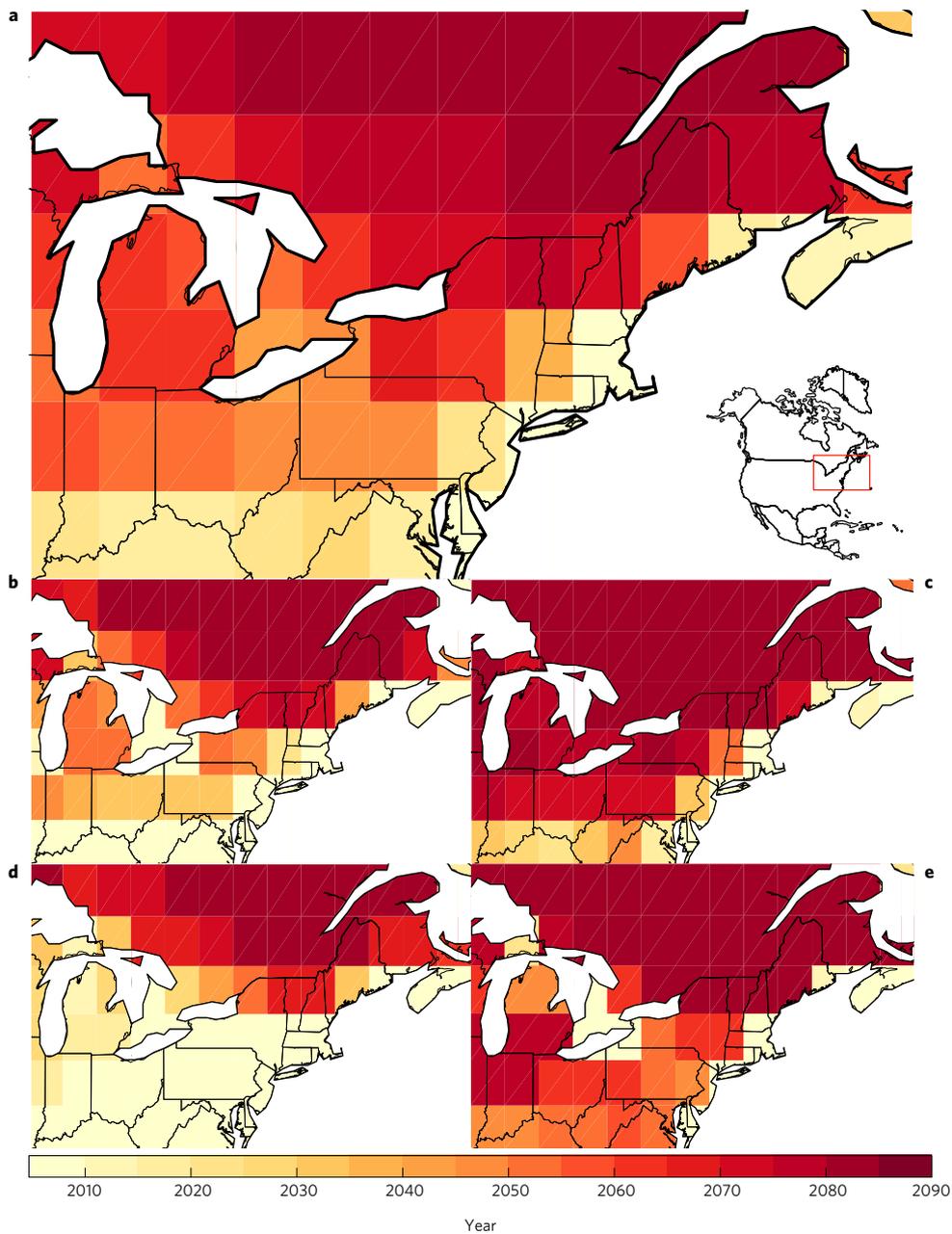


Figure 2 | Projected year of emergence of SPB-suitable climate, defined as the year for which minimum phloem temperature of -10°C is not reached in the following decade. **a, Mean of full set of 162 model runs (27 GCMs, 2 emissions scenarios and 3 K values). **b**, 25th percentile of the full set. **c**, The same as **b** but for the 75th percentile. **d**, Minimum of internal variability range across 60 runs (10 CSIRO-MK3 ensemble members, 2 emissions scenarios and 3 K values). **e**, The same as **d** but for the maximum.**

