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Ignoring biotic interactions overestimates climate change effects: The potential response of the spotted nutcracker to changes in climate and resource plants

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Abstract

Aim: Projecting future distributions of species under climate change remains a particular challenge for species that are trophically interacting. Interaction partners are often assumed to react differently to climate change, causing spatial mismatches in future distributions and increased extinction risks. We compare potential direct effects of climate change with combined direct and indirect effects mediated via food plants on a highly specialized bird species.

Location: Europe.

Taxon: European spotted nutcracker (*Nucifraga caryocatactes*).

Methods: We used climate-based species distribution models to project probabilities of occurrence of European spotted nutcrackers and their main food sources, Swiss stone pine (*Pinus cembra*) and common hazel (*Corylus avellana*) under climate change. We combined direct climate change effects on the bird and indirect effects via the food plants by calculating the probabilities of plants and nutcrackers occurring together.

Results: We find considerable projected northward shifts in future occurrences of nutcrackers under climate change and similar effects on hazel. In contrast, projections for Swiss stone pine indicate minor altitudinal upward shifts. Combined projections of direct and indirect effects of climate change indicate less pronounced shifts of nutcrackers' occurrences, due to relatively small changes in pine's occurrences and to suitable hazel occurrence shifts.

Main conclusions: Our study suggests that potential effects of climate change on the future distribution of the nutcracker might be overestimated when ignoring trophically interacting plants in future projections. Models of direct effects of climate change on nutcrackers' occurrence probabilities project greater range losses than models of combined direct and indirect effects via resource plants. Therefore, considering biotic interactions does not necessarily increase the risks that climate change may impose on species distributions, but could reduce overestimation of potential range losses in rapidly changing environments.

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KEYWORDS

biotic interactions, climate change, *Corylus*, *Nucifraga*, nutcracker, *Pinus*, resource plants, species distribution models

1 | INTRODUCTION

Interactions between species are a crucial component of resilient ecosystems, but they are often neglected in assessments of possible effects of climate change (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013). Species range shifts lead to major changes in ecosystem structure, function and species' interactions when interacting species respond differently to climate change (Walther et al., 2002), causing predominantly negative consequences for biodiversity (Blois et al., 2013; Böhning-Gaese & Lemoine, 2004). Shifts in geographic ranges in response to anthropogenic climate change such as upward shifts in tree line and northward shifts of range boundaries have already been observed (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Maggini et al., 2011). For interacting species, such range shifts could lead to a mismatch of the areas where each of the species is able to persist (Kissling et al., 2010; Schweiger et al., 2012). In mutualistic animal–plant interactions such range shifts have more negative impacts on animals' than on plants' survival (Schleuning et al., 2016; Stewart et al., 2015), which makes animal species that rely on specific plant resources especially vulnerable to climate change due to the combined direct and indirect effects of climate change.

The European spotted nutcracker (*Nucifraga caryocatactes* L. 1758) depends on three plants providing seed sources for its winter caches, which may render the bird especially vulnerable to indirect climate change effects via its food plants. Additionally, nutcrackers prefer mountain habitats which are suggested to be particularly at risk of extensive species losses under climate change (Kissling et al., 2012; Sekercioglu, Schneider, Fay, & Loarie, 2007). Already Gregory et al. (2009) found that the nutcracker is one of the bird species which most declined with global warming between 1980 and 2005.

The nutcracker's main seed sources in their European range are Swiss stone pine (*Pinus cembra* L. 1753) and common hazel (*Corylus avellana* L. 1753) (Bauer & Glutz von Blotzheim, 1993; Mattes & Jenni, 1984). The birds cache the seeds which they use as primary food source throughout the year. Additionally, the amount of energy-rich seeds determines their breeding success as sole food for fledglings during the winter (Neuschulz, Mueller, Bollmann, Gugerli, & Böhning-Gaese, 2015). The nutcracker is a highly effective seed disperser that far surpasses the dispersal rate of most tree species (Lorenz, Sullivan, Bakian, & Aubry, 2011; Swanberg, 1956), providing its resource plants with the possibility to undergo upward and northward range shifts (Theurillat & Guisan, 2001; Kharuk, Ranson, Im, & Dvinskaya, 2009; but see also Neuschulz, Merges, Bollmann, Gugerli, & Böhning-Gaese, 2018).

Here, we analyse projected future changes in the distributional range of the nutcracker in Europe using species distribution models

(SDMs). We compare projections based on direct effects of climate change with projections based on combined direct and indirect effects of climate change via potential occurrence changes of the three tree species as the nutcracker's main food sources.

Classical SDMs link occurrence data to abiotic environmental variables (Elith & Leathwick, 2009), assuming that biotic interactions are unimportant at large scales and equally strong across the species' range (Kissling et al., 2012; Pearson & Dawson, 2003). A common approach to integrate interacting species into SDMs is based on a secondary combination of separate distribution models. In previous studies the projected probabilities of occurrence are converted into presence–absence distribution maps where a threshold is used to determine which probability of occurrence is considered to be a presence. Only after this conversion is the distribution of the target species restricted to the distribution of its interaction partners (Schweiger et al., 2012; Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008). Some studies, however, suggest that, as the rules of transformation from probabilities of occurrence to presence–absence data are an important source of model variability (Araújo, Whittaker, Ladle, & Erhard, 2005), the use of estimates of change in probabilities of occurrence might provide more robust forecasts (Araújo, Williams, & Fuller, 2002). Here, we combine the species' occurrence probabilities in a manner that uses actual probabilities of occurrence for both the separate projections of direct climate change effects and combined projections of direct and indirect climate change effects to give a more nuanced projection of future trends.

