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Forest management could counteract distribution retractions forced by climate change

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Abstract. Climate change is expected to drive the distribution retraction of northern species. However, particularly in regions with a history of intensive exploitation, changes in habitat management could facilitate distribution expansions counter to expectations under climate change. Here, we test the potential for future forest management to facilitate the southward expansion of an old-forest species from the boreal region into the boreo-nemoral region, contrary to expectations under climate change. We used an ensemble of species distribution models based on citizen science data to project the response of *Phellinus ferrugineofuscus*, a red-listed old-growth indicator, wood-decaying fungus, to six forest management and climate change scenarios. We projected change in habitat suitability across the boreal and boreo-nemoral regions of Sweden for the period 2020–2100. Scenarios varied in the proportion of forest set aside from production, the level of timber extraction, and the magnitude of climate change. Habitat suitabilities for the study species were projected to show larger relative increases over time in the boreo-nemoral region compared to the boreal region, under all scenarios. By 2100, mean suitabilities in set-aside forest in the boreo-nemoral region were similar to the suitabilities projected for set-aside forest in the boreal region in 2020, suggesting that occurrence in the boreo-nemoral region could be increased. However, across all scenarios, consistently higher projected suitabilities in set-aside forest in the boreal region indicated that the boreal region remained the species stronghold. Furthermore, negative effects of climate change were evident in the boreal region, and projections suggested that climatic changes may eventually counteract the positive effects of forest management in the boreo-nemoral region. Our results suggest that the current rarity of this old-growth indicator species in the boreo-nemoral region may be due to the history of intensive forestry. Forest management therefore has the potential to compensate for the negative effects of climate change. However, increased occurrence at the southern range edge would depend on the dispersal and colonization ability of the species. An increase in the amount of set-aside forest across both the boreal and boreo-nemoral regions is therefore likely to be required to prevent the decline of old-forest species under climate change.

Key words: citizen science; climate change; dead wood; forestry; habitat management; polypore fungi; volunteer recording.

Introduction

Land use and climate change are predicted to be the two major drivers of biodiversity change in terrestrial ecosystems over the coming century (Mantyka-Pringle et al. 2015). Much work has focused on predicting biodiversity responses to future climate change (Bellard et al. 2012), but land use changes have largely been neglected in the forecasting literature, despite the potentially stronger influence of land use on species distributions (Titeux et al. 2016). Moreover, macroclimate effects occur at the continental or region scale, while land use effects occur at the landscape or even smaller scale (Pearson and Dawson 2003), meaning that the utility of national or landscape scale forecasts are likely to be greatly enhanced by the inclusion of land use effects. The interactive effects of land use and climate change on biodiversity are likely to be particularly important in forecasting, as the implementation of appropriate conservation measures has the potential to minimize climate change impacts (Stralberg et al. 2015). Alternatively, species may suffer negative impacts from both (e.g., Jetz et al. 2007).

Future land use changes are likely to be closely tied to climatic changes, both in terms of direct environmental responses to changing climatic conditions and due to societal aims to reduce carbon emissions. For example, in boreal forest, increased biomass extraction can facilitate an economic shift away from fossil fuels (Gauthier et al. 2015). However, in countries such as Sweden, the highly developed forestry industry has already led to the loss of species-rich old-forest (Gauthier et al. 2015), and is likely to continue doing so unless the management changes (Mönkkönen et al. 2014). Although it has been suggested that, in the short to medium term, forest

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management is likely to have a greater impact on biodiversity than climate change (Pawson et al. 2013), for some forest species, the long-term impacts of climate change are predicted to be far greater (Meller et al. 2015). The ability to balance economic demands with biodiversity conservation requires an understanding of how species respond to different forest management practices, and the interactive responses to climate change (Mazziotta et al. 2015). Previous studies have addressed one or other of these effects on boreal forest species (e.g., Mönkkönen et al. 2014), but there is a dearth of studies using realistic forest management and climate change scenarios to address the effects and interactions of both at a large scale.

The likely effects of forest management and climate change on species occurrence can be efficiently studied using indicator species, the occurrence of which indicates the naturalness of an ecosystem (Nitare 2000, Niemelä 2005). In forest ecosystems, dead-wood decaying fungi make excellent indicator species due to their strong association with natural old-forest (Lonsdale et al. 2008). They also perform important ecosystem functions as dead wood decomposers (Lonsdale et al. 2008). It is clear that the indicator species are negatively affected by forestry (Nordén et al. 2013), but the role of macro-climatic effects in determining occurrence has received little attention (Heilmann-Clausen and Boddy 2008, but see Bässler et al. 2010). In Sweden, the absence or rarity of many dead-wood decaying indicator species from the southern, boreo-nemoral region is assumed to be primarily due to a history of highly intensive forestry (Nordén et al. 2013), yet the role of macroclimate has not been studied. If species absence is due primarily to forestry, then there is the potential for changes in forest management to facilitate increased occurrence of the species in the boreo-nemoral region, which would run contrary to expectations of a northward distribution contraction under climate change. Conversely, if absence is due primarily to climate, or the interactive effects of forestry and climate, then a greater focus on conservation may be required throughout the species range to mitigate the likely negative effects of climate change.

The aim of this study was to test for differences among large scale scenarios of forest management and climate change on the suitability for *Phellinus ferrugineofuscus*, a dead-wood old-growth indicator fungus that occurs primarily in the boreal region and shows sparse occurrence in the boreo-nemoral region (Fig. 1; Ryvarden and Melo 2014). We tested the hypothesis that forest management has the potential to facilitate increased occurrence at the species southern range edge, contrary to expectations that climatic changes should drive a northward retraction. We used an ensemble of species distribution models fitted to citizen science data (Mair et al. 2017) to forecast habitat suitability over the coming century across the boreal and boreo-nemoral regions of Sweden. Forest projections were based on realistic, national management scenarios that allowed us to test how varying the level of timber extraction and the area of forest set aside from production may affect species occurrence. We compared scenarios with only legally protected reserves set asides from production (3.6% forest set aside) against scenarios that included voluntarily set-aside and clear-cut retention forests (Gustafsson et al. 2012) to increase the total amount set aside to 16%. This is close to the Aichi Biodiversity Target 11 aim of ≥17% of terrestrial habitat protected, which was adopted by the Convention on Biological Diversity (CBD) in 2010 and aims to halt the loss of biodiversity (CBD 2010). Climate change projections allowed us to determine the interactive effects of forest management and varying magnitudes of climate change. In order to assess potential distributional changes, we compared changes in suitability in the northern boreal region, where the species is widely distributed, against changes in the southern boreo-nemoral region, where the species' prevalence is low (Fig. 1).

