The potential effect of climate change on the geographical distribution of insect pest species in the Swedish boreal forest

Anouschka R. Hof\textsuperscript{a,b,*} and Anna Svahlin\textsuperscript{b}

\textsuperscript{a}Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), Umeå SE 901 83, Sweden; \textsuperscript{b}Landscape Ecology Group, Department of Ecology and Environmental Science, Umeå University, Umeå SE 901 87, Sweden

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With the expected rising temperatures, outbreaks of insect pests may be more frequent, which can have large consequences on forest ecosystems and may therefore negatively affect the forestry sector. In order to be better able to predict where, but not if, outbreaks may occur in future we investigated the potential future (2070) geographical distribution of 30 prospective insect pest species (Coleoptera and Lepidoptera) by applying species distribution modelling. We also assessed the geographical extent to which the boreal forest in Sweden may be affected. We found that numerous species may experience large increases in their potential distribution in future, which may result in outbreaks in “new” areas. It is therefore likely that more trees will be infested by pests in future, which may have large implications for the Swedish forestry sector.

Keywords: climate change; forestry; insects; Norway spruce; pests; Scots pine; species distribution modelling

Introduction

Global climate change is predicted to cause changes in abiotic factors that will indirectly effect species distributions and alter species communities around the world, which may lead to changes in species compositions (Hughes 2000; Walther et al. 2002). These changes are traceable and already visible in many ecosystems across the world and amongst different taxa (Hughes 2000; Walther et al. 2002). It has for instance been shown that in northern Europe it is likely that generalist species will increase in number, whilst more specialist species (species with special requirements concerning abiotic factors, habitat or food supply) are likely to decline or go extinct (Hof et al. 2012). However, the interaction between temperature and shifts in species distributions is not straightforward. Species might for instance have temperature thresholds that keep them from changing their distributional pattern until that threshold value is reached (Walther et al. 2002). A better understanding of how species may shift their distribution in the face of future climate change is not only highly valuable for species conservation; it can also be paramount for the preservation of natural resources and for local communities that depend on those natural resources (Huntington & Fox 2005; Larsen et al. 2014).

The Swedish economy is largely dependent on the forestry sector and forestry-related products comprise an important part of the gross national product (Swedish Forest Agency 2012). Norway spruce (\textit{Picea abies} denoted as “spruce”) and Scots pine (\textit{Pinus sylvestris} denoted as “pine”) are the two economically most important tree species for forestry (Swedish Forest Agency 2012). However, climate change is expected to affect the forestry sector. There is no certainty in how pine and spruce may react to climate change and responses may differ depending on management strategies (Schlyter et al. 2006). There are indications that tree species like spruce might be more sensitive to early spring frost because warm temperatures early in the year will cause buds to burst in a period when the likelihood of frost is higher (Langvall 2011). Since it is expected that climate change will come with warmer weather conditions and less precipitation in large parts of Sweden according to for instance the HadGEM2-ES model from the Hadley Global Environment Model- Earth System, increased stress levels for tree species are to be expected (Rebetez & Dobbertin 2004; Schlyter et al. 2006). However, climate change will not only affect trees and the distribution of tree species (Iverson & Prasad 1998). The boreal ecosystem has already shown many responses to climate change in the past decades (Soja et al. 2007). Extreme fire events have for instance been occurring in Alaska, Canada and Siberia and severe outbreaks of insect pests are more common. Such events may alter the entire ecosystem (Soja et al. 2007). Further climate change will likely continue to have an impact on disturbances such as the frequency of forest fires (Stocks et al. 1998), the level of wind throw and, perhaps most
important of all, on pest infestations (Logan et al. 2003). Although the risk of storm and wind damage might increase, differences in anthropogenic decisions, for example, in rotation time, land-use change and forestry practice, can affect the extent of the damage caused by such events (Schlyter et al. 2006). However, increased stress levels will likely enhance the sensitivity of tree species to pest species (Schlyter et al. 2006; Jönsson et al. 2009). Furthermore, it is predicted that a number of pest species will be able to expand their geographical range due to climate change (Hughes 2002; Vanhanen et al. 2007; Jönsson et al. 2009). The effects of these changes may have large consequences for the forestry sector.