2 | MATERIALS AND METHODS

We projected current and future probabilities of occurrence of the nutcracker and its main food sources, Swiss stone pine and common hazel, using SDMs (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000; Willis et al., 2015).

2.1 | Data

We used presence–absence data of the European nutcracker from the second European Breeding Bird Atlas (Hagemeyer & Blair, 1997) obtained from the Global Biodiversity Information Facility (GBIF.org, 2016). The data for the atlas have been collected from 1972 to 1995 with a core fieldwork period from 1985 to 1988. The available spatial resolution is 0.5° × 0.5° latitude–longitude. A comparison with more current point observation data showed that although the EBCC data was collected more than 20 years ago it is still valid at the available resolution. We obtained plant occurrence data from chorological

maps from the European Atlas of Forest Tree Species (Caudullo & de Rigo, 2016; Enescu, Houston Durrant, Rigo, & Caudullo, 2016). These maps provide a synthetic overview of the plants' distribution ranges compiled from multiple sources. The main fieldwork period was during the National Forest Inventories from 1993 to 2009. We set the geographic limits for the plants' projections to the nutcracker's European range of the EBCC atlas, spanning between the Atlantic Ocean in the West over the Mediterranean Sea in the South to 30° East.

We extracted current climate data and projections of future conditions from WorldClim 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Current data represent the time period of 1960–1990. Future nutcracker distributions were projected for 2070 (average for 2061–2080). We used future climate databased on all four representative concentration pathways (RCP2.6, 4.5, 6.0 and 8.5) produced by general circulation models (GCMs) for climate change projections in the IPCC Fifth Assessment report (IPCC, 2013). We used the mean of two different GCMs, the MIROC5 (model for interdisciplinary research on climate) and the CCSM4.0 (community climate system model) (IPCC, 2014), to increase the validity of our results. All species and climate data were rescaled to a spatial resolution of 0.5° × 0.5° latitude–longitude.

2.2 | Modelling

We used two approaches, Boosted Regression Trees (BRT) and Maximum Entropy (MAXENT), to model distributions of the three focal species. By using two reliable modelling algorithms we intend to increase the robustness of our results. Compared to other existing SDM methods, BRTs provide outstanding predictive discrimination (Elith et al., 2006), while MAXENT tends to have high predictive accuracy (Merow, Smith, & Silander, 2013). MAXENT estimates environmental suitability for the species to occur, which we considered as equivalent to the probabilities of occurrence estimated by BRT for comparison. We will further refer to both model outputs as probabilities of occurrence, however, we acknowledge the initial difference between the models' intent. The nutcracker has exceptional dispersal ability and transports the plants' seeds across large distances (Didier, 2001), so we assumed unlimited dispersal for all species. All analyses were conducted in R 3.3.3 (R Core Team, 2017), using the package 'biomod2' 3.3–7 for building SDMs (Georges & Thuiller, 2013).

To calibrate the SDMs, we chose a set of predictor variables for both the bird's and the plants' projections showing low variance inflation factors (VIF < 3 following Zuur, Ieno, and Elphick (2009), using the R-package 'usdm' 1.1–18 by Naimi, Hamm, Groen, Skidmore, and Toxopeus (2014)) and low collinearity (pairwise Pearson $|r| < .7$ following Dormann et al. (2013)). Based on these conditions and with biological relevance in mind, we chose the variables temperature seasonality (bio4), mean temperature of the wettest quarter (bio8), mean temperature of the warmest quarter (bio10), precipitation seasonality (bio15), precipitation during the driest quarter (bio17) and altitude.

Model evaluation was based on several accuracy measures. The area under the curve (AUC) of receiver operating characteristic (ROC) is a measure of discrimination capacity between presences and absences where values >0.8 are considered good and values >0.9 excellent (Elith, Kearney, & Phillips, 2010; Pearce & Ferrier, 2000). The true skill statistic (TSS) indicates a prediction success rate where a model is considered to perform accurately if it scores >0.5 at least (Allouche, Tsoar, & Kadmon, 2006; Herkt et al., 2017). Both measures are based on sensitivity representing the models' ability to correctly predict a known occurrence and specificity representing the ability to correctly predict a known absence (Liu, White, & Newell, 2011). We used a 5-fold systematic spatial blocking technique using the 'blockCV' package 1.0.0 (Valavi, Elith, Lahoz-Monfort, & Guillera-Aroita, 2019) based on Roberts et al. (2017). We ran the models with different parameters for the three species and chose the final settings for each based on the highest evaluation scores achieved (see Table 1).