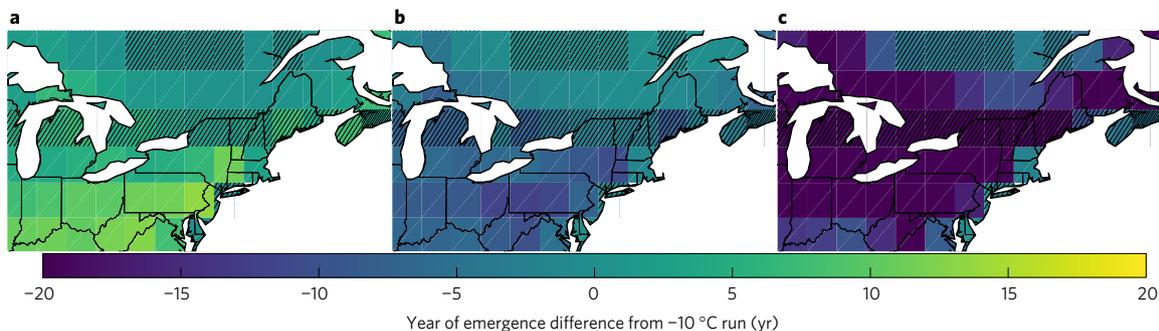


Figure 3 | Projected year of emergence of SPB-suitable climate using alternative definitions of SPB suitability. **a-c, Next-best range-predicting temperatures of -9°C (**a**) and -11°C (**b**), and the lethal temperature of -16°C (**c**). Results are presented as differences compared with the main results using -10°C (Fig. 2). Stippling indicates grid cells for which results are highly robust (difference < 5 years across all alternative definitions).**

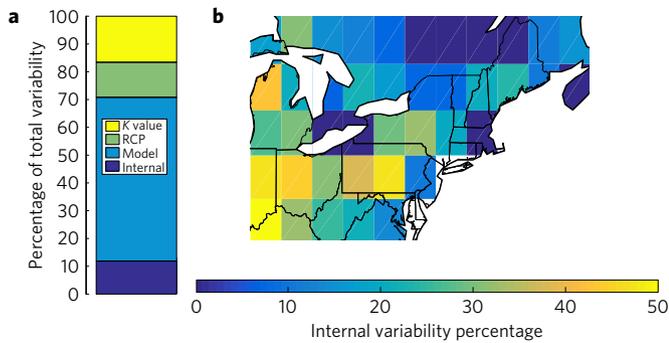


Figure 4 | Drivers of uncertainty in projected year of emergence of SPB-suitable climates. **a**, Estimated partitioning of total year of emergence uncertainty into its four components: internal variability (dark blue), differences between GCMs (light blue), emissions scenarios (RCP, green) and K values (yellow). **b**, Estimated percentage of the total uncertainty resulting from internal variability across the study region, ranging from 10–50% among non-coastal grid cells. Although reduction of all sources of uncertainty is technically challenging, uncertainty due to internal variability is theoretically irreducible and therefore unavoidable in setting adaptation priorities and strategies (see Supplementary Information).

species in its historical range²², and tree attacks have recently been documented for the first time in red and white (*P. strobus*) pines on Long Island, New York and Connecticut (personal communication). Although successful reproduction of SPB in white pine has not yet been documented, a moderate density of more suitable pitch and red pine across the region may provide a pathway for expansion (Supplementary Fig. 6, see Supplementary Information).

Pine-sparse hardwood forests in the northern United States may present a barrier to continued SPB dispersal into the red and jack pine forests further north. However, SPB has already traversed large pine-sparse regions in the eastern United States, and forests further north feature a higher, more continuous density of pine (Fig. 5b). The Great Lakes pine forests are separated to the south and east by a larger pine-sparse zone. Our projections indicate that the pine-dense Canadian forests north of the Great Lakes will become climatically suitable by 2050–2080, opening a plausible route for SPB spread to these forests (Fig. 5a).

