Geographical variability of spruce bark beetle development under climate change in the Czech Republic

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ABSTRACT: Climate change is expected to influence the distribution and population dynamics of many insect pests, with potential severe impacts on forests. Spruce bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) is the most important forest insect pest in Europe whose development is strictly regulated by air temperature. Therefore, climate change is anticipated to induce changes in the pest's distribution and development. We used the PHENIPS model to evaluate climate change impacts on the distribution and voltinism of spruce bark beetle in the Czech Republic. Two future time periods – 2025–2050 (near future) and 2075–2100 (distant future) – are addressed. The period 1961–1990 is used as the reference. We found that while a two-generation regime dominated in the Czech Republic in the reference period, significant three-generation regime regions are projected to appear in the near future. In the distant future, the three-generation regime can be expected to occur over all existing coniferous stands in the Czech Republic. The analysis of altitudinal shift of *n*-generation regime regions indicates noticeable expansion of *Ips typographus* development to higher elevations, leading for example to disappearance of one-generation regime regions in the distant future. Uncertainties and limitations of the presented findings are discussed as well.

Keywords: bark beetle altitudinal shift; climate change scenario; *Ips typographus* generations; temperature increase

Responses of forest pests to changing climate are extremely rapid in comparison with the inherent adaptive capacity of forest trees. It is assumed that insect herbivores will respond faster to climate change, and given the host plants that are available in new areas of the pest potential occurrence, some species may extend their distributional ranges rapidly (Rouault et al. 2006). This issue has become of key importance in assessing climate change impacts on forestry, agriculture and other sectors (MacLeod et al. 2002; Olfert, Weiss 2006; Baier et al. 2007; Trnka et al. 2007). The increased air temperature can influence pest populations mainly by (*i*) prolonged vegetation season and availability of host plants, (*ii*) accelerated development of a single generation in multivoltine species, (*iii*) lower mortality rate during winter, and (*iv*) overall change in the pest development (Porter et al. 1991). Climate change can also influence insect emergence and first appearance after hibernation, which may depend on a combination of day length and temperature thresholds. The dormancy phase, which is essential to many species in temperate regions for the completion of their life cycles and endurance of low temperatures during the winter season, could be influenced as well (Netherer, Schopf 2010). In contrast, the "growth-differentiation balance" hypothesis (Herms, Mattson, 1992) indicates that moderate water stress as well as plant exposure to increased levels of atmospheric CO_2 are likely to

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stimulate plant defence and resistance to the colonization by phytophagous insects.

Spruce bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) is anticipated to benefit mainly from an accelerated developmental rate, thus allowing for the earlier completion of life cycles and establishment of additional generations within a season (Lange et al. 2006). Climate change is also expected to influence the pest swarming activity, diapause and winter mortality. The temperature regime during autumn could have a decisive impact on the size of the swarming population in the next spring (Jönsson et al. 2009).

An abiotic stress affects the interplay between susceptibility of vegetation and activity of insect pests (Jönsson et al. 2009). It is projected that severe regional heat waves may become more frequent in a changing climate (Meehl, Tebaldi 2004), thereby increasing the spruce susceptibility to bark beetle attacks. In addition, forest stands damaged by wind are especially important precursors to outbreaks as they quickly provide large quantities of optimal breeding material (e.g. Grodzki et al. 2006). Thus a projected increase in the windstorm frequency (Giorgi, Coppola 2007) could also escalate the bark beetle threat to forests in future.

The purpose of this paper is to analyze how *I. typographus* development can be influenced by climate change in the Czech Republic and to describe the spatial variability of expected changes. In particular, we:

- calculated the climatic potential for the development of a certain number of bark beetle generations in the Czech Republic for the reference and future climates using a climate change scenario with high spatial resolution;
- produced maps describing the regions where certain numbers of *I. typographus* generations are expected to develop;
- described the interannual variability of modelled bark beetle development under the reference, near future and distant future climates;
- identified the elevation ranges of *n*-generation regime regions in the reference, near future and distant future periods.