Every year the Swedish forest industry sustains large economic losses due to pest species (Paine et al. 1997; Swedish Forest Agency 2009) and it is estimated that an outbreak of a pest species can cost hundreds of thousands Swedish kronor (Swedish Forest Agency 2009). Warmer weather conditions are likely to have an impact on pest species (Hughes 2000; Schlyter et al. 2006; Jönsson et al. 2009). As an example, future climate change is predicted to benefit bark boring pest species. It is for instance expected that the spruce bark beetle (Ips typographus) is likely to increase its geographic range, its number of generations per summer (predicted second generation in the southern part of Sweden), and its number of large outbreaks (Jönsson et al. 2009). Swarming of bark boring beetles and the development from eggs to adults is directly dependent on accumulated degree days, where a certain degree day threshold needs to be crossed. Climate change can cause an increase in the number of swarming periods (i.e. two periods become possible if swarming can start earlier) and reach the degree days threshold for faster development (Jönsson et al. 2009). Most species of bark boring beetles breed in galleries made in the phloem part of dead or dying trees (Weslien & Schroeder 1999). In their larval stage they also use the wood as food supply (Paine et al. 1997). Some of the bark boring species can have devastating effects on trees since they infest and kill standing/living trees (Paine et al. 1997; Schroeder et al. 1999; Jönsson et al. 2009). Furthermore, many of the aggressive bark boring beetles carry fungi (e.g. heterobasidiomycetous fungi) that help them overcome the defence system of trees (Paine et al. 1997; Kirschner et al. 2001). It is thus clear that future climate change can increase the damage to trees through, amongst others, the predicted positive effect of increased temperatures on bark boring beetles. Since pine and spruce are the most important tree species for Swedish forestry, any threat that may occur in the face of climate change is important to explore. This study therefore investigates the potential effect of future climate change on the distribution of a number of pest insects, which will give a better indication on where outbreaks from which species may occur in future.

**Materials and methods**

We assessed the potential future distribution of 30 species listed as possible pest species that have negative impacts on spruce or pine (Table 1, SLU 2014), in the boreal forest region in Sweden (here defined as the region of Norrland (Figure 1)). In total 8 species are from the order Lepidoptera and 22 species from Coleoptera, mostly representing true weevils or snout beetles from subfamilies like the Scolytinae (bark beetles) and the Lamiinae (flat-faced longhorns) (Table 1). Occurrence data for the species have been obtained through the Global Biodiversity Information Facility (http://data.gbif.org) for the period 1990–2011. To eliminate potential bias in the data set, a raster with a 10 km$^2$ grid-cell size was used to randomly extract one occurrence point per grid-cell in ArcGIS whilst further analyses took place at the $\sim$1 km$^2$ scale. We used the Species Distribution Modelling (SDM) algorithm MaxEnt version 3.3.3.k (Phillips et al. 2006) to predict the current and future geographic distribution of the species, since it has shown to generally outperform other algorithms (Elith et al. 2006; Hijmans & Graham 2006). SDMs are widely used to predict the impact of climate change on species distributions (e.g. Virkkala et al. 2010; Araújo et al. 2011). Their general approach is to identify important variables amongst those entered in the model that strongly correlate with species occurrences. Based upon the variables that determine most of the variation in species presence, SDMs predict the highest likelihood of species presence throughout a defined region in a specific time (Phillips et al. 2006). MaxEnt applies maximum entropy, which assumes that the probability distribution with the largest entropy, that is, with the largest average amount of information per variable, is the most reliable to identify species’ distributions. Areas predicted to be suitable for the species to occur are limited to those areas that have environmental values that fall within the extent of environmental values of locations where species are present (Elith et al. 2011). The main limitation of the use of SDMs is that the possibility to introduce many biotic and abiotic factors other than environmental variables is limited. Future predictions of, for instance, food availability, interspecific competition, and presence of predators are usually not available. Also, MaxEnt does not take the potential presence of a species in a neighboring grid-cell, each grid-cell being $\sim$1 km$^2$ which was the same as the scale of the environmental variables, into account. For example, the distance to the nearest population is not considered, only how suitable each grid-cell is for the species based on the environmental variables. Furthermore, it is not possible to account for population dynamics in such models. Although such variables are dynamically related with species abundance and important in assessing species distributions, they often have to be neglected due to their complex nature and...
Table 1. Basic information and model outcomes of the species studied (n = 30). N λ shows the mean number of derived variables (parameters) used in the final MaxEnt models. Pred. = Most important predictor variable as determined by jackknife in MaxEnt: (1) mean temperature of the warmest quarter, (5) maximum temperature of the warmest month, (8) annual mean temperature, (10) mean temperature of the warmest quarter, (11) mean temperature of the coldest quarter. Current: estimated mean percentage of the area of boreal forest in Norrland that may be affected in future, with standard deviation in brackets. Future: predicted mean percentage of the area of boreal forest in Norrland that may be affected in future, with standard deviation in brackets. V: Wilcoxon signed-rank test outcome between the difference between the current and future predicted mean percentage, df = 9 for all species. P: italic font denotes significance.