METHODS

Model indicator species and landscape

Phellinus ferrugineofuscus is a polyporous fungus associated with Norway spruce, *Picea abies*. It is classified as near threatened (NT) in Sweden because of negative effects of forestry (Artdatabanken 2015) and has been

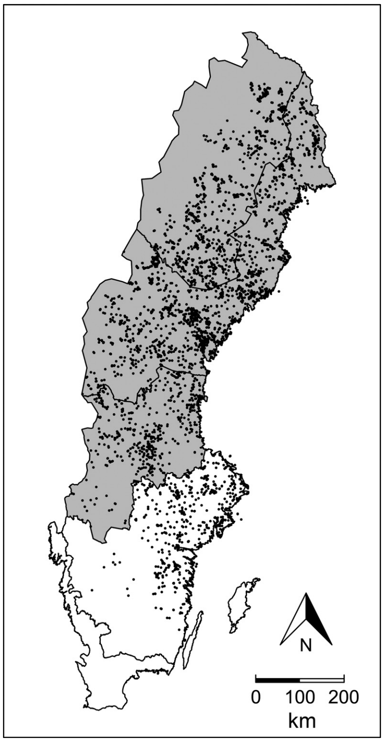

FIG. 1. Observed 100-m grid cell resolution occurrences of *Phellinus ferrugineofuscus* 2000–2013 (N = 5317) obtained from Swedish Lifewatch (see footnote 4). The northern boreal region is shown in gray and the southern boreo-nemoral region is white.

widely used as an old-forest indicator species in conservation inventories in the Nordic countries (Nitare 2000, Niemelä 2005). The occurrence of *P. ferrugineofuscus* depends upon the local availability of dead spruce wood and connectivity to old spruce-dominated forest (Nordén et al. 2013). The species is a good candidate for citizen science data collection as fruiting bodies are large and persist for a few years, and are easy to distinguish from other species in the field.

Phellinus ferrugineofuscus has a northern boreal distribution in Sweden, as can be identified from presence-only observations by citizens and national conservation inventories by the forestry sector (Fig. 1). The southern boreo-nemoral region, where the species is rare, consists of a wide mixture of deciduous and coniferous dominated forest, which is highly productive and heavily exploited for timber. The northern boreal forest is coniferous dominated and, although also heavily exploited, contains most of the country's old growth forest. Since the species occurrence is negatively affected by intensive forestry (Edman et al. 2004, Nordén et al. 2013), the relative importance of forest management history and macro-climate in determining the species distribution within Sweden is currently unclear.

The distribution of *P. ferrugineofuscus* extends beyond Sweden; according to Ryvarden and Melo (2014), the species follows natural stands of *Picea* as far south as France. Publicly available observations of *P. ferrugineofuscus*, however, come primarily from Sweden (data *available online*).[4] In Appendix S1, we show that the Swedish observation data used here capture the climatic range of the species from the available European observation data (see footnote 3 and Andrew et al., *in press*) relatively well (Appendix S1: Figs. S2 and S3). We also show that in the species projections there is limited extrapolation beyond the climatic range used in model fitting (Appendix S1: Figs. S4–S6), justifying our focus on the extent of species occurrence in Sweden for fitting the model (see Mair et al. 2017).

Species distribution models

We used five species distribution models using a combination of presence-only (PO) and presence–absence (PA) citizen science observations of *P. ferrugineofuscus* (Mair et al. 2017). The models applied were a generalized linear model (GLM) using PA data, a point-process Poisson model using both PA and PO data (here termed the PA/PO model; Fithian et al. 2015), a Bayesian occupancy model using repeat visit data (Kéry et al. 2010), MaxEnt using PO data with a random background (Phillips et al. 2006), and MaxEnt using PO data and the target group background (TGB) approach (Phillips and Dudik 2008). These models were selected to encompass a range of data requirements and assumptions about recording bias (for further details, see Mair et al. 2017).

In brief, species presence-only observation data were downloaded from the Swedish Lifewatch website for the period 2000–2013 at a grid cell resolution of 100 m (Mair et al. 2017; Lifewatch *available online*).[5] In total, occurrences in 5317 cells were recorded (Fig. 1). A presence–absence data set was established based on observation records from eight polypore recorders. These data were at the 100-m resolution and covered 15,508 grid cells spread across the study region (mapped in Mair et al. 2017). The repeat-visit detection/non-detection data used in the occupancy model were based on presence-only records of 35 old-forest indicator species of dead-wood-dependent fungi from the LifeWatch website (see footnote 4). The detection of indicator species other than the focal species represented the non-detection of the focal species.

Species occurrence was modelled as a function of living spruce volume, connectivity to old spruce forest, mean annual temperature (averaged over 1989–2010), summed precipitation May–November (averaged over 1989–2010), a temperature–precipitation interaction, and a wetness index. Full details of model selection procedures and final model parameters are given in Mair et al. (2017) and details of variables are in Appendix S2. Mair et al. demonstrated that these models based on citizen science data were able to reproduce species projections from a Bayesian state-space model for colonization–extinction dynamics based on systematically collected field data.