Although SPB has already been detected in western Connecticut in 2015, we project these areas to be climatically suitable for SPB only after 2025. Long-range SPB dispersal is poorly understood²³ and may occur over greater distances than previously thought²⁴ (for example, 2010, Fig. 1a). These earlier-than-predicted sightings could reflect a tendency of SPB to disperse far beyond its climatically constrained range²², as observed in New Jersey in 2014 (Fig. 1a), but fail to survive a subsequent winter and establish stable populations. In this case, our model might accurately project longer-term range expansion despite omitting shorter-term leaps. By contrast, sustained future SPB presence in these areas would suggest that our model underestimates the pace of expansion. Continued SPB monitoring will enable a rigorous assessment of this aspect of our model's performance and further research into the relationship between long-term and intermittent range expansions.

Further ecological and climatological factors not simulated in our study, such as drought, fire and community-level interactions, may affect future SPB range expansion. By mid-century, the northeastern United States is likely to experience elevated drought risk and 10–40 additional extreme heat days per year¹⁵. Some forest types are more susceptible to attack by bark beetle when stressed by drought and extreme heat²⁵; however, the link between drought and SPB may be weaker²⁶ or more nuanced²⁷ than for other beetle species. In contrast to some conifer-infesting beetles, SPB has not been strongly linked to natural or prescribed fire²⁸. However, this association may become clearer if fire regimes shift under climate change. Although SPB may encounter suppression by or release from predators and competitors in newly suitable areas, SPB's primary predator (*Thanosimus dubius*) is widely distributed in eastern North

multi-run mean years of SPB-suitable climate emergence across the study region (Fig. 5a). These forest type ranges are expected to shift under climate change²⁰, but because projected changes in dominant species are small through 2100²¹, we approximated them as static in our analysis. We also mapped the basal area density of the various pine species over the study region to identify pine-sparse areas that may inhibit further SPB spread (Fig. 5b).

By 2050, 78% of the 124,000 km² range of pitch pine (*Pinus rigida*) forests extending from southern Maine to eastern Ohio are projected to feature newly SPB-suitable climates. This forest ecosystem is particularly vulnerable to SPB and has already suffered unprecedented widespread tree mortality in New Jersey and New York^{6,11}. Our projections demonstrate a significant risk to pitch pine forests within 35 years, including broad disruption of local ecosystem services⁷, shifts in forest structure⁸, and threats to native biodiversity⁹.

By 2080, we project that SPB-suitable climates will reach 71% of the red pine (*P. resinosa*) and 48% of jack pine (*P. banksiana*) forest ranges that extend across more than 706,000 km² in the northeastern United States northwards through subarctic Canada (Fig. 5a). It is uncertain whether SPB will thrive in forests dominated by these pine species. However, SPB is highly polyphagous among pine

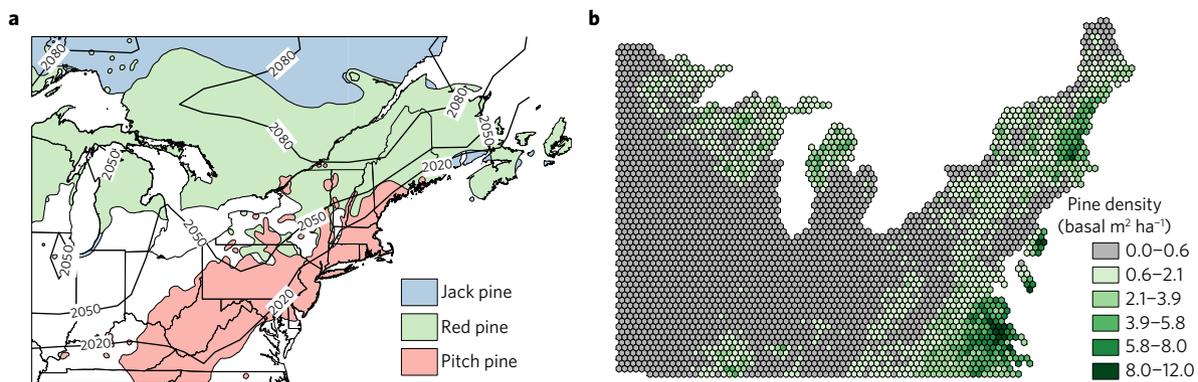


Figure 5 | Projected SPB expansion into ranges of forest types with suitable dominant pine species. **a**, Lines of equal year of emergence of SPB-suitable climate (black lines) and ranges of forest types defined by dominant pine species across the northeastern United States and southeastern Canada. Climates suitable for SPB are projected to reach 78% of previously unaffected North American pitch pine (red, *Pinus rigida*) forests by 2050, and 71% of red pine (green, *P. resinosa*) and 48% of jack pine (blue, *P. banksiana*) forests by 2080. **b**, Aggregate basal area density (m² ha⁻¹) of selected *Pinus* species across the northeastern United States. SPB has already dispersed across large areas of low pine density along its expansion trajectory.