| Species                          | Affects | N   | AUCCORR | N λ | Pred. Current Future | Future V | P    | Future V | P    |
|----------------------------------|---------|-----|---------|-----|---------------------|----------|------|----------|------|
| **Coleoptera**                   |         |     |         |     |                     |          |      |          |      |
| Acanthocinus aedilis             | Pine    | 672 | 0.700   | 35  | 10                  | 25 (10)  | 95   | 4        | 0.002 |
| Cryphalus abietis                | Both    | 87  | 0.868   | 23  | 1                   | 0 (0)    | 26   | 16       | 0.002 |
| C. saltuarius                    | Spruce  | 60  | 0.743   | 8   | 8                   | 92 (5)   | 49   | 18       | 0.037 |
| Dendroctonus micans              | Spruce  | 65  | 0.773   | 10  | 1                   | 54 (8)   | 90   | 5        | 0.002 |
| Ips acuminatus                   | Pine    | 140 | 0.799   | 37  | 1                   | 25 (6)   | 85   | 13       | 0.002 |
| Ips sexdentatus                  | Pine    | 54  | 0.715   | 8   | 1                   | 33 (14)  | 56   | 16       | 0.002 |
| I. typographus                   | Spruce  | 346 | 0.774   | 50  | 1                   | 17 (3)   | 98   | 3        | 0.002 |
| Phaenops cyaneus                 | Pine    | 165 | 0.878   | 40  | 1                   | 6 (3)    | 85   | 13       | 0.002 |
| Pissoides pini                   | Pine    | 327 | 0.731   | 28  | 1                   | 19 (6)   | 100  | 0        | 0.002 |
| Pissoides pinophilus             | Pine    | 86  | 0.718   | 10  | 5                   | 27 (9)   | 97   | 2        | 0.002 |
| Pityogenes bidentatus            | Pine    | 258 | 0.772   | 38  | 8                   | 44 (8)   | 100  | 1        | 0.002 |
| P. chalcographus                 | Spruce  | 409 | 0.759   | 27  | 10                  | 36 (10)  | 90   | 11       | 0.002 |
| Pityogenes quadridens            | Pine    | 147 | 0.808   | 29  | 1                   | 22 (5)   | 99   | 1        | 0.002 |
| P. poligraphus                   | Spruce  | 188 | 0.796   | 31  | 8                   | 77 (5)   | 98   | 1        | 0.002 |
| Tetropsis castaneum              | Spruce  | 638 | 0.720   | 27  | 8                   | 12 (2)   | 73   | 11       | 0.002 |
| Tetropsis fuscom                  | Spruce  | 336 | 0.788   | 24  | 8                   | 6 (1)    | 76   | 13       | 0.002 |
| Tominus minor                    | Pine    | 176 | 0.803   | 34  | 5                   | 60 (8)   | 80   | 13       | 0.002 |
| Tominus piniperda                | Pine    | 357 | 0.749   | 38  | 10                  | 22 (8)   | 99   | 1        | 0.002 |
| Trypodendron lineatum            | Both    | 303 | 0.746   | 23  | 10                  | 31 (5)   | 98   | 3        | 0.002 |
| **Lepidoptera**                  |         |     |         |     |                     |          |      |          |      |
| Bupalus piniaria                 | Pine    | 613 | 0.765   | 25  | 10                  | 8 (1)    | 91   | 2        | 0.002 |
| D. pini                         | Pine    | 382 | 0.809   | 34  | 10                  | 4 (1)    | 96   | 2        | 0.002 |
| Epinotia pygmaeacea              | Spruce  | 189 | 0.885   | 31  | 10                  | 6 (2)    | 52   | 22       | 0.002 |
| Lymantria monacha                | Both    | 430 | 0.831   | 37  | 10                  | 2 (0)    | 58   | 10       | 0.002 |
| Panolis flammea                  | Pine    | 500 | 0.779   | 30  | 10                  | 8 (1)    | 91   | 1        | 0.002 |
| R. buoliana                      | Pine    | 59  | 0.831   | 5   | 11                  | 1 (0)    | 32   | 4        | 0.002 |
| Rhyacionia duplica               | Pine    | 53  | 0.913   | 23  | 10                  | 8 (2)    | 88   | 4        | 0.002 |
| Z. ratzeburgiana                 | Spruce  | 245 | 0.857   | 38  | 1                   | 6 (2)    | 98   | 1        | 0.002 |