Forest management scenarios

We used the species distribution models to project habitat suitability in response to forecasts of forest management and climate change. Forest projection data were available from the Swedish Nationwide Forestry Scenario Analysis 2015 (NFSA; Claesson et al. 2015, Eriksson et al. 2015). Projections were made for the National Forestry Inventory (NFI) plots (see Appendix S3: Fig. S1 for the distribution of NFI plots; Fridman et al. 2014) and initialized from the state observed in 2008–2012. We used projection data for a total of 29,892 NFI plots located across Sweden and representing 22.4 million ha of productive forest land. Data on projected changes in living and dead wood spruce volume and forest age were available for each plot for every fifth year from 2020 to 2110 (for details on how dead wood data was used when making projections, see *Species projections*). We used projections of the living spruce volume and forest age to calculate connectivity (for details see Mair et al. 2017). For additional information on total wood volume extracted and so forth, see Claesson et al. (2015). We wrote our own software to simulate the decomposition of the dead wood on the NFI plots using the one-time chronosequence method described in Harmon et al. (2000).

[4] www.gbif.org

[5] www.analysisportal.se

For the NFSA projections the RegWise software (version 2.2) was used. RegWise is a software component within the Heureka suite of forest decision support tools (Wikström et al. 2011). The core of Heureka is made up of empirical individual tree growth (see Fahlvik et al. 2014), ingrowth (Wikberg 2004), and mortality (Elfving 2014) models simulating tree layer development in five-year time steps. In RegWise, forest management actions are steered by a rule-based simulation framework. The harvest level, and consequently the development of the forest, is controlled by stated management programs (silviculture and harvest activities) and the predicted growth in each time period. Different management programs are stated for, e.g., different forest owner categories and tree species mixtures, in accordance with what was observed at the NFI plots during the last 5–10 yr. Tree retention practices at final felling were also included (Roberge et al. 2015).

In NFSA, different scenarios were applied concerning the intensity of harvest and the forest area set aside from timber production for nature conservation purposes. The six scenarios consider both forest management and climate change effects (Table 1). The "baseline" scenario assumes that over the coming 100 yr, 84% of the land is used for wood production and 16% is set aside from forestry. This 16% comprises legally protected reserves, forest that is voluntarily set aside from production, and clear-cut retention forestry. The scenario assumes that 100% of tree growth is cut. Tree growth rates were assumed to vary with climate, and three climate scenarios were applied to this baseline forest management scenario. These were (1) constant present data climate (100ConstClim), (2) moderate climate change, representative concentration pathway (RCP) 4.5 (100RCP4.5), and (3) a higher rate of climate change, RCP 8.5 (100RCP8.5; Table 1). Three alternative forestry practices were then forecast assuming climate scenario RCP 4.5. These were (1) timber extraction reduced to 90% of tree growth (90RCP4.5), (2) timber extraction increased to 110% of tree growth (110RCP4.5), and (3) twice the amount of forest set aside from production (totaling 32%), with the additional set-aside forest classed as legally protected reserves, voluntary set-aside forest or clear-cut retention forest in the same proportions as the original 16% (Cons100RCP4.5).

Voluntary set-aside and clear-cut retention forest practices may not be strictly adhered to in reality in the long term. As a result, forest classed as voluntary set-aside or retention forest may in fact be managed as production forest now or in the future, and so 16% may be an overestimate of the amount of forest actually set aside from production. Therefore we also tested the effect of removing voluntary set-aside and retention forest practices across all six scenarios. In these simulations, only legally protected reserves were set aside from production, which composed 3.6% of the landscape. To do this, we replaced projection data from the voluntarily set-aside and clear-cut retention forest plots with projection data from production forest plots. Each voluntary set-aside or retention forest plot was replaced with the spatially nearest production forest plot. Nearest spatial neighbor was used in order to maintain the landscape-scale spatial structure of, for example, tree composition.

Climate change data

The climate change scenarios applied were RCP 4.5, which assumes a radiative forcing of 4.5 W/m^2 by 2100, and RCP 8.5, which assumes a higher rate of climate change, with radiative forcing of 8.5 W/m^2 by 2100 (van Vuuren et al. 2011). For both RCP scenarios, five different global climate models were used from the CMIP5 archive (Taylor et al. 2012) were used (Appendix S4), as different models make different assumptions. To increase the spatial resolution in the climate scenarios, data from the global models where used to force the regional climate model RCA4 (Strandberg et al. 2014). To further increase the resolution and reduce model biases the results were bias adjusted using a distribution based scaling (DBS) method (Yang et al. 2010*a*, *b*). The reference data set for the DBS calibration procedure was the same as used for the development of the species distribution models (Appendix S2: *Climate data*). In this way, the climate scenario data have the same mean climate during the reference period, as well as the same spatial resolution of 6.25 × 6.25 km for the whole period 1970–2100. Monthly total precipitation were summed over the period May–November, and monthly mean temperature data were averaged across each year, to match the climate variables used during species distribution model fitting.

Table 1. Layout of the experimental design based on the two factors, percentage extraction of tree growth (forest management) and climate, and the corresponding scenario acronyms.

	Climate		
Tree growth extraction (%)	Constant present day climate	RCP4.5	RCP8.5
90		90RCP4.5	
100	100ConstClim	100RCP4.5 Cons100RCP4.5	100RCP8.5
110		110RCP4.5	

Note: For the combination 100% tree growth extraction and RCP4.5, an additional conservation scenario (Cons100RCP4.5) was devised, see *Forest management scenarios* for details.

The downscaled climate projection data show large interannual variability therefore in order to project the responses of species to climate change over the long term, we calculated climate averages over a 20-yr interval (IPCC 2013).For each climate model separately, projection data were averaged over a 20-yr moving window, such that for a particular year, we took the average of the 20 yr immediately prior. This corresponded to the ~20-yr averaging period applied to the climate data used in species distribution model fitting.

We matched the forest scenario assumptions to the climate change scenario (Table 1). For 100ConstClim we applied the observed climate data for the present day (1980–2010 averages), which were also used for model fitting.

Species projections

We used each of the five species distribution models to project habitat suitability in response to the six scenarios of forest management and climate change (MaxEnt models predict relative suitability, while the other models predict probability of occurrence, therefore we use the general term “suitability” throughout). Projections were made at each of the NFI plots for every fifth year for the period 2020–2100. In the case of the scenarios that incorporated a climate change component, projections of species habitat suitability were made for each of the five climate projections separately.