America²⁹ and has not strongly influenced recent expansion. Finally, while our analysis projects future change in SPB-suitable areas, the degree of SPB damage to forests depends on outbreak intensity, which is linked to climate, forest conditions and management, and SPB population dynamics¹⁸. Further monitoring and research are needed to understand how these factors may affect the regional impacts of SPB into the future (see Supplementary Information).

Our study reveals a plausible new threat from SPB to vast areas of pine forest in eastern North America by 2050 and into subarctic Canada after 2080 under continued climate change. Meaningful global greenhouse gas emissions mitigation can reduce the projected risks only after 2050, as projected warming is largely independent of emissions scenario for the coming few decades³⁰. Further monitoring and research concerning the additional determinants of SPB range not simulated in our projections, such as the suitability of northern pine species and the role of drought, will improve the understanding of SPB's implications for northern pine forests. Despite these uncertainties, our results suggest that the mounting threat posed by SPB to regional ecosystems, biodiversity and economies is likely to become increasingly relevant to forestry managers and policymakers as climate change proceeds.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

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Author contributions

C.L. and E.C. conceived and coordinated this research and performed modelling and analysis. A.W.D.A. and K.D. contributed data and methods. All authors discussed the results and wrote the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Correspondence and requests for materials should be addressed to C.L.

Competing financial interests

The authors declare no competing financial interests.

Methods

The dynamics of phloem heating and cooling in response to winter temperature variation is an important determinant of the minimum winter temperature that an overwintering SPB is exposed to. To simulate the thermal buffering of tree stems, we modelled phloem temperatures using a linear Newtonian heat flux model with thermal buffering coefficient values (K values) representative of regional forest structure¹⁴. This phloem temperature model was used for both historical and projected future temperatures.

For the historical portion of our analysis, we drove the phloem temperature model using bias-corrected historical air temperature data with 30 km grid resolution at three-hourly intervals from North American Regional Reanalysis³¹ (see Supplementary Information). To identify the critical minimum phloem temperature for SPB in New Jersey, we mapped the presence or absence of SPB based on aerial pest detection surveys over 2002–2014³² (data missing for 2006) onto the annual minimum phloem temperature grids. We then estimated the probability of SPB occurrence at minimum temperatures ranging from -20 to -2 °C as the number of cells with SPB divided by the total number of cells with given minimum temperature. The probability of SPB occurrence dropped to 0 for all temperatures less than -16 °C, indicating a lethal minimum temperature.

To select the phloem temperature that best predicted the northern range limit of SPB, we assessed a window of seven candidate temperatures (-8 through -14 °C) centred on the temperature of peak probability of SPB occurrence (-11 °C). We collated 36 annual grid cells with active SPB populations across 6 longitudinal bins and for each cell observed the southernmost latitude at which each of 7 candidate critical temperatures occurred at the cell's longitude (to account for varying climates from coastal to interior New Jersey). We then fitted linear trends to scatter plots of the latitude of northernmost SPB populations versus latitudes of the candidate minimum temperatures (Supplementary Fig. 2). A linear regression with slope of 1, intercept of 0, and r^2 of 1 would indicate perfect correspondence in space between the northern limit of SPB range and southernmost occurrence of that candidate minimum temperature (see Supplementary Information). We found that the critical temperature of -10 °C best matched these criteria, with slope of 1.00, $r^2 = 0.34$, and an intercept of ~ 0.4 ° of latitude (Fig. 1c, Supplementary Fig. 2 and Supplementary Table 3, see Supplementary Information). Two other candidate temperatures (-9 °C and -11 °C) satisfied these criteria nearly as well, so we treated them as alternative plausible range-predicting temperatures in the sensitivity analysis.