Note: Fine spatiotemporal resolution (Anderson & Raza 2010; Barve et al. 2011). Predictions generated by SDM therefore show the potential distribution based on the input variables and not necessarily the realized distribution. This is important to keep in mind when interpreting spatial and temporal predictions based on correlative models (Dormann et al. 2012).

MaxEnt generates predictions based on species occurrences that are provided by the user. Absence records are taken randomly from the extent of the geographic region used to train the model (Phillips et al. 2006; Elith et al. 2011). However, different results may be obtained when using different geographical extents (Anderson & Raza 2010; Barve et al. 2011). Using a large extent and consequently having a large variety in the climatic conditions used to generate predictions, can lead to an overestimation of the area predicted to be suitable for the species modelled. On the other hand, when a small geographic extent is used, one risks that the breadth of the climatic conditions used to generate the prediction does not capture the full climatic envelope of the species concerned. This leads to underestimations (Thuiller et al. 2004). Although our study site was limited to Norrland, we included the area south of Norrland, incorporating the whole of Sweden, Denmark and parts of countries like Germany and Poland (Figure 1), in our models since (1) many species in northern Europe are expected to shift or expand their geographic ranges to higher latitudes (Hof et al. 2012) and (2) since it is essential to incorporate areas in the modelling that have environmental conditions that are currently not present in the study region but may be present in future.
Incorporating the entire native ranges of the species was unfortunately not possible due to lack of detailed occurrence data and lack of data on the presence of boreal coniferous forests in future (see below) south of our geographic extent. However, since our region of interest, Norrland, is well north of the southern boundary of the geographical extent, possible errors in the prediction due to not capturing the full climatic envelope of the species were thought to be small under the Representative Concentration Pathway (RCP) 4.5 scenario (see below) but may have caused some underestimations of species presence, especially in the southern parts of the study region, under the RCP 8.5 scenario (see below), which should be taken into account when interpreting the resulting species distribution maps.

We used the 4.5 and 8.5 RCPs of the downscaled general circulation model Hadley Global Environment Model- Earth System for the year 2070. The RCP 4.5 scenario is based on the assumption that the total radiative forcing is stabilized soon after 2100. The long-run radiative forcing target level will not be surpassed (Thompson et al. 2011). The RCP 8.5 scenario is based on the assumption that greenhouse gas emissions will be increasing over time and will lead to high greenhouse gas concentration levels (Riahi et al. 2011). The 19 bioclimatic variables, derived from monthly temperature and rainfall values during 1950–2000, which are described and available at http://www.worldclim.org/futdown.htm, were used in the models at the 30 arc-seconds (~1 km²) scale. Unfortunately there are currently no future scenarios for the distribution of pine and spruce separately available. However, Wolf et al. (2008) used a dynamic vegetation model (LPJ-GUESS) to project transient impacts of changes in climate on vegetation of northern Europe for the year 2080. The resulting vegetation projection provided continuous data of biomass of the main vegetation zones, of which boreal coniferous forest, consisting of Scots pine and Norway spruce, is one. We deemed the year 2080 close enough to the year 2070 to use these data. These data were available at the 25 arc-minutes scale and interpolated to the 30 arc-seconds scale in ArcGIS (10.2 by ESRI) by means of the natural neighbour method.