We applied mechanistic assumptions in order to incorporate aspects of the species’ ecology that were not captured in the correlative structure of the models (Kearney and Porter 2009). First, the species could not occur in plots where there was no dead wood. Second, the species could not occur where the forest age was 25–64 yr old due to dead wood dynamics (we assumed that any retained dead wood has decomposed 25 yr after cutting, and that further dead wood takes a minimum of 64 yr to accumulate and become suitable for colonization; see Mair et al. [2017] for details). Third, suitabilities in clear-cut retention forest (one of the sub-categories within forest set aside from production) were reduced to 1/10th of the projected values, in order to account for edge effects (Ruete et al. 2016). Following this, suitabilities were averaged across the five climate projection models.

Projections of habitat suitability at each plot were then scaled up to reflect the area of land each plot represents, given their uneven distribution across the country. Scaled up projections were summarized across the boreal and boreo-nemoral regions separately, and were separated into production and set-aside forest. In order to take an ensemble modelling approach, we averaged across projections from the five species distribution models. Results are presented as mean suitabilities and as relative change over time from 2020. Relative change over time was used to facilitate comparison of temporal change among scenarios.

RESULTS

Spatial variation in species’ response to climate and forest scenarios: Projections in the boreal vs. boreo-nemoral regions

Ensemble model projections of the relative change in *Phellinus ferrugineofuscus* habitat suitabilities in response to future forest management and climate change scenarios showed more positive changes in the boreo-nemoral region compared to the boreal region (Fig. 2).

In the boreal region, increases were projected in set-aside forest, while changes in production forest were overall small or negative (Fig. 2a). Projected trends indicated a negative effect of climate change; overall habitat suitability showed a large increase assuming no climate change (100ConstClim), a small increase under moderate climate change (100RCP4.5), and a decline under more rapid climate change (100RCP8.5). Changing the volume of timber harvested had relatively little effect on overall habitat suitability trends (100RCP4.5 vs. 90RCP4.5 vs. 110RCP4.5). In contrast, doubling the amount of forest set aside from production resulted in the largest overall increase in habitat suitability (Cons100RCP.45).

In the boreo-nemoral region, set-aside forest was also projected to show increases in suitability across all scenarios (Fig. 2b). Production forest showed little change, except for under no climate change (100ConstClim) and with lower timber extraction (90RCP4.5), where overall increases were projected (Fig. 2b). Overall habitat suitability trends again showed a negative effect of climate change (100ConstClim > 100RCP4.5 > 100RCP8.5). Despite overall increases being projected even under rapid climate change, the levelling off toward the end of the projection period suggests the potential for future declines. In this region, reducing the volume of timber extracted resulted in a large overall increase in habitat suitability (90RCP4.5). Again, doubling the amount of forest set aside from production resulted in the largest overall increases in habitat suitability (Cons100RCP4.5).

The mean suitabilities revealed two important elements. First, the projected suitability in production forest was homogeneously very low across all scenarios and both regions (Fig. 3). Although there was an increase between the first and last year for some scenarios (e.g., no climate change; 100ConstClim), the final suitabilities remained very low in production forest. Secondly, although there were substantial increases in set-aside forest in the boreo-nemoral region over time, within each scenario, suitabilities in set-aside forest were consistently higher in the boreal region than the boreo-nemoral. Thus set-aside forest in the boreal region remained the most suitable for the species. Having said this, mean suitabilities in set-aside forest in the boreo-nemoral region in 2100 were similar to mean suitabilities in set-aside forest in the boreal region in 2020. This suggests that, by the end of the projection period, species occurrence could increase in the boreo-nemoral region,