MATERIAL AND METHODS

Climate change scenario used

The reference and future climate data were originally calculated using the global circulation (climate) model (GCM) ARPEGE-Climat V4 (Déqué 2007) in an experiment performed by CNRM/Météo-France. Because of the rather coarse resolution of the GCM (~50 km over Central Europe), a regional climate model (RCM) ALADIN-Climate/CZ (Farda et al. 2010) was used for the additional downscaling of GCM data. The IPCC A1B emission scenario was adopted for information on the future development of greenhouse gas emissions. The scenario represents a medium variant of greenhouse gas emissions. The RCM covers Central Europe with horizontal spatial resolution of 10 km. The data used in this study comprise a subset of ALADIN's entire integration domain covering the Czech Republic. This data was developed in the framework of the CECILIA (Central and Eastern Europe Climate Change Impacts and Vulnerability Assessment, www.cecilia-eu.org) 6FP Project.

Modelling approach

The analysis of bark beetle development was based on the model PHENIPS – A Complex Phenological Model of *I. typographus* (Baier et al. 2007). The used stage-specific developmental thresholds were proposed by Wermelinger and Seifert (1998).

A general principle of the PHENIPS model is as follows: maximum daily air temperature indicates the year day of infestation onset, while mean bark temperature determines the development of particular developmental stages of parental generations. The onset of host tree infestation in spring is estimated using the lower threshold of 16.5°C for flight activity and the mean thermal sum of 140 degree-days from the beginning of April. Parental beetles occur after the thermal sum of 557 degree-days accumulated above 8.3°C needed for total development is reached. Discontinuance of the reproductive activity of beetles occurs at a day length shorter than 14.5 h (August 22 in the study region). Mean bark temperature is calculated by regression of daily mean air temperature and solar radiation. The equation proposed by Baier et al. (2007) has been used without any modification. The egg stage is assumed to require 12% of the total development time, while 35% is attributed to the larval stage and 13% to the pupal stage. The longest stage is maturation feeding, i.e. the period starting with the emergence of adult beetles from their brood trees until the establishment of another generation.

As the PHENIPS model was not originally designed for investigating *I. typographus* development under climate change, we describe how the climate change scenario data were adapted to this purpose.

All climate data needed – daily solar radiation, daily mean and maximum air temperature – were available at all grid points (10 × 10 km spatial resolution) of the aforementioned RCM. Climatic time series of the reference period (1961–1990) were interpolated into RCM grid points from the neighbouring meteorological stations. Future time series for the periods 2021–2050 and 2071–2100 were originally simulated at RCM grid points. Such data allowed for using the PHENIPS model to calculate the total number of degree-days indicating the number of *I. typographus* generations developed at each grid point. The calculations were conducted for an average climate of the reference, near future and distant future periods (30-year average climate data).

To produce seamless maps describing the regions with *n*-generation regime of *I. typographus* in the Czech Republic, the acquired degree-day sums were interpolated using kriging with external drift (Matheron 1973) over the whole country while using elevation as the predictor variable. Subsequently, the division of interpolated degree-days by 557 yielded the number of fully developed generations at each location in the country.

An increase in the number of generations and spatial variability of such increase are described. Changes in other parameters (onset of infestation, completion of individual developmental stages, etc.) are not presented in this study.

RESULTS

Geographical variability of bark beetle development

Discrete regions with climatic potential allowing for the development of *n*-generations of *I. typographus* (*i*) under the reference (1961–1990), (*ii*) near future (2021–2050), and (*iii*) distant future climates (2071–2100) are presented in Fig. 1. It is important to note that the presented calculations represent an average climate of the investigated 30-year periods, and thus the influence of inherent interannual climate variability should be considered.

(*i*) As can be seen, regions allowing for the development of two bark beetle generations dominated in the Czech Republic under the reference climate. Three generations developed at low altitudes representing 5.4% of the coniferous forests in the Czech Republic (Table 1). One generation was allowed to complete development at an elevation above 775 m