In MaxEnt we mostly used the default settings; we used the default convergence threshold \(10^{-6}\), maximum number of iterations (500) values, we applied hinge features, and we kept the maximum number of background points at 10,000. A degree of spatial autocorrelation between climatic variables is unavoidable. However, testing for spatial autocorrelation for presence-only data is not possible (Dormann et al. 2007). We therefore did not pre-select variables, judging all

![Figure 1. The study region displayed in dark grey.](image-url)
included variables to potentially be biologically meaningful and taking advantage of the regularization application of MaxEnt. This application reduces potential over-fitting of large numbers of auto-correlated variables (Phillips et al. 2006) and deals with the selection of environmental variables (regulating some to zero). The application has shown to perform well (Hastie et al. 2009; Elith et al. 2011) and is thought to be more stable than, for instance, stepwise regression, when correlated variables are present. This reduces the need to remove correlated variables, or to use PCA to select a few dominant axes (Elith et al. 2011). Furthermore, by giving more weight to variables that exhibit high correlation with the occurrence data, MaxEnt minimizes autocorrelation between variables (Elith et al. 2011). In order to avoid under and over-fitting, we did not rely on the default setting in MaxEnt but tuned the regularization multiplier for each species, evaluating the performance of multipliers 0.5, 1, 2, 4, 6, 8 and 10 (Merow et al. 2013; Radosavljevic & Anderson 2014). Unfortunately, independent data were not available to assess whether there was spatial bias in the occurrence data used and to assess model performance. It was also logistically not possible to gather independent data as recommended by Halvorsen et al. (2014). Therefore, we divided the occurrence datasets in calibration sets and evaluation sets geographically, by longitude, to avoid environmental dependency between the calibration (approximately two-thirds of the data) and evaluation sets (approximately one-third of the data) based on recommendations from Radosavljevic and Anderson (2014). We evaluated model performance of the different regularization multipliers, using the calibration data set, by calculating cumulative binomial probability distributions for each species and obtaining a *p*-value of test-significance, based upon recommendations by Peterson et al. (2011). The binomial was based on the number of successes – that is, the number of correctly predicted occurrences in the evaluation data set by the model outcome of the calibration data set – out of the total number of occurrences in the evaluation data set, and the probability of success – that is, the proportion of the area predicted to be suitable (Peterson et al. 2011). We determined binary suitable/unsuitable area by applying cut-off thresholds, so that the difference between sensitivity and specificity was minimized, to the continuous suitability predicted by MaxEnt (Cantor et al. 1999). This method was chosen since it has shown to be one of the superior methods to transform continuous probabilities of species occurrence to binary presence/absence occurrence (Liu et al. 2005). Upon finding the most suitable regularization multipliers and assessing the significance of the model performances, the calibration and the evaluation data sets were combined to run the final models. These runs were replicated ten times, using bootstrap, for each species under current climatic conditions and for each RCP. We therefore created in total 30 predictions per species, of which 10 were based on current conditions and 20 were based on future predictions. We then also used the Area Under the Curve (AUC) of a Receiver Operating Characteristic plot (Phillips et al. 2006) to assess the accuracy of the final predictions, after correction (AUC CORR) for presence-only based models following, and based upon, recommendations from Halvorsen (2013). The performance of the models was classified based on Halvorsen (2013). Those that had an AUC CORR score > 0.700 and ≤0.900 were classified as useful, and with a score > 0.900 as good. By overlapping the model outcomes, that is, the potential geographic distributions of the insects, with the distribution of needle leaved forest, we were able to calculate how much more area may be infested by insects in future. The overlap between the predicted current and potential future ranges of the pest species with the boreal forest were calculated in R version 3.1.1 (R Core Team 2014). The average of the replicates was used for displaying purposes.