2.3 | Modelling interaction partners

We integrated the occurrence probabilities of the food plants into the occurrence probabilities of the nutcracker by calculating the combined probability of the species occurring together for each of our projections (see Figure 1). We standardized all projected occurrence probabilities, dividing the probabilities by the maximum in each data set, because the projected probability for the Swiss stone pine only reached a maximum of 0.5 (while others reach higher), but the projected current range fitted the current realized range. We estimated the combined probability of occurrence (\bar{P}_{int}) of the bird (P_{Nc}) and all food plants (P_{Pc}, P_{Ca}) as the product of each pair of interacting species' occurrence probabilities. We obtained probabilities of the nutcracker occurring together with each of the food plants separately. To estimate the combined effects of all food plants on the nutcracker's occurrence probability, we summed up all combined occurrence probabilities and divided the result by the maximum number of food plants occurring within one grid cell (P_{Pmax}):

$$\bar{P}_{int} = \frac{P_{Nc} \times P_{Pc} + P_{Nc} \times P_{Ca}}{P_{Pmax}} = \frac{P_{Nc} \times (P_{Pc} + P_{Ca})}{2}$$

In addition to reflecting the probabilities of food sources to be present, this calculation gives more weight to those areas where more than one food source is available, which further increases the probability of the focal species to be able to persist even if one food source decreases.

For these calculations, we make the simplifying assumption that the three species' occurrences are mathematically independent from each other. We are aware that this is not the case and that a tight dependency between plant and bird occurrences implies lower combined probabilities of occurrence, thus the true probability of co-occurrence is greater than the calculated value for \bar{P}_{int} . To address this issue we decided to rescale all models before further analysis. We divided all future and current projections by the maximum probability

of occurrence of their respective current climate projections, ensuring that all projected probabilities of occurrence for all models range between 0 and 1.

To assess the projected changes in occurrence probabilities in relation to the current range as well as to potential future ranges, we chose two subsets of our study extent in addition to the full European extent for the assessment. First, we chose a subset representing changes in all areas currently being or in the future becoming suitable for the nutcracker in Europe. This was done by selecting those grid cells with projected probabilities of occurrence in either one of the scenarios larger than the prevalence of the nutcracker in the EBCC dataset (similar to the approach for threshold selection by Liu, Berry, Dawson, and Pearson (2005)). For the second subset, we restricted our resulting maps to areas currently inhabited by the nutcracker by selecting those grid cells

with presences in the EBCC data set, representing changes in the current range. We calculated the differences between current and future projected probabilities of occurrence for both areas and compared the differences using a Wilcoxon rank sum test, including a Bonferroni correction for significant p -values to correct for multiple testing due to the number of grid cells included into the test for significance (Mangiatico, 2015).

3 | RESULTS

All projections showed good performances, indicated by high AUC and TSS scores for the plant's projections and slightly lower performance scores for the nutcracker projections and the combined projections (Table 2). The TSS score of the BRT combined projection

	<i>N. caryocatactes</i>	<i>P. cembra</i>	<i>C. avellana</i>
BRT			
Trees	2,500	2,500	2,500
Bag fraction	0.5	0.5	0.5
Cross-validation folds	3	3	3
Learning rate	0.001	0.001	0.001
Interaction depth	7	10	8
Minimum number of observations in the terminal nodes of the tree	5	8	8
MAXENT			
Iterations	2,500	2,500	2,500
Linear features	-0.1	-0.1	-0.1
Regularization parameters	-0.1	-0.1	-0.1
Beta-multiplier	1	1	1
Prevalence	0.5	0.5	0.5
Threshold features, sample number	80	-	80
Hinge features, sample number	15	-	15
Quadratic features, threshold	-	-	10
Product features, threshold	-	-	80

TABLE 1 Model parameters for the Boosted Regression Trees (BRT) and Maximum Entropy (MAXENT) species distribution models of the European spotted nutcracker (*Nucifraga caryocatactes*), Swiss stone pine (*Pinus cembra*) and common hazel (*Corylus avellana*)

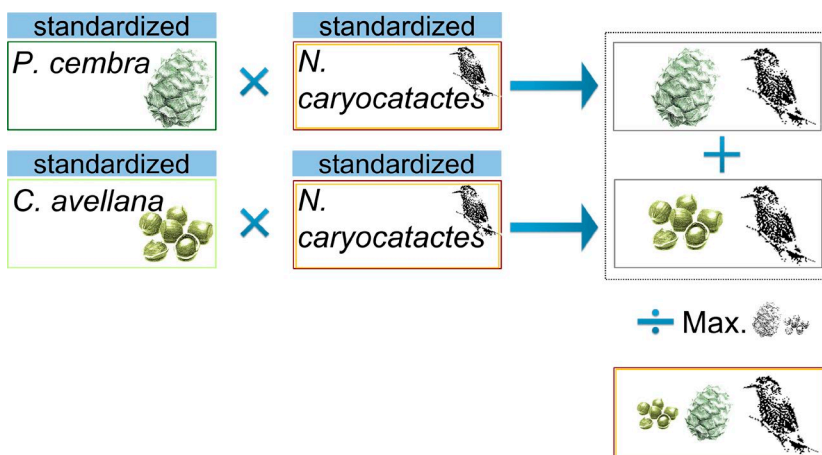


FIGURE 1 Schematic overview of the combination of direct and indirect climate change effects under each RCP. European spotted nutcracker (*Nucifraga caryocatactes*), Swiss stone pine (*Pinus cembra*) and common hazel (*Corylus avellana*). We standardized all species' projected probabilities of occurrence and multiplied each plant data set with each of the nutcracker's, calculating areas where each food plant occurs together with the nutcracker. We summed up the combined probabilities and divided the sum by the maximum (Max.) number of resource plants occurring together. We receive probabilities of occurrence for the nutcracker's minimum and maximum range under combined direct and indirect effects of climate change [Colour figure can be viewed at wileyonlinelibrary.com]

closely resembles that of the direct effects projection of the nutcracker, while the ROC score as well as both MAXENT combined projection scores show slightly lower evaluation scores than the direct effects projections. All models show high accuracy regarding the projections of species' current ranges, however, MAXENT projections tend to underestimate current ranges while BRT models slightly overestimate them at the range edges.