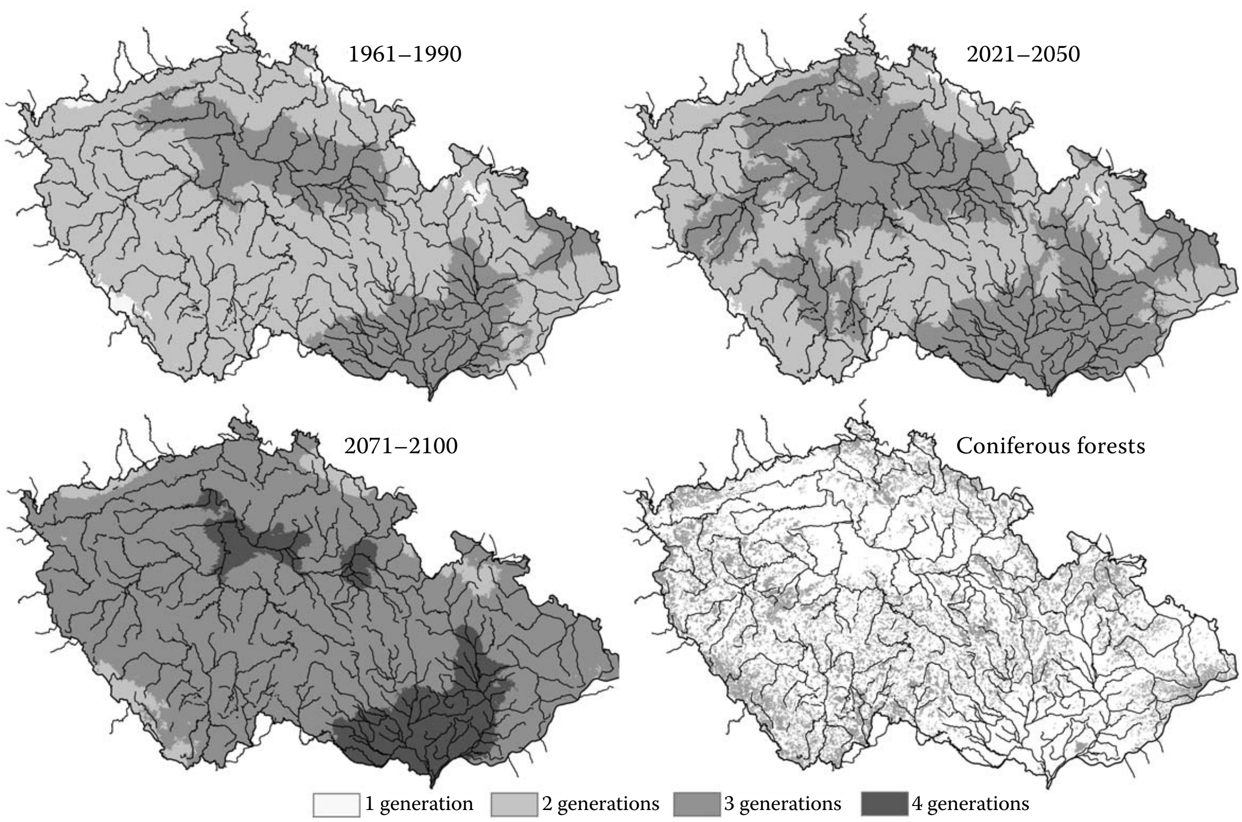

Fig. 1. Regions allowing for the development of *n*-generations of *Ips typographus* in the Czech Republic under the ALADIN-Climate/CZ climate change scenario. Distribution of coniferous forests is based on CORINE Land Cover 2000 classification (Source: European Environmental Agency)

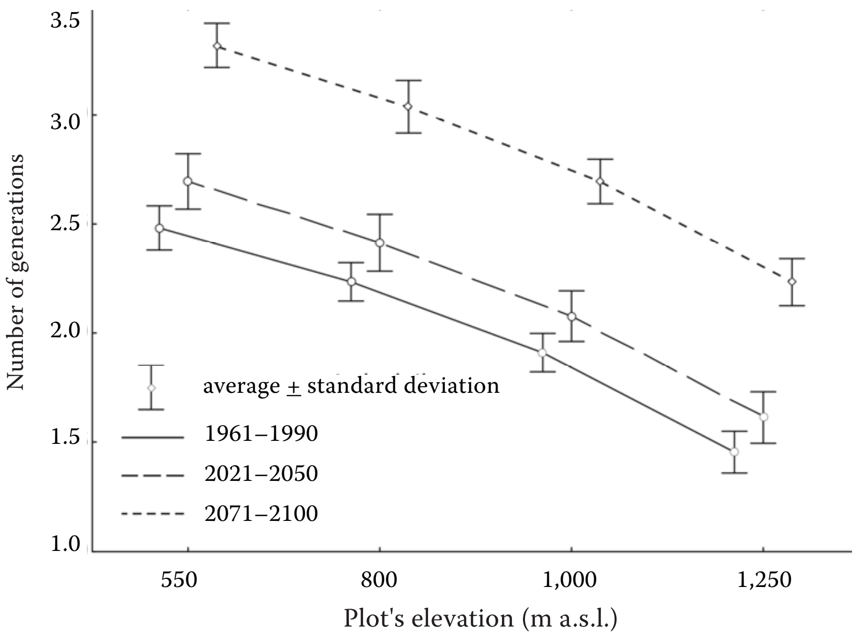

Fig. 2. Mean values and standard deviations of modelled bark beetle (*Ips typographus*) development at four points in the Czech Republic under the reference, near future and distant future climates. ALADIN-Climate/CZ climate change scenario is used for the description of future time periods

a.s.l. (95% quantile of the elevation range), representing about 4.6% of the coniferous forests in the country (Fig. 1; Tables 1 and 3).