**Results**

The models of three species, *Hylobius abietis*, *Monochamus sutor*, *Rhagium inquisitor*, were not useful (mean AUC CORR < 0.700). These species were therefore left out of the further analyses. Models for the other species were useful, of which one was good (Table 1). For most species the environmental conditions will likely improve in large parts of Norrland in future. Assuming that species will be able to disperse and are not restricted by other ecological filters such as for example interspecific competition, pathogens or predators (Svenning et al. 2014), most species were predicted to be able to significantly expand their distribution range (Table 1). Some species will probably be able to substantially expand their geographic range, such as *Zeiraphera ratzeburgiana* (RCP 4.5: + 92 percentage-points (Wilcoxon: *V*₉ = 0, *p* = 0.002), RCP 8.5: + 80 percentage-points (Wilcoxon: *V*₉ = 0, *p* = 0.002)), and *Dendrolimus pini* (RCP 4.5: + 92 percentage-points (Wilcoxon: *V*₀ = 0, *p* = 0.002), RCP 8.5: + 91 percentage-points (Wilcoxon: *V*₀ = 0, *p* = 0.002)). In contrast, *Cryphalus saltuarius* was predicted to significantly loose parts of its range in boreal forest in future, both under the RCPs 4.5 and 8.5 (RCP 4.5: −44 percentage-points (Wilcoxon: *V*₀ = 48, *p* = 0.037), RCP 8.5: −83 percentage-points (Wilcoxon: *V*₀ = 55, *p* = 0.002)). The average range gain for Coleoptera was 34 percentage-points under the RCP 4.5 and 28 percentage-points under the RCP 8.5. For Lepidoptera the figures were respectively 43 percentage-points and 45 percentage-points.

**Figure 2(a)** shows in which regions boreal forest is currently predicted to be affected by how many pest species. **Figure 2(b) and 2(c)** show the same for future. The potential spread of each species throughout Norrland
is visualized in the supplementary material. These results can be used to predict the potential spread of insect pests in order to understand which areas may most likely be affected currently and in the future, or are least likely to be affected, but should be seen as an indication of higher likelihood of presence/absence rather than as a factual presence/absence of the species. The mean temperature of the warmest quarter and the annual mean temperature were most often the most explanatory variables in the models (Table 1). For 75% of the Lepidoptera and...
32% of the Coleoptera species the mean temperature of the warmest quarter was the strongest predictor. The annual mean temperature was the strongest predictor for 37% of the Coleoptera. Species responded positively to increasing temperatures; see as an example the response of the predicted distribution of *Pityogenes chalcographus* to an increase in the mean annual temperature in Figure 3.

**Discussion**

The results show, as predicted, strong indications for possible major changes in potential distribution patterns for most species assessed. A future warmer climate is likely to benefit the majority of the species assessed since most are predicted to expand their range extensively. The majority of the species are temperature dependent based upon our models: the mean temperature of the warmest quarter and the annual mean temperature were frequently largely explaining the current distribution of the species. These findings are confirmed in literature for many insects (e.g. Wermelinger & Seifert 1999; Bale et al. 2002). The development from eggs to adults is for species like *I. typographus* faster and their reproduction is more successful under higher temperatures (Wermelinger & Seifert 1999; Jönsson et al. 2009). This indicates that a temperature threshold currently limits the distribution of numerous pest species in Sweden, but this threshold will most likely be exceeded by 2070. Although the potential geographic distribution range of most of the species assessed may expand to a large extent, our results do not give any indications on the likelihood of outbreaks, nor where outbreaks will occur. Instead, our study gives an indication of which regions of boreal Sweden will have suitable climatic characteristics in future for a number of species, and thus where outbreaks are more likely to occur providing that other requirements are met. Insect outbreaks are more common under warmer climate regimes with a higher occurrence of stressed or damaged trees (Jakuš 1998; Jurec et al. 2006). Trees may suffer from stress or damage by drought more often during warm periods (Schlyter et al. 2006; Langvall 2011), and will simultaneously be more sensitive to insect pests (Schlyter et al. 2006; Jönsson et al. 2009). It is therefore highly likely that more pine and spruce stands will be infested by pests in a warmer future, which might have large implications for the Swedish forestry sector. Based on our results, we predict that especially the higher elevation regions and the northern parts of Sweden may increasingly suffer from outbreaks in the future. These areas have so far not been severely affected by many species, but they become climatologically suitable for a larger number of species which may result in higher incidences of outbreaks. Economic damage caused by insect pests in forestry is therefore thought to increase. It must however be noted that it is envisaged that the productivity of both pine and spruce may increase with rising temperatures (Kellomäki & Kolström 1994). Processes may act differently in different regions throughout Sweden in the future; whilst frost events during summer may increasingly damage seedlings in southern Sweden due to for instance earlier bud-burst, this is not the case in northern Sweden where the damage of frost events may even decrease in future (Langvall 2011). Some of these envisaged positive effects of climate change on pine and spruce in boreal Sweden may therefore reduce the negative effects of insect pests.