The climate-only projections of the nutcracker show north- and upward shifts with stronger decreases in the southern range than increases in the north (Figure 2i,k) and an overall decreasing range size. A projected complete loss of lower mountain ranges as climatically suitable habitats in the future is accompanied by minor increases of occurrence probabilities at higher altitudes in the Alps (Figure 2e,g).

Similar to the nutcracker, the hazel is projected to strongly increase its occurrence probabilities north of its current range with decreased occurrence probabilities in southern range parts (Figure 3j,l). The hazel's central European occurrence probabilities, however, are projected to remain unchanged. The Swiss stone pine shows only slight changes in probability of occurrence between the grid cells, but no range shifts are projected (Figure 3i,k).

Combined projections for the nutcracker and its food plants give lower probabilities of occurrence in lower mountain ranges of central Europe and highest probabilities of occurrence in the Alps (compare Figure 2b,d). Future projections show smaller magnitudes of range losses and gains than climate-only projections, although occurring within the same regions (compare Figure 2j,l). Although probabilities for combined projections range between 0 and 1, like the probabilities for climate-only projections, overall the projected probabilities of occurrence are lower for combined than for climate-only projections.

Integrating food resources into range projections for the nutcracker leads to a reduced decline in future occurrence probability (Figure 4). For all projections, the changes in probability of occurrence differ significantly between climate-only models and combined models (see *p*-value indicators from Wilcoxon rank sum test depicted in Figure 4). Additionally, the variabilities in projected changes are higher in climate-only models than in combined models. The median changes within the whole study area only differ slightly in all projections (Figure 4a,b). In contrast, median changes in probability of occurrence within the current range of the nutcracker

(Figure 4e,f) and in all areas now or in the future suitable for the bird (Figure 4c,d) show greater declines in climate-only projections than in combined projections.

4 | DISCUSSION

The integration of biotic interactions into projections of species ranges is widely acknowledged to play a crucial role in estimating species' occurrence probabilities and responses to climate change (Araújo & Luoto, 2007). In our study, climate-only projections show high probabilities of occurrence throughout the current range, while projections that combine direct climate change effects and indirect effects mediated via the resource plants give higher probabilities of occurrence in areas where population densities of the nutcracker are reported to be highest (Bauer & Glutz von Blotzheim, 1993). Trophic interactions seem to influence the species' occurrence not only at small scales, but throughout the projected range, as suggested by Wisz et al. (2013). In our case, however, the resource plants appear not to restrict the bird's range but its population density or probability of occurrence, while climatic factors define its range limits. While combined projections show slightly lower evaluation scores than models of direct climate change effects, presumably as an effect of combined factors decreasing each model's performance, all indices are above the threshold for good model performance (AUC > 0.8, Elith et al., 2010; Pearce & Ferrier, 2000; TSS > 0.5, Allouche et al., 2006; Herkt et al., 2017). Thus we consider the combined models useful for further interpretation. Combining direct and indirect effects of climate change on species in a sensible way provides a more holistic approach to estimate a species' possible response to changing environmental conditions. While previous studies mostly found that interacting plants impose additional restrictions on the animal partners in their potential responses to changing climates (e.g. Schweiger et al., 2012; Schweiger et al., 2008), our study suggests that ignoring the resource plants might lead to an overestimation of climate change effects on the nutcracker's distribution in Europe. Our results also show direct negative impacts of climate change on the nutcracker in combined projections, but the negative change is projected to be lower when including the resource plants. The widespread occurrence of hazel could provide a stable food resource throughout the nutcracker's current and future range. However, nutcracker

TABLE 2 Model evaluation for the models of European spotted nutcracker (*Nucifraga caryocatactes*), Swiss stone pine (*Pinus cembra*), common hazel (*Corylus avellana*) and combined direct and indirect effects (combined projections). True skill statistic (TSS), area under the curve (AUC) of receiver operating characteristic (ROC), including standard deviation (\pm SD) for Boosted Regression Trees (BRT) and Maximum Entropy (MaxEnt) models.

	<i>N. caryocatactes</i>	<i>P. cembra</i>	<i>C. avellana</i>	Combined projections
BRT				
TSS \pm SD	0.593 \pm 0.0206	0.990 \pm 0.00172	0.842 \pm 0.0132	0.594 \pm 0.0238
ROC \pm SD	0.896 \pm 0.00581	0.998 \pm 0.000715	0.975 \pm 0.00213	0.870 \pm 0.00743
MaxEnt				
TSS \pm SD	0.603 \pm 0.0824	0.940 \pm 0.00405	0.708 \pm 0.0132	0.537 \pm 0.0273
ROC \pm SD	0.882 \pm 0.00683	0.993 \pm 0.0	0.921 \pm 0.00480	0.817 \pm 0.0106