Future daily phloem temperatures over 2006–2090 were projected independently for 27 CMIP5 GCMs³³ under the RCP4.5 and 8.5 emissions scenarios³⁴ (Supplementary Table 1) in conjunction with the phloem temperature model. Model-specific mean temperature biases due to factors such as varying parameterization schemes and internal model dynamics ranged from 3–5 °C relative to the National Centers for Environmental Prediction (NCEP) reanalysis³⁵. To correct these biases, we divided the daily maximum and minimum temperature distributions for NCEP reanalysis and each model into ten 10-percentile bins and corrected the mean bias between the model and the reanalysis for each bin¹⁷ (Supplementary Fig. 4). This method accounts for generally larger bias near the high and low tails (Supplementary Fig. 5). Residual biases were minimal except on the periphery of the study area.

Year of emergence of an SPB-suitable climate was estimated as the first year in which the critical minimum temperature of -10 °C was not reached in the following decade. This ten-year window was chosen as it could be applied consistently to each annual time step over 2006–2080. We present the mean year of emergence across all -10 °C runs in Fig. 2a. To examine the sensitivity of these multi-run mean results to varying plausible definitions for the emergence of SPB suitability, we recomputed the year of emergence projections for the next-best range-predicting temperatures of SPB's northern frontier (-9 °C and -11 °C, Fig. 3a,b). We also examined the results using the lethal minimum temperature of -16 °C (ref. 13) (Fig. 3c and Supplementary Information). The alternative results (Fig. 3) are presented as differences in the multi-run mean year of emergence from

the -10 °C result in Fig. 2a. Projections using the next-best predictors of SPB's northern frontier (-9 °C and -11 °C, Fig. 3a,b) differed from those under the -10 °C definition by ≤ 2 years on region-wide average, indicating low sensitivity of the results to alternative range-predicting temperatures. Projections based on the lethal minimum temperature (-16 °C, Fig. 3c)^{13,14} as opposed to the range-predicting temperatures were 14 years earlier on region-wide average; these results may be considered an earliest plausible projected timeline of SPB emergence (see Supplementary Information).

Total uncertainty in the year of emergence projections was estimated by considering the full set of 162 model runs generated from the combination of 27 CMIP5 GCMs, 2 emissions scenarios (RCP4.5 and 8.5) and 3 K values. We presented the 25th and 75th percentiles of this full set as the central range of year of emergence results (Fig. 2b,c). To estimate the partitioning of the total uncertainty into its constituent sources, we employed two different methods. For the emissions scenario, GCM and K value sources, we estimated the percentage of uncertainty arising from each source as its year of emergence range over the year of emergence range of the full set (see Supplementary Information). For internal variability, we applied a similar method using a suite of 60 results based on a 10-member ensemble of the Commonwealth Scientific and Industrial Research Organisation (CSIRO)-MK3 GCM³⁶ driven by the 2 emissions scenarios and 3 K values (Fig. 2d,e). We present these rescaled partitioned uncertainties in Fig. 4a, along with a map of the internal variability ratio in Fig. 4b (see Supplementary Information).

Lines of equal year of emergence were fitted to the multi-run mean year of emergence maps and were manually smoothed in some areas to reduce implausible precision induced by the contour fitting algorithm, especially near coastal grid cells (Fig. 5a). Data on the spatial extent of pitch, red and jack pine forests were obtained from the US Forest Service Forest Inventory and Analysis Program (Fig. 5a)³⁷, and we mapped basal area density of pine species using a derived raster imputation basal area map also from the US Forest Service (Fig. 5b)³⁸. The area of forest newly climatically suitable for SPB was calculated as the suitable area in 2050 (for pitch pine) or 2080 (for red and jack pine) minus the suitable area in 2007 (no jack or red pine forests were suitable for SPB in 2007).

Data availability. The daily minimum temperature data that support the findings of this study are available from the Coupled Model Intercomparison Project Phase 5 archive, located at http://cmip-pcmdi.llnl.gov/cmip5/data_portal.html. These data were processed as described in the Methods. The SPB aerial detection survey, forest range and pine basal area density data are available from the United States Forest Service at <https://foresthealth.fs.usda.gov/portal/Flex/IDS>, <https://www.fs.fed.us/foresthealth/technology/adsm.shtml>, <http://www.fs.fed.us/ne/delaware/4153/global/littlefia/index.html>, and <https://www.fs.usda.gov/rds/archive/Product/RDS-2013-0013>.

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