We highlight the significance of a possible future expansion of the distribution range of a few species in combination with a warming climate. One of the Coleoptera assessed was *I. typographus*. This species is considered as one of the most damaging pest species in Europe (Christiansen & Bakke 1988). It can cause substantial damage to spruce stands and its ability for rapid population increase can lead to outbreaks (Wermelinger 2004). Damaged or weakened spruce stands are particularly susceptible to outbreaks, such as after natural disturbances like drought or storm events (Wermelinger 2004). Such outbreaks rarely occur in Scandinavia today (Eidmann 1992; Eriksson et al. 2005), probably because current climatic conditions only allow the species to reproduce once a year (Sauvard 2004). Outbreaks of *I. typographus* are thought to be increasingly common in Scandinavia in future because of improving climatic conditions which allow the species to reproduce more often (Jönsson et al. 2009; Öhrn 2012). We show that the species will also likely expand its geographical range extensively, but in those new areas, they may still only reproduce once a year. The improving climatic conditions for *I. typographus* at lower elevations or in southern parts of Sweden, along with the predicted increase in extreme weather events (Larsen et al. 2014), may make Scandinavian spruce stands more likely to be affected by this species in future than at present. Similar patterns have been observed for species such as *Polygraphus poligraphus* and *P. chalcographus*. Studies
throughout Europe show that *P. poligraphus* attacks living trees under stressed conditions (i.e. air pollution or drought) (Jakuš 1998). In Sweden, the species usually attacks small to middle sized trees that already sustained some stress. Warm and dry summers can raise stress levels and can therefore induce more attacks (Swedish Forest Agency 2000). *P. chalcographus* often occurs together with *P. poligraphus* and attacks living trees (Schroeder et al. 1999; Swedish Forest Agency 2000). In the south of Europe, outbreaks that cause damage to trees occur more commonly, where a combination of windbreak and high temperatures in summer have shown to lead to larger populations of the species, resulting in greater damage to forest ecosystems (Jurc et al. 2006). Both species only reproduce once a year under the currently relatively cold climatic conditions in Scandinavia (Swedish Forest Agency 2000). However, they may, similarly to *I. typographus*, also reproduce twice a year in a future, warmer Scandinavia (Jurc et al. 2006). In addition, we predicted that both species may expand their range northward. Pine and spruce stands may therefore be affected at higher latitudes and altitudes than is currently the case. Furthermore, stands at lower latitudes and altitudes may be subjected to an increasing number of outbreaks due to possible increased reproduction capacity of pest species.

One of the Lepidoptera assessed was *Rhyacionia buoliana*. Although this species can already be found throughout Sweden, it is more abundant in the south of the country where it attacks young pine stands (Lindelöw 2015). This species can cause extensive malformations of current-year shoots of pine by tunnelling in the core and has been classified as a major pest to both lodgepole and Scots pine (Lindelöw & Björkman 2001). Although the species is univoltine, that is, only one generation a year, it has been suggested that climate change may benefit it, potentially leading to an increased number of outbreaks (Heeley et al. 2003). We predict that it may also be able to expand its geographic range extensively. This species has already shown its capacity to cause large damages in young pine shoots in newly reached areas in the boreal forest (Heeley et al. 2003). Potential damage in pine plantations in Northern Sweden, where it has not caused many problems, is thus to be expected.