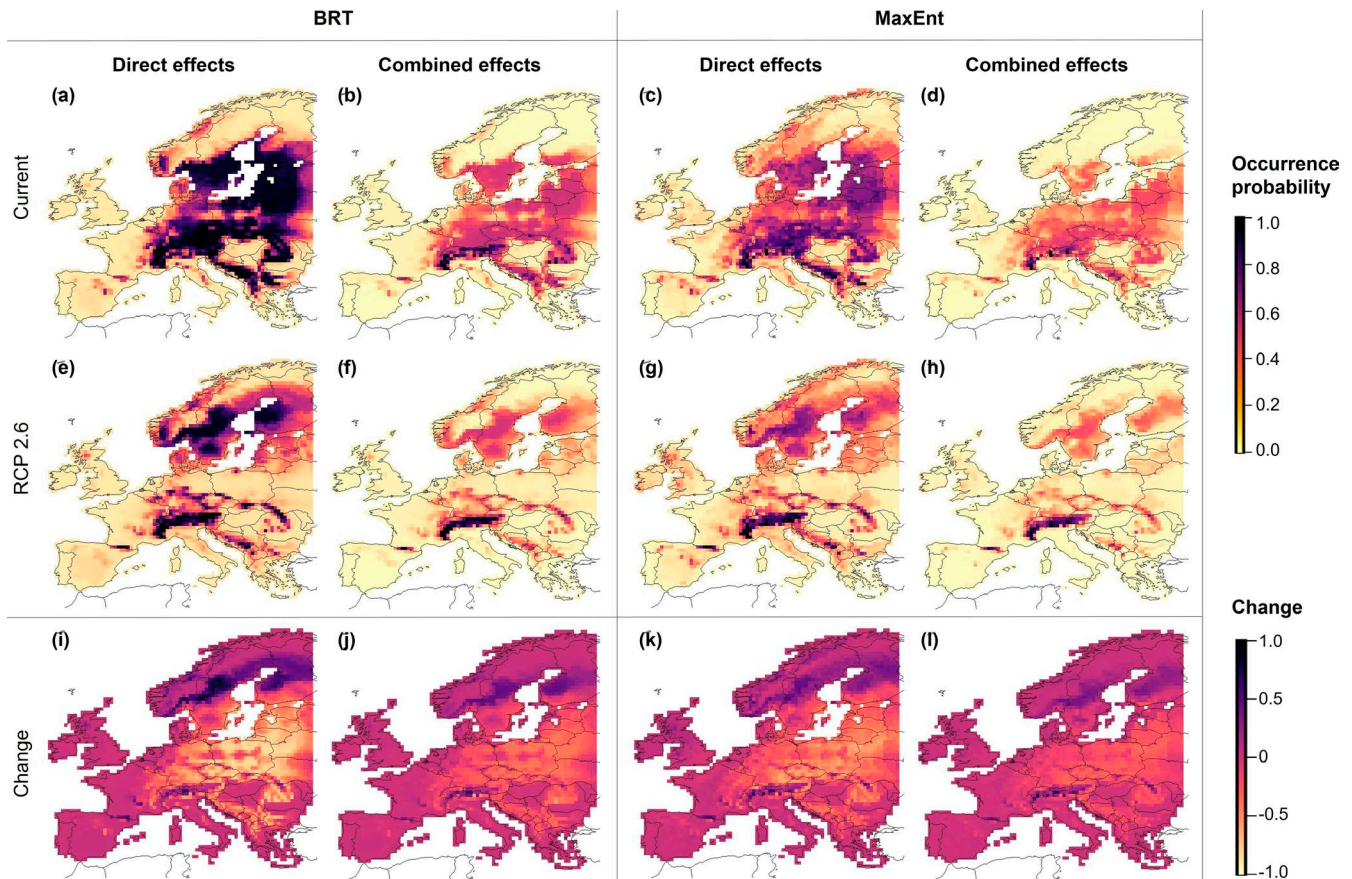


FIGURE 2 Projected probabilities of occurrence of the nutcracker (*Nucifraga caryocatactes*) for 2070 under representative concentration pathway (RCP) 2.6. (a)/(b), (e)/(f), (i)/(j) projections from Boosted Regression rTrees (BRT); (c)/(d), (g)/(h), (k)/(l) projections from Maximum Entropy (MaxEnt); (a)/(e)/(i), (c)/(g)/(k): projections of direct climate change effects; (b)/(f)/(j), (d)/(h)/(l): projections of combined direct and indirect effects of climate change; (a)/(b), (c)/(d): current climate projections; (e)/(f), (g)/(h): RCP 2.6 projections for 2070; (i)/(j), (k)/(l): change in probabilities of occurrence; upper legend: occurrence probabilities for (a)–(h), lower legend: change in occurrence probabilities for (i)–(l) [Colour figure can be viewed at wileyonlinelibrary.com]

population densities are far lower in lower mountain regions without pine trees (Mattes, 1982), which is reflected in our combined models' results that give lower probabilities of occurrence there. Accordingly, the concentration of projected climate-driven range losses in lower mountain ranges leads in sum to less negative change in combined than in climate-only projections. The nutcracker's core area with highest population densities in the Alps is projected to remain stable under climate change both for the nutcracker and its food plants.