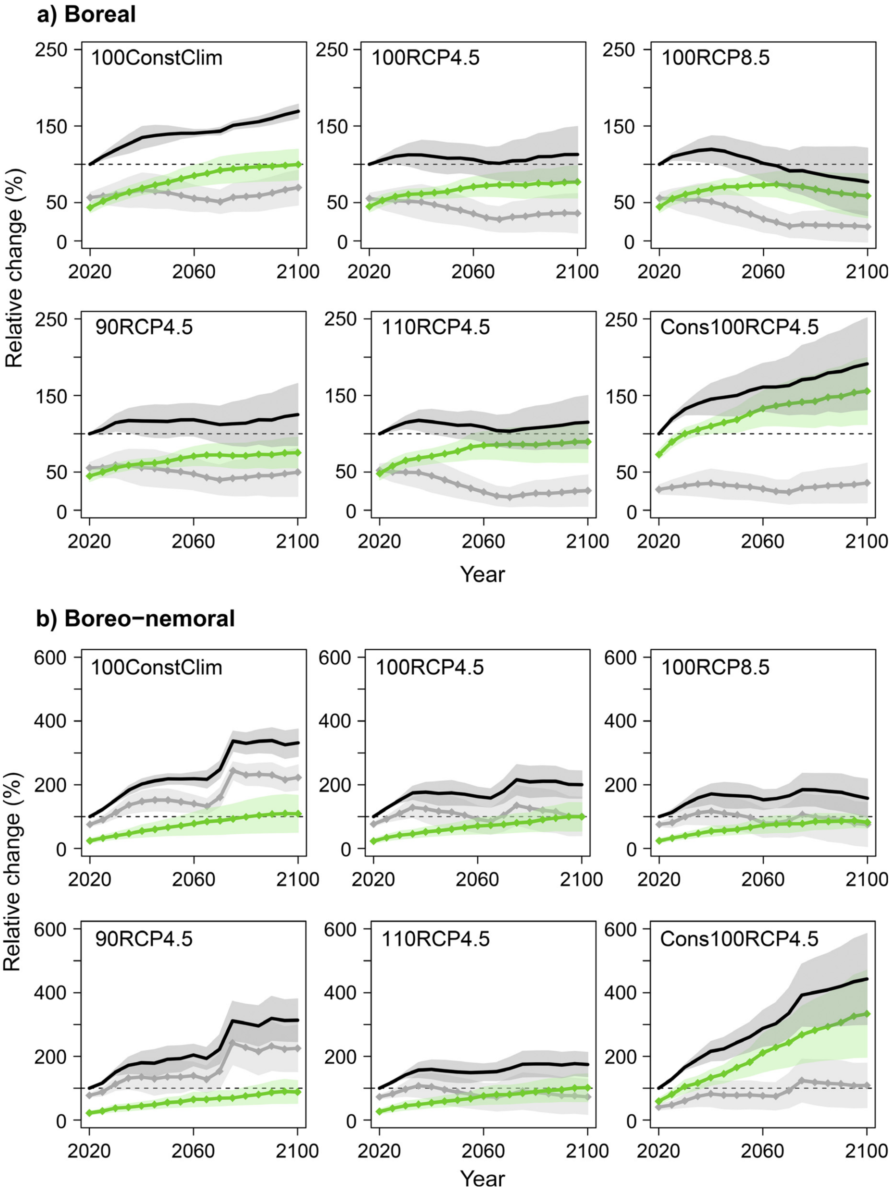

FIG. 2. Relative change in *Phellinus ferrugineofuscus* habitat suitability in response to the six projected forest management and climate change scenarios for the (a) boreal and (b) boreo-nemoral region. The relative change (mean ± SD [shaded areas]; across five species distribution models) is presented for all forest (black), production (gray), and set-aside (green) forest separately. The dashed black line shows the total habitat suitability in 2020, against which relative change is calculated. Note the varying scales on the *y*-axes between panels a and b. Forest management scenarios are described in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

which is the species' southern range edge within Sweden. The explanation is the projected increase in spruce volume, see *Underlying forest and climate projection data*.

The negative effect of climate change on suitabilities projected in 2100 was more pronounced in the boreal region than in the boreo-nemoral. In set-aside forest, mean suitabilities in the boreal region decreased with increasing radiative forcing (100ConstClim vs. 100RCP4.5 vs. 100 RCP8.5; Fig. 3b). In contrast, in the boreo-nemoral region, there was little difference in mean suitabilities in set-aside forest among climate change scenarios, which was due to projected increase in spruce volume (see *Underlying forest and climate projection data*).

Reducing the amount of set-aside forest across all scenarios

When only legally protected reserves were set aside from production, the projected trends for *P. ferrugineofuscus* were considerably less positive (Fig. 4). In the

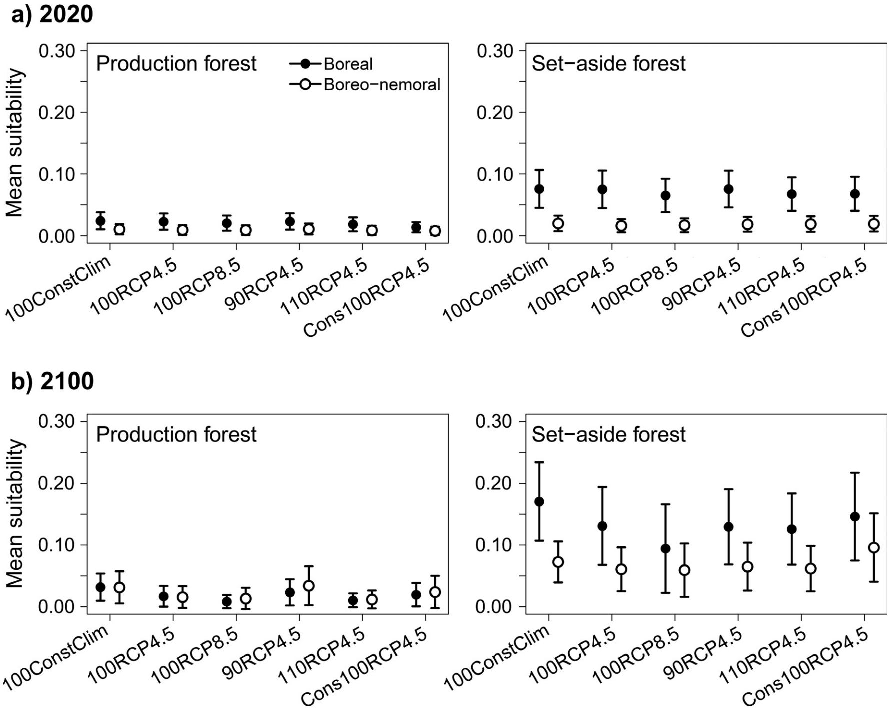

FIG. 3. Habitat suitability (mean ± SD; across five species distribution models) for *Phellinus ferrugineofuscus* in the boreal (solid points) and boreo-nemoral (open points) regions separately for (a) 2020 and (b) 2100, separating out production and set-aside forest.

boreal region, there was again a negative effect of climate change and little effect of varying rate of timber extraction. However, overall increases were only observed under no climate change (100ConstClim; Fig. 4a). In the boreo-nemoral region, differences among scenarios were similar to previously, although increases in set-aside forest were generally small and the overall trends were driven by changes in production forest (Fig. 4b). Projections indicated that legally protected reserves alone were not sufficient to increase or even maintain habitat suitabilities under most scenarios.

Mean suitabilities showed similar differences among scenarios and regions compared to those projected when voluntarily set-aside and clear-cut retention forest were also set aside from production (Fig. 5). However, suitabilities were higher in set-aside forest in 2100, because of the exclusion of lower quality clear-cut retention forest.

Overall trends across boreo-nemoral and boreal regions combined

Projected trends across the boreal and boreo-nemoral regions combined (the full extent of the study area) showed that despite increases in the boreo-nemoral region, overall *P. ferrugineofuscus* trends were dominated by projections in the boreal region (Fig. 6). Habitat suitability was projected to increase under no climate change (100ConstClim), show less of an increase under RCP 4.5 (100RCP4.5), and was projected to go to into decline under RCP 8.5 (100RCP8.5; Fig. 6a). When only legally protected reserves were set aside from production forest, no overall change was projected under RCP 4.5 (100RCP4.5) and a greater decline was projected under RCP 8.5 (100RCP8.5; Fig. 6b). Overall trends highlighted the importance of set-aside forest for species persistence and the large positive effect of increasing the amount of forest set aside from production.