From the examples given above we suggest that the potential expansion of the geographic range of insect pest species, caused by a warming climate, can potentially have a large impact on the forestry sector. However, there were some limitations to our study. Firstly, we did not use scenarios of the future distribution of pine and spruce but rather the one scenario of the distribution of boreal forest that was available. However, both pine and spruce are found in similar climatic regions in Sweden and forestry practices largely determine the distribution and abundance of both tree species. We therefore think that our use of the scenario of the future distribution of boreal forest gives a fair indication of where we may expect to find pine and spruce in future as well. We were also restricted by the geographic extent of the future projection of the boreal forest; the full climatic envelope of the species studies were therefore not always captured, which may have caused some underestimations of species presence in the southern parts of the study region under the RCP 8.5 scenario. Secondly, species distribution models indicate where in space and in time, in this case, climatic conditions are similar to where species have been found. It must therefore be noted that the accuracy of predictions generated by SDM is highly dependent on the availability of accurate and unbiased species occurrence data. Although we made an effort to reduce potential bias present in the datasets, due to the frequent low number of occurrences and patchy availability of data, predictions should be seen as an indication of higher likelihood of presence/absence rather than as a factual presence/absence. Furthermore, there are multiple other factors that drive the distribution of species. We did not account for the dispersal rate of species. Not only are the dispersal rates for many species unknown, poorly documented or highly fluctuating, insects are amongst the taxa that are frequently, unintentionally, introduced to new areas by humans. Roques et al. (2009) report for instance that approximately 90% of the alien invertebrates present in Europe were unintentionally introduced through human activity. Such unintentional introductions of insects often occur via “stowaway” or via the transport of for instance compost, plants, fruit and vegetables (Roques et al. 2009). Both Coleoptera and Lepidoptera are apt dispersers with reported dispersal rates between 5–470 km/year for the first and 3–170 km/year for the latter (Liebhold & Tobin 2008). We therefore envisage that all species may potentially reach the whole study region, which spans approximately 1000 km from south to north, since a dispersal rate of roughly 15 km/year would suffice even for species that currently do not occur in the region, whilst the vast majority of the species we included in our study already do. However, it must be noted that the regions in the south that were predicted to be suitable for the species studied to occur will likely face potential attacks sooner than the regions in the north. As the vast majority of Swedish forests are highly impacted by forestry, human actions will also contribute to the distribution of insect pests. The landowner will decide how the land will be used, which tree species will be present and what method will be used for harvesting. All these management decisions and strategies also affect the likelihood of insect pest species to spread across the landscape, since specific species are dependent on specific tree hosts.

Lastly, this study did not take some important species interactions into account, which is often inherent for studies that apply SDM to get a better understanding of the impact of climate change on species distributions’ (Anderson & Raza 2010; Barve et al. 2011). Inter and
intra-specific competition over food resources may for instance affect the abundance of species (Bulleri et al. 2008). Also, the resistance of a tree largely determines its susceptibility to attacks (Christiansen et al. 1987); the presence of pests may for instance attract other pests. Pheromones used by pioneer beetles attract other beetles (Rudinsky 1962; Wood 1982). Forestry-related practices may also affect the predator–prey interaction between, for instance, bark boring beetles and their predators (Schroeder et al. 1999; Swedish Forest Agency 2000). Many of the predators of bark boring beetles are more sensitive to forestry than the bark boring beetles themselves, depending on different dormancy strategies. This means that forestry practices can favour bark boring beetles by removing tree trunks and consequently by removing their predators (Schroeder et al. 1999). Therefore, management decisions and strategies made by the forestry industry are important for controlling the future spread of insect pests. Boreal forest stands should be managed in a way that reduces their susceptibility to infestations and outbreaks. Here we highlighted which parts of Sweden may become increasingly suitable for a number of insect species to occur and this may better indicate where potential insect pests may affect boreal forests in future. This information is therefore potentially valuable for the Swedish forestry sector in developing proactive management strategies that reduce the impact of these future risks.

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ORCID

Anouschka R. Hof  http://orcid.org/0000-0001-6743-0089

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