The nutcracker's core area in the Alps relies on the occurrence of the Swiss stone pine. Currently the birds are dispersing stone pines above and beyond the plants' current range (Didier, 2001; Kharuk et al., 2009), providing them with the possibility to shift their ranges with climate change. These events however appear to be rare and might only occur frequently during mast seeding years (Neuschulz et al., 2018). Previous studies found significant variation in stone pine growth driven by climatic factors (Carrer, Nola, Eduard, Motta, & Urbinati, 2007; Holtmeier & Broll, 2007), highlighting possible effects of climate change on individual trees. Today's seedlings are growing under climatic conditions that are probably different to those in the future (Hickler et al., 2012), and as the stone pine needs 40–60 years to mature and produce seeds

(Ulber, Gugerli, & Bozic, 2004) our projections looking ~50 years into the future give only rough estimates of climate change effects.

Our projections suggest that the stone pine might be able to persist in its current range under climate change, providing a safe core area for the nutcracker. In contrast to our results, a small-scaled future trends analysis for the Swiss stone pine by Casalegno, Amatulli, Camia, Nelson, and Pekkarinen (2010) suggests heavy losses of suitable areas. The difference to our results could be driven by differences in the spatial scales of the analyses. Mountainous areas show high levels of climatic variation across small spatial scales where increases in large-scale average temperatures can be overruled by local microclimate and topography (Holtmeier & Broll, 2005). Such small-scale effects could not be captured by the coarse scale of our study, which calls for more detailed investigations that integrate direct and indirect effects at different levels of spatial scale.

Besides the changing temperature and precipitation regimes assessed in our study, other factors affected by climate change limit plant growth as well (Anfodillo et al., 1998; Wieser et al., 2009). Extreme weather events strongly affect species ranges, especially in timberline ecotones like the nutcracker's core area (Easterling et