(*ii*) In contrast to the reference climate, three-generation regime regions were projected to develop in 27% of the present coniferous forests in the country in the near future, mostly at altitudes between 188 and 485 m a.s.l. (Tables 1 and 3). The two-generation regime is expected to move to higher altitudes, such as the Moravian-Silesian Beskids Mts. with elevations in a range of 399–851 m a.s.l. The area with climate allowing for the development of a single *I. typographus* generation is expected to recede to 1.6% of the total coniferous forest in the country, mainly in the Hrubý Jeseník, Krkonoše and Krušné hory Mts. as well as in the Bohemian Forest (Šumava Mts.) (Fig. 1; Tables 1 and 3).

(*iii*) Projections to the distant future (2071–2100) are subjected to great uncertainty due to both the inherent uncertainty of climate modelling and expected changes in spruce distribution in the country. In any case, three-generation regime regions are projected to come to dominate in almost 90% of all present coniferous forests in the Czech Republic (Table 1). Under the theoretical assumptions of unchanged spruce distribution, a fourth generation is projected to develop in a region covering 19% of the present distribution of coniferous forests at low altitudes. The two-generation regime will move to the highest mountains in the country. The one-generation regime will disappear completely (Fig. 1; Table 1).

Interannual variability of modelled bark beetle development

All the presented results were calculated using average climate data for three 30-year time periods. To complement this information, we investigated the temporal variability of bark beetle development at several grid points of the RCM used. We selected four grid points arranged at an elevation gradient from 550 to 1,250 m a.s.l. Several measures of variability were calculated to describe the bark beetle development under the reference, near future and distant future climates (Fig. 2; Table 2).

Table 1. Proportion of the Czech Republic area (variant 1) and of coniferous forests in the Czech Republic (variant 2) with climatic conditions allowing for the appearance of regions with *n*-generation regime of *Ips typographus*. The projection is based on the ALADIN-Climate/CZ climate change scenario

Time period	1st generation		2nd generation		3rd generation		4th generation	
	1	2	1	2	1	2	1	2
1961–1990	1.7	4.6	70.2	90.0	28.1	5.4	0.0	0.0
2021–2050	0.7	1.6	45.9	71.4	53.4	27.0	0.0	0.0
2071–2100	0.0	0.0	4.3	10.9	80.9	87.2	14.8	1.9