Underlying forest and climate projection data

The underlying forest management and climate change scenarios provide insights into the projected habitat suitability trends. Across all forest management scenarios, living and dead spruce volume, stand age, and connectivity were higher and showed greater increases over time in set-aside forest than in production forest (Appendix S4: Fig. S1). Living and dead spruce volumes were projected to be higher and show greater increases in the boreo-nemoral region relative to the boreal, for all scenarios (Appendix S4: Fig. S1). Connectivity projections were generally similar between the boreal and boreo-nemoral regions. In contrast, for set-aside forest, stand age was consistently higher in the boreal region than the boreo-nemoral, but was similar between the two regions for production forest. Both mean annual temperature and summed precipitation

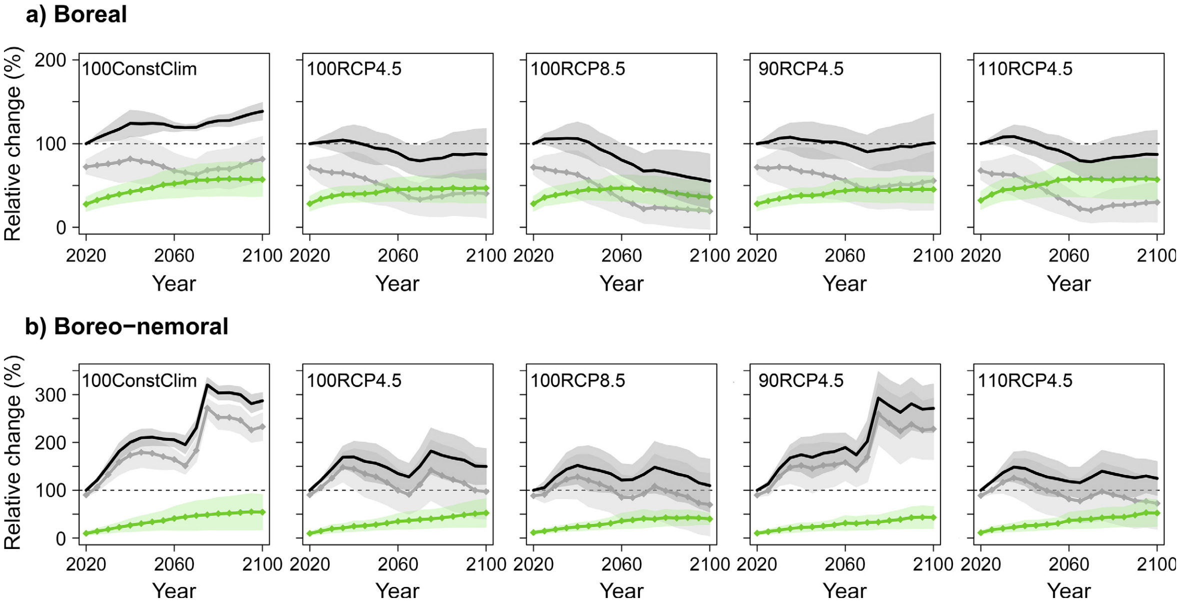

FIG. 4. Relative change in *Phellinus ferrugineofuscus* habitat suitability in response to the six projected forest management and climate change scenarios for the (a) boreal and (b) boreo-nemoral region, when only legally protected reserves are set aside from production. The relative change (mean ± SD [shaded areas] across five species distribution models) is presented for all forest (black), production (gray), and set-aside (green) forest separately. The dashed black line shows the total habitat suitability in 2020, against which relative change is calculated. Note the varying scales on the *y*-axes between panels a and b. [Color figure can be viewed at wileyonlinelibrary.com]

May–November were projected to increase on average across the study region from 2020 to 2100 (Appendix S4: Fig. S2). Larger increases were projected for both variables in the RCP 8.5 scenario compared to the RCP 4.5 scenario. Temporal trends showed spatial similarity, with both the boreal and boreo-nemoral region projected to experience an increase in both climate variables.

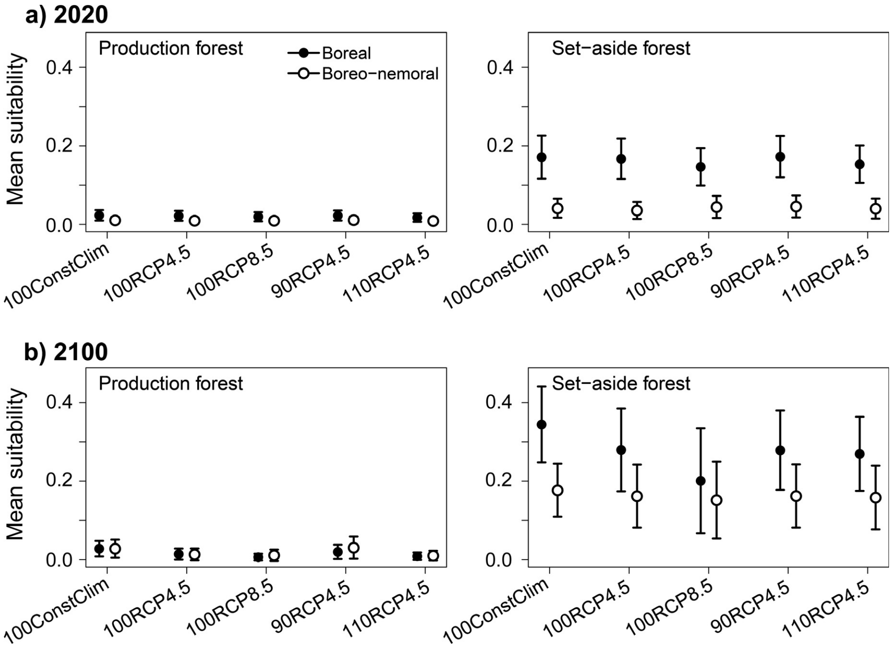

FIG. 5. Habitat suitability (mean ± SD; across five species distribution models) for *Phellinus ferrugineofuscus* in the boreal (solid points) and boreo-nemoral (open points) regions separately for (a) 2020 and (b) 2100, when only legally protected reserves are set aside from production.