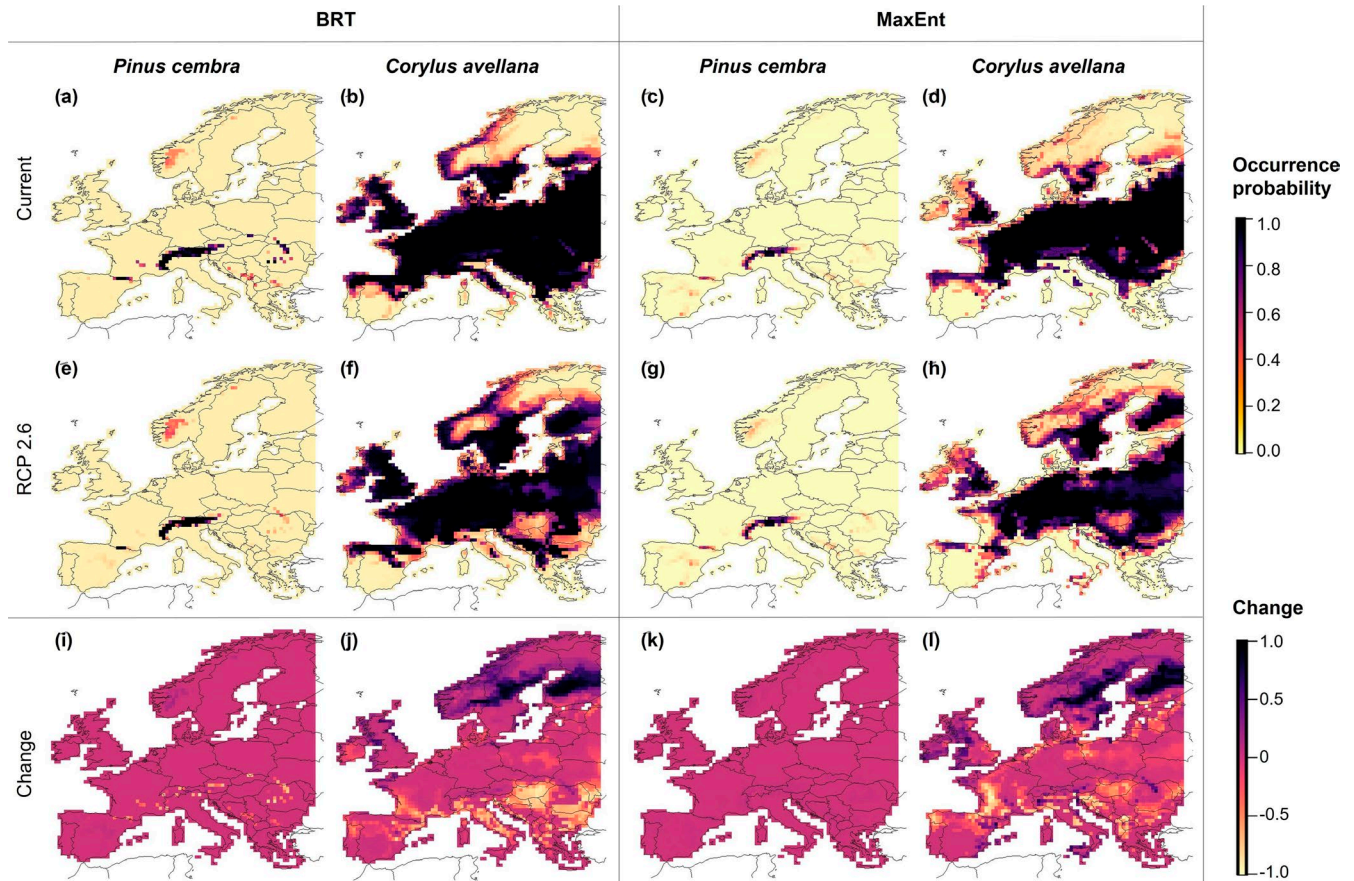


FIGURE 3 Projected occurrence probabilities of the nutcracker's associated food plants for 2070 under representative concentration pathway (RCP) 2.6. (a)/(c), (e)/(g), (i)/(k): projections for Swiss stone pine (*Pinus cembra*); (b)/(d), (f)/(h), (j)/(l): projections for common hazel (*Corylus avellana*); (a)/(b), (e)/(f), (i)/(j): projections from Boosted Regression Trees (BRT); (c)/(d), (g)/(h), (k)/(l): projections from Maximum Entropy (MAXENT); (a)/(b), (c)/(d): current climate projections; (e)/(f), (g)/(h): RCP 2.6 projections for 2070; (i)/(j), (k)/(l): change in probability of occurrence; upper legend: occurrence probabilities for (a)–(h), lower legend: change in occurrence probabilities for (i)–(l) [Colour figure can be viewed at wileyonlinelibrary.com]

al., 2000), and are projected to increase in intensity and frequency under climate change (Gimmi, Wohlgemuth, Rigling, Hoffmann, & Bürgi, 2010; Zumbrunnen, Bugmann, Conedera, & Bürgi, 2009). Such local events could lead to increased tree mortality rates, giving way for pioneer species to establish to a disadvantage for the nutcracker (Boden, Pyttel, & Eastaugh, 2010; Hättenschwiler & Körner, 1995).

Additional biotic factors apart from the trophic interactions analysed in our study influence species ranges under climate change (Rosenzweig et al., 2007; Wieser et al., 2009). Under warming conditions invading deciduous trees have an advantage and outcompete slow-growing pine species (Fischelli, Frelich, & Reich, 2014; Gimmi et al., 2010). Understorey vegetation and seed predation have been shown to be more influential on stone pine establishment than climatic factors (Neuschulz et al., 2018). Also, there are unknown effects of pathogenic fungi and insects which depend on stand density as well as climatic conditions (Merges & Neuschulz, 2018). The species are currently in a state where neither pathogens nor competitors pose a threat for the Swiss stone pine, but changing climate and phenology could lead to unknown effects.

Although we find some direct and indirect influences of climate on the distribution of the stone pine, its current distribution is largely

shaped by historic human influences (Casalegno et al., 2010; Didier, 2001). The nutcracker's occurrence data show presences further north than its food sources. A likely reason for this discrepancy could be plantations of Siberian stone pine (*Pinus sibirica*) in Finland and Sweden (Bauer & Glutz von Blotzheim, 1993) which the nutcracker also uses as a food source. Some authors argue that the development of forest structures at higher altitudes does not depend on bioclimatic factors altogether (Holtmeier & Broll, 2007), but on forest management practices that have shaped alpine ecosystems (Motta & Lingua, 2005). The recent establishment of the Swiss stone pine at higher altitudes might merely be a re-establishment where currently decreasing human pressure has previously suppressed forest growth (Wieser et al., 2009). These discussions emphasise that human land use, especially forest management and grazing regimes, will play a fundamental role in the conservation of plant habitats (Casalegno et al., 2010), and thus also determine the abilities of associated animal species to persist under climate change.

The consideration of biotic interactions is crucial for the successful protection of target species. While in some cases the dependency on resource plants might pose an additional threat (Schweiger et al., 2012), our results show that ignoring the availability of host plants