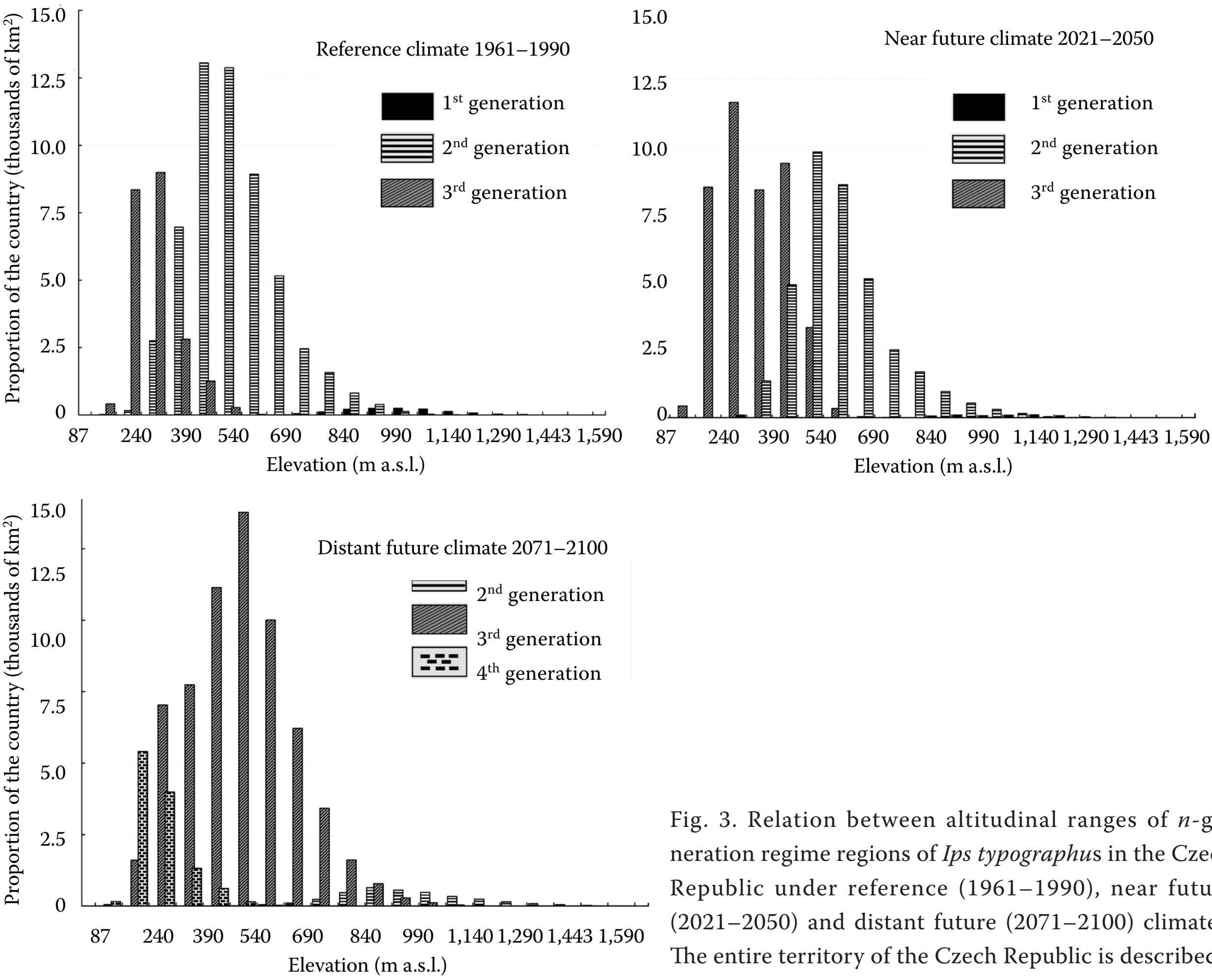

Fig. 3. Relation between altitudinal ranges of *n*-generation regime regions of *Ips typographus* in the Czech Republic under reference (1961–1990), near future (2021–2050) and distant future (2071–2100) climates. The entire territory of the Czech Republic is described

As can be seen, the range of 5–95% quantiles in the reference period is the lowest compared to both future time slices – it ranges from 0.73 to 0.85 generation (range 0.11). The variability slightly increases in the future, ranging from 0.95 to 1.19 generation in the near future (range 0.24) and from 0.84 to 1.0 generation in the distant future (range 0.16). No specific response of variability to elevation has been observed.

Bark beetle development in relation to elevation of the Czech Republic

This analysis aims to assess altitudinal shifts of *n*-generation regime regions during all investigated time periods. A high correlation of air temperature (the main driver of bark beetle development) with elevation suggests that calculated degree-days will be driven also by elevation. Such a relationship is

Table 2. Variability of modeled bark beetle (*Ips typographus*) development in terms of number of generations developed at four points in the Czech Republic under the reference, near future and distant future climates. ALADIN-Climate/CZ climate change scenario is used for the description of future time periods

Elevation (m a.s.l.)	Geomorphological unit	1961–1990				2021–2050				2071–2100			
		med.	5%	95%	IQR	med.	5%	95%	IQR	med.	5%	95%	IQR
550	Javorníky Mts.	2.45	2.01	2.85	0.40	2.70	2.15	3.18	0.37	3.30	2.87	3.72	0.38
800	Slavkovský Forest	2.24	1.84	2.61	0.37	2.40	1.86	3.05	0.34	3.03	2.56	3.56	0.28
1,000	Bohemian Forest	1.95	1.48	2.21	0.35	2.14	1.53	2.48	0.32	2.66	2.26	3.18	0.30
1,250	Giant Mts.	1.49	1.00	1.80	0.27	1.64	1.15	2.19	0.38	2.23	1.79	2.63	0.39

med. – median; IQR –inter-quartile range (75–25%)