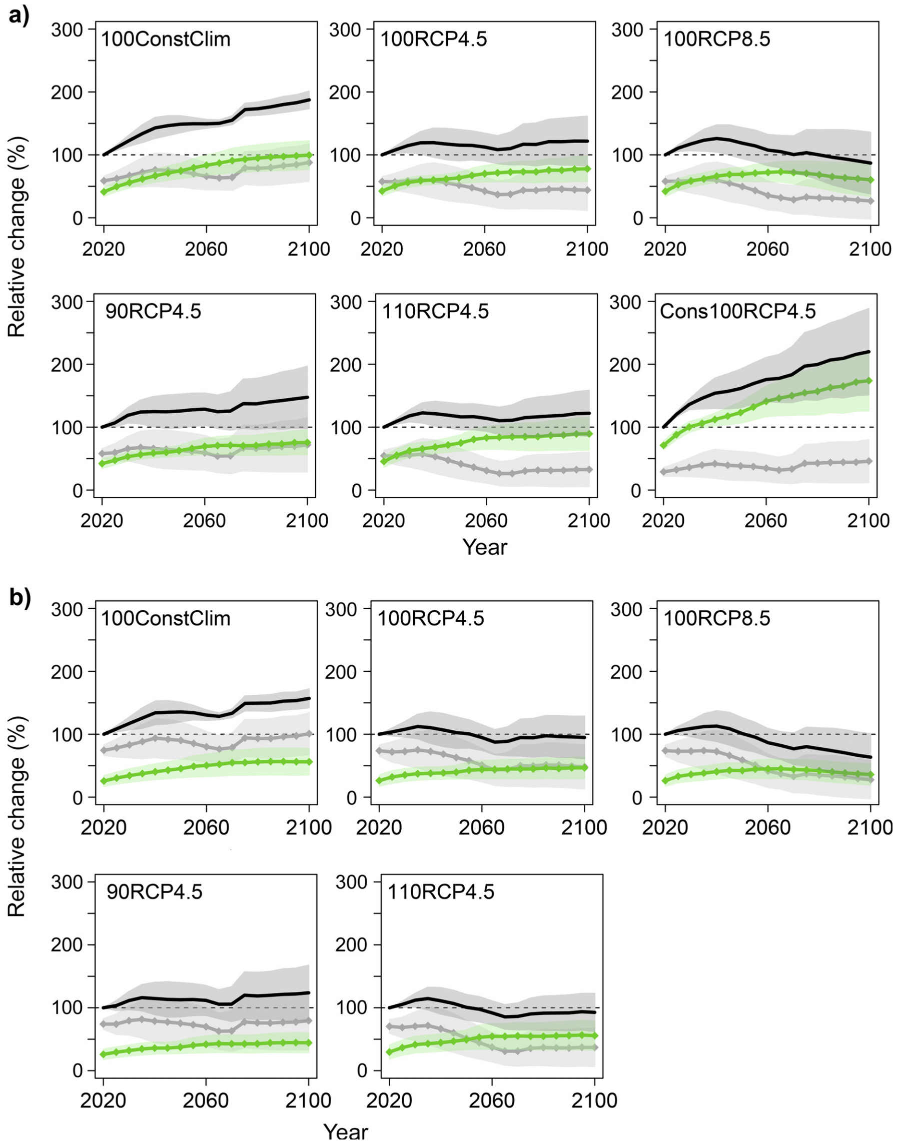

FIG. 6. Relative change in *Phellinus ferrugineofuscus* habitat suitability in response to the six projected forest management and climate change scenarios for the boreal and boreo-nemoral regions combined for (a) 16% of forest set aside from production (legally protected reserves, voluntary set-aside, and clear-cut retention forest) and (b) only legally protected reserves set aside from production. The relative change (mean ± SD [shaded areas]; across five species distribution models) is presented for all forest (black), and for production (gray) and set-aside (green) forest separately. The dashed black line shows the total habitat suitability in 2020, against which relative change is calculated. [Color figure can be viewed at wileyonlinelibrary.com]

Variation among species distribution models

There was broad agreement among the species distribution models in projected trends over time (Appendix S5: Figs. S1 and S2). However, there was variation among models in the absolute amount of change over time (Appendix S5: Figs. S1 and S2). For example, projections suggest that the GLM was more sensitive to forest variables than the other models, as the GLM projected larger increases in response to an increase in the amount of set-aside forest (Cons100RCP4.5; Appendix S5: Fig. S1; see Mair et al. [2017: Supporting Information] for model response curves). On the other hand, the PA/PO model and MaxEnt random background appear to be more sensitive to climate, as these models projected the largest declines in response to climate change (100RCP8.5; Appendix S5: Fig. S1). The effect of variation among models can be seen in the ensemble projections. Particularly noticeable are the fluctuating projections in production forest in the boreo-nemoral region (Figs. 2b and 4b vs. Appendix S5: Fig. S1b), which are due to the use of the "relative change" scale exaggerating the small changes in low projected suitabilities that occur in response to changes in underlying forest data (Appendix S4: Fig. S1a).

Discussion

We used an ensemble modelling approach to show that, under large-scale scenarios of forest management and climate change, forest management has the potential to facilitate an increase in occurrence at the southern range edge of an old-forest indicator species in Sweden. Greater relative increases in habitat suitability were projected in the southern boreo-nemoral region, where the species is currently rare, compared to the northern boreal region, where the species is more widespread. Although set-aside forest in the boreal region was consistently the most suitable, the projected increases in set-aside forest in the boreo-nemoral region suggested that forest management could facilitate increased occurrence at the southern range edge, which would run counter to the northward distribution retractions that are the well-established expectation under climate change (Thomas et al. 2006). Previous studies have shown that the interaction between temperature and precipitation can result in multi-directional range shifts (VanDerWal et al. 2013), but we show that land use could also be the basis for nonconforming distribution changes.