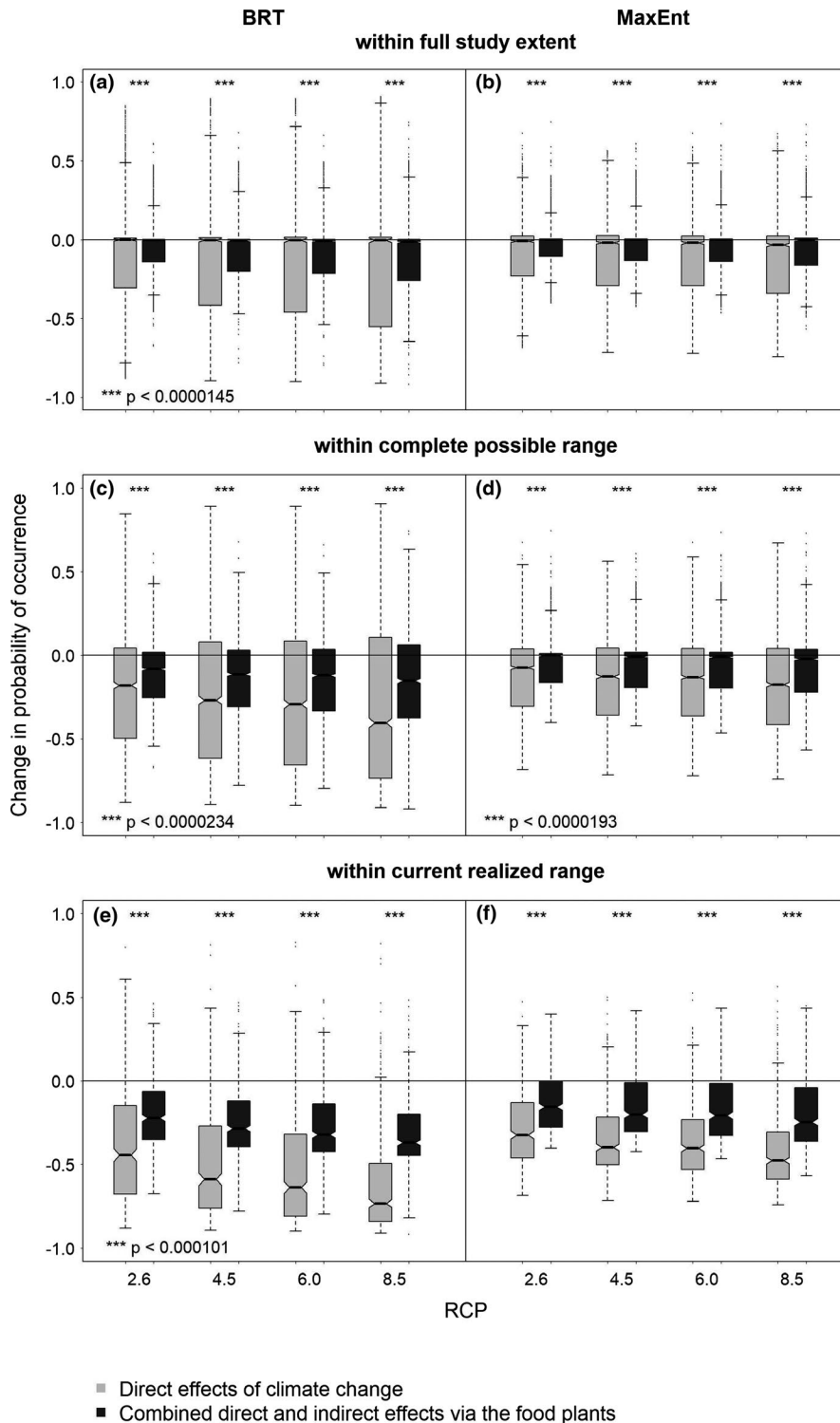


FIGURE 4 Boxplots of changes in probabilities of occurrence of the nutcracker (*Nucifraga caryocatactes*) over all representative concentration pathways (RCPs) in 2070. Light grey: projected direct effects of climate change; dark grey: combined projected direct and indirect climate change effects via the food plants; (a), (c), (e): projections from Boosted Regression Trees (BRT); (b), (d), (f): projections from Maximum Entropy (MAXENT); (a), (b): changes within all of Europe; (c), (d): changes within all areas currently being or in the future becoming suitable for the nutcracker in either one of the RCP scenarios; (e), (f): changes within the nutcracker's current realized range; notches indicate 95% confidence interval of the difference between two medians; ***: indicates highly significant differences between the boxplots of direct and combined direct and indirect climate change effects, p-values indicate Bonferroni corrected significance thresholds

may lead to overestimation of potential range losses. Our study emphasizes the importance of considering the responses of interaction partners when investigating the effects of climate change, especially for developing conservation strategies. A better understanding of biotic interaction networks increases the success of conservation strategies and the ability to protect ecosystem services (Potts et al., 2010; Schweiger et al., 2012), especially in highly heterogeneous mountain areas, where the small-scale consequences of climate

change on specific species are still poorly understood (Boden et al., 2010).

5 | CONCLUSION

Biotic interactions are an important factor in species' response to climate change. Our study suggests that, when considering the

direct links between the animal species and its resource plants as well as direct climate change effects, the inclusion of interaction partners into future projections could reduce overestimations of potential range losses. For the nutcracker, projected replacements of tundra ecosystems by forests (Hickler et al., 2012) and an increasing proportion of Swiss stone pine at higher altitudes in the Alps (Didier, 2001; Schröter et al., 2005) could offer new habitats in the future. Vice versa, the nutcracker provides its food plants with 'extraordinary colonization capacity' (Didier, 2001), giving them a high potential for quick responses to climate warming. Increasing seed production due to increasing summer temperature might shorten the interval between good seed years (Holtmeier & Broll, 2007) and increases tree growth (Motta & Nola, 2001), offering further potentially positive effects of climate change. However, shifts from boreal to temperate vegetation in lower mountain ranges and southern latitudes might lead to range decreases as well (Hickler et al., 2012) and effects of climate change on tree pathogens are yet unknown. Furthermore, in recent decades human land use has been shown to be the most influential factor in determining species ranges, emphasizing the need for conservation strategies that consider these multiple anthropogenic effects. Overall, the case of the European spotted nutcracker and its resource plants suggests that considering trophic interactions in modelling species responses to climate change might help reduce overestimations of potential range losses, thus stressing that species interactions should be taken into account in future models of climate change effects as well as in conservation strategies.

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DATA AVAILABILITY STATEMENT

All data used in this study were obtained from third parties and are available online. Data on the European spotted nutcracker are available from the Global Biodiversity Information Facility (GBIF.org, EBCC data: <https://doi.org/10.15468/dl.cxntbz>), data on the tree species' ranges were extracted from the European Atlas of Forest Tree Species (San-Miguel-Ayanz et al. 2016, forest.jrc.ec.europa.eu/en/european-atlas/). Climate data were obtained from WorldClim 1.4 (Hijmans et al., 2005, worldclim.org/version1).

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**BIOSKETCHES**

Eva Katharina Engelhardt is mainly interested in climate and land use change effects on species and biodiversity. She is a PhD student who has conducted this work as her Master's thesis.

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Author contributions: E.K.E., E.L.N. and C.H. conceived the ideas; E.K.E. analysed the data; and E.K.E. led the writing with contributions from E.L.N. and C.H.

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