Table 3. Elevation ranges (m a.s.l.) of *n*-generation regime regions in the reference (1961–1990), near future (2021–2050) and distant future (2071–2100) climates

	1st generation			2nd generation			3rd generation			4th generation		
	5%	med.	95%	5%	med.	95%	5%	med.	95%	5%	med.	95%
1961–1990	775	1,000	1,275	310	490	775	176	252	410	–	–	–
2021–2050	885	1,100	1,350	399	550	851	188	319	485	–	–	–
2071–2100	–	–	–	650	879	1,193	247	458	700	168	230	384

med. – median elevations (m) and 5–95% elevation quantiles of *n*-generation regime regions are stated; – sign indicates that the n^{th} generation is not allowed to develop in the respective time period

influenced by solar irradiation that is used to calculate the mean bark temperature. As the spatial variability of projected temperature increase is very low (up to just 0.5°C in both near and distant future climates), the correlation coefficient between degree-days and elevation remains more or less constant in all investigated time periods.

The comparison of altitudinal ranges of *n*-generation regime regions indicates that while two- and three-generation regime regions are relatively well separated (Fig. 2), the four-generation regime region that is projected to appear in the distant future almost thoroughly overlaps in altitude with the three-generation regime region.

The presented projections of *I. typographus* development suggest a discernible upward trend towards higher altitudes. While the area allowing for the development of one bark beetle generation occurred above 775 m a.s.l. (5% quantile of the elevation range) under the reference period, it is projected to recede to elevations above 885 m a.s.l. in the near future and it disappears completely in the distant future. Similar development has been projected for the remaining generations (Table 3).

DISCUSSION

This paper provides essential information on the potential impacts of climate change on spruce stands in the Czech Republic due to changes in *I. typographus* development. We stated that the 3rd bark beetle generation would be critical in the Czech Republic, even in the near future period (2021–2050). The four-generation regime regions were projected to appear in the distant future only marginally at the lowest elevations. Regional impact studies from Slovakia or Sweden (Hlásny, Turčáni 2009; Jönsson et al. 2009) as well as recent observations of bark beetle development during hot years in Central Europe support such findings.

An important fact is that the climate change induced pressure of bark beetles is expected to increase in spruce stands naturally dominated by broadleaves, i.e. outside the range of the spruce natural distribution, where spruce can be considered as highly vulnerable. In addition, stands at the lower range of the spruce present distribution at lower elevations are anticipated to suffer from heat and drought stress (Colwell et al. 2008; Jump et al. 2009), thereby increasing spruce susceptibility to the bark beetle attack (Dutilleul et al. 2000). From this aspect, a radical near-term decrease in the spruce proportion in favour of naturally dominating broadleaves appears inevitable. Nevertheless, the fact that *I. typographus* preferably feeds on spruces older than 60 years as well expected improvement in growth conditions for spruce at high elevations (Walther 2004; Hlásny et al. 2011) suggest that spruce could remain a part of the species composition of forests in this country.

The role of natural enemies (biological control agents) and their role in pest control (e.g. Kenis et al. 2004; Wegensteiner 2004) have not been fully understood yet in the context of climate change. Bark beetle parasitoids and predators could play a role in the future as climate change driven agents or simply respond to the population sizes and preferences of their hosts.

Another fact which has not been addressed is that bark beetle parent females produce sister broods which contribute to population growth and size (Anderbrant 1989). Usually, parent beetles re-emerge 2–3 weeks after the initial attack and establish one sister generation at least. This fact has not been considered in the presented projections, although the PHENIPS model provides capabilities for modelling the sister brood development.

A portion of uncertainty in the applied spatial modelling comes from the use of spatial interpolation of data distributed at grid points of the regional climate model used. Therefore, while the produced maps are supposed to describe the main tendencies and spatial patterns on the scale of the entire Czech Republic, their use at finer scales is limited. The use of kriging with external drift, which allows for using secondary variables (elevation in this study), linearly correlated with interpolated degree-days, is supposed to markedly improve the interpolation compared to a univariate approach (e.g. Vizi et al. 2011). Regardless of the uncertainty due to interpolation, we emphasize that only a single climate change scenario has been used in this study. Therefore, the uncertainty of future climate development ensuing from the use of various global and regional climate models, as well as of various emission scenarios, has not been investigated. Hence the distant future projections could be subjected to particularly large uncertainty potentially exceeding the ranges of uncertainty due to the interpolation of relatively dense source data.

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