The projected increase in habitat suitability in the boreo-nemoral region reflects an increase in the projected spruce volume and forest age in set-aside forests. Our results therefore support the assumption that the current rarity of the species in this region is due to a history of intensive forest management that has reduced the amount of natural old-growth forest and the availability of dead wood (Nordén et al. 2013, Gauthier et al. 2015). Indeed, the suitability of production forest was very low across both regions and all scenarios (Peltoniemi et al. 2013), indicating that the species is largely restricted to set-aside forest. As a result of this very low suitability in production forest, we found that in both the boreal and boreo-nemoral regions, varying the amount of timber harvested had little effect on mean habitat suitabilities. However, varying the amount of timber harvested did affect the projections of overall relative change due to production forest showing more positive trends in relative suitability when the amount of timber harvested was reduced. Reducing the amount of timber harvested left more old-forest uncut, to the benefit of the study species. Therefore, although these trends are driven by changes in the suitability of production forest where the species rarely occurs, varying the amount of timber harvested is likely to have some effect on the overall occurrence of the study species.

Projections indicated a strong effect of climate change, and our results suggest that the species is likely to suffer negative consequences of climate change throughout its range. Our findings are supported by previous work which showed that, for the majority of wood-decaying species studied, climate change was likely to have a negative effect due to increased decomposition rates reducing the length of time that dead wood was available (Mazziotta et al. 2016). The authors of this study concluded that an increase in set-aside forest would increase dead wood availability, and therefore compensate for the likely negative effects of climate change on wood decaying species in boreal forests. Our results support this conclusion; we show that under RCP 4.5, legally protected reserves alone are likely insufficient to maintain habitat suitabilities for the species into the future, however increasing the area of forest set aside from production results in more positive projection trends across the whole study area. Somewhat unexpectedly, our results also indicated that the negative effects of climate change were more evident in the boreal region than in the boreo-nemoral; there were larger declines in habitat suitability toward the end of the projection period under RCP 8.5 in the boreal compared to the boreo-nemoral region. We suggest that this is likely due to the fact that initial habitat suitabilities in the boreo-nemoral were so low that the potential for improvements in forest condition were huge, and as a result, the continuously improving forest conditions dominated the projection trends in this region. In contrast, the boreal region had a much higher initial suitability for the species, resulting in smaller relative improvements in forest condition, which allowed the negative effects of climate change to become evident in this region.

Our results strongly support the importance of set-aside forest for the persistence of old-forest associated species (Junninen and Komonen 2011). Projections assuming 16% of forest set aside from production, which is close to the Aichi Biodiversity Target 11 of ≥17% adopted by the CBD in 2010 (CBD 2010), showed that legally protected reserves complimented with voluntary set-aside forest that remains uncut in the coming century will increase the species viability. Mean habitat suitabilities were higher in set-aside forest consisting of only legally protected reserves compared to set-aside forest consisting of a mixture of management types, indicating that legally protected reserves are the most suitable habitat type for the study species. However, the addition of voluntarily set-aside forest resulted in much more positive projection trends overall, emphasizing the benefit of an increase in the total area of forest set aside from production for species conservation. Voluntarily set-aside forests tend to be smaller than reserves, with a different structure and tree composition, and so they can increase the diversity of habitats supporting forest biodiversity (Simonsson et al. 2016). However, the positive projections we obtained when 16% of forest was set aside from production rely on strict adherence to setting aside forest over the coming century. There is some concern among non-governmental environmental organizations, first that 16% is an overestimate of the amount of forest currently set aside and second that not all voluntarily set-aside forest will remain uncut over the coming century. Moreover, we consider that setting aside 32% of forest, which resulted in by far the greatest projected increases in overall habitat suitability, is likely to be too costly to be implemented. In addition, although we reduced the suitabilities in clear-cut retention forest to 1/10th of the projected values in order to account for negative edge effects in forest fragments (Ruete et al. 2016), this may nevertheless overestimate suitability. Our projections may therefore be overly optimistic.

Furthermore, the ability of the species to respond to an increase in forest age and dead wood volume in set-aside forest depends upon the species dispersal and colonization abilities, and this in turn will depend upon the connectivity of old-growth forest at the landscape scale (Nordén et al. 2013). The re-colonization of restored forest by red-listed species of dead-wood-dependent fungi is slow (Pasanen et al. 2014). Moreover, species interactions and competition influence fungal communities (Ottosson et al. 2014), and could limit species occurrence. Thus, the positive trends projected in the boreo-nemoral region may not be realized.

A further conservation concern is the potential conflict between the conservation of spruce-associated species and the conservation of deciduous-associated species in the boreo-nemoral region. The boreo-nemoral region is currently biodiverse due partly to the occurrence of deciduous tree species, and it is already recommended that, for conservation purposes, spruce should be actively removed from deciduous forest reserves (SEPA 2013). An increase in spruce volume in naturally developing forest may therefore be of benefit to spruce-associated indicator species such as *P. ferrugineofuscus*, but deciduous-associated species may subsequently suffer. A possible solution could be to cut spruce without selling it, thereby providing habitat for species associated with dead spruce wood.

In summary, our results (1) support previous studies showing that *P. ferrugineofuscus* is mainly restricted to set-aside forest and (2) suggest that the current species rarity in the boreo-nemoral is due to the history of intensive forest management in that region. As a result, (3) improved forest conditions through management action could facilitate increases in *P. ferrugineofuscus* occurrence at its southern range edge, contrary to expectations under climate change. We found that (4) the species is likely to be negatively affected by climate change but (5) an increase in set-aside forest area resulted in more positive projections, suggesting that conservation action could buffer the species to some extent against the negative effects of climate change. Finally, (6) such positive responses to conservation action would require that voluntarily set-aside forest is strictly adhered to. We conclude that an increase in the amount of set-aside forest to the level of the Aichi 17% target (CBD 2010) could increase the viability of species negatively affected by forestry across both the boreo-nemoral and boreal regions and that there is therefore potential for conservation action to mitigate the negative effects of climate change.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1541/full

Data Availability

Data associated with this paper have been deposited in the Environmental Climate Data Sweden depository https:/doi.org/10.5879/ECDS/2017-03-23.1/1