Received: 10 October 2023 | Revised: 12 February 2024 | Accepted: 5 March 2024

DOI: 10.1111/ddi.13834

RESEARCH ARTICLE

Diversity and Distributions WILEY

Underprediction of extirpation and colonisation following climate and land-use change using species distribution models

Alistair G. Auffret[1] | Hedvig Nenzén[1,2] | Ester Polaina[1]

[1]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Alistair G. Auffret, Department of Ecology, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden.
Email: alistair.auffret@slu.se

Funding information
Vetenskapsrådet, Grant/Award Number: 2020-04276; Svenska Forskningsrådet Formas, Grant/Award Number: 2015-1065

Editor: Martin Jung

Abstract

Aim: To evaluate the performance of species distribution models in predicting observed colonisations, persistences and extirpations in response to changes in climate and land use over a multi-decadal period.

Location: Sweden.

Methods: We use historical (early 20th century) land use and climate data to build species distribution models for 84 plant species across three provinces of Sweden. Model performance was then evaluated internally using a subset of the historical data for cross-validation, as well as by using the models to project occurrences to the modern day and validating them with observed occurrences from 1990 to 2020. We then analysed predicted and observed occurrences in the modern period in terms of persistence, extirpation (local extinction) and colonisation in relation to species' habitat and climate associations.

Results: We found overall high agreement between evaluation methods, although internal evaluation gave consistently higher values for model performance (using true skill statistic, TSS). Overall, extirpations were worst predicted, with on average fewer than one-third of each species' extirpations being foreseen by the models. Colonisations were better predicted, while persistences were relatively well-predicted. Predictive accuracy of colonisations was higher for species with relatively warmer temperature associations (climate-driven expansion), while extirpations were better predicted in cool-related species (retractions at cool edges). Colonisations of forest-associated species were more common than predicted (underpredicted), despite widespread patterns of afforestation. Assessing grid-cell level turnover, we found that in grid cells that experienced the largest changes in terms of climate and land use, predicted extirpations were less likely to have happened.

Main Conclusions: We found that commonly applied modelling approaches have limited ability to predict observed changes in species occurrences, especially extirpations. This suggests that we should take predictions of future biodiversity loss very seriously. However, the ability for species to (at least temporarily) persist in unsuitable conditions could be an opportunity for biodiversity conservation.

KEYWORDS
biodiversity, climate change, extinction debt, habitat destruction, land-use change, plants, SDMs

1 | INTRODUCTION

Anthropogenic pressures on the environment have caused wholesale changes in species occurrences across the world (IPBES, 2019). Ongoing and future environmental change, particularly habitat destruction and climate warming, are predicted to result in significant losses of biodiversity worldwide unless serious action is taken (Leclère et al., 2020; Urban, 2015). However, several analyses of biodiversity change in response to the environmental perturbations that have already happened have identified no strong negative pattern in species richness over time at local scales (Antão et al., 2020; Vellend et al., 2017). Understanding discrepancies in expected and observed biodiversity change in response to changes in the environment is vital, because accurate predictions of ecological responses to future change are needed to inform the conservation strategies that are designed to protect nature (Asamoah et al., 2021; Leclère et al., 2020).

Species distribution models, which in their various forms relate environmental conditions to species occurrences and use them to predict occurrences in other regions or time periods, are a common tool in global change ecology. Perhaps most visibly, they have been used to predict widespread extinctions and biodiversity loss in future climates (Thomas et al., 2004; Warren et al., 2018). Although communicating the general risk of future environmental change for biodiversity is important, it is usually not possible to independently verify the predictions being made (Araújo et al., 2005). Traditionally, species distribution models are internally cross-validated, using data from the majority of the study region to create the model, and then evaluating the accuracy of predictions made by the model in the remaining area. However, internal cross-validation practices are prone to error, as shown by models built using nonsense variables receiving validation scores higher than those built using true environmental variables (Fourcade et al., 2018). One recommended way to evaluate model performance is to instead predict occurrences in the same region at a different time period, and then evaluate prediction accuracy in this independent test data (Araújo et al., 2019). Evaluations using such forecasting (building a model based on historical and predicting later occurrences) or hindcasting (building a model based on modern and predicting historical occurrences) techniques have shown general agreement between predicted and observed changes in species' ranges and abundances, but with large variation across species (Illán et al., 2014; Rapacciuolo et al., 2012; Soultan et al., 2022).

Understanding the climate and habitat associations of the species for which predicted occurrences are more or less accurate can give valuable insights for species distribution modelling. In plants, longer-lived, woody species and those that are effective seed dispersers generally appear to produce more accurate models (Dobrowski et al., 2011; McCune et al., 2020; Syphard & Franklin, 2010). However, in an era of environmental change, it can also be of interest to compare species' associations with the environmental changes being studied. For example, as the climate warms, we might expect expanding, warm-adapted species to be better predicted by species distribution models (Talluto et al., 2016). When considering multiple species, it may also be informative to understand if the amount of environmental change that has taken place in a particular location affects the rate of correct or incorrect predictions of occurrence.

Although climate change is likely the most common context in which predictive species distribution models are created, it is only one of a number of serious threats to biodiversity worldwide. In particular, habitat destruction through land-use change is generally considered to be the most significant driver of biodiversity change today (IPBES, 2019; Newbold et al., 2016). Habitat availability is also an important mediator of climate-driven distribution changes (Mair et al., 2014; Platts et al., 2019), and so consideration of both of these main drivers of global change is preferable. This is true both for predicting future changes in biodiversity (Asamoah et al., 2021), and also for model evaluation, as loss of a particular habitat might affect predictability of specific species responding to climate change.

In this study, we use historical (mid-1900s) climate, landscape and species occurrence data to fit species distribution models for 84 plant species in three regions of southern Sweden. We then use these models to predict modern-day occurrences based on current environmental data, using observation data from 1990 to 2020 data to evaluate predictive accuracy. The study area has undergone large-scale loss (largely abandonment) of grassland habitat and experienced significant climate warming, which has been reflected in changes in plant community composition (Auffret et al., 2018; Auffret & Thomas, 2019a). It is not our intention to build the most perfect models for distribution forecasting, but rather we aim to identify sources of prediction biases in a common modelling approach, based on relevant environmental variables that are available in our study region for both time periods. After building our models based on the historical data, we use both traditional internal cross-validation evaluation measures within the same time period and validation using modern-day observed occurrence data to investigate the accuracy of the models in predicting change (Figure 1). To identify sources of uncertainty and error, we then look into how species' occurrence predictions relate to their climatic niches (the average and range of temperatures experienced by each species over its range) and their habitat associations (proportions of each species' national populations restricted to grassland and forest habitat). Finally, we evaluate how prediction accuracy of extirpation, colonisation and persistence across all species is affected by the amount of environmental change that has occurred within each grid-cell landscape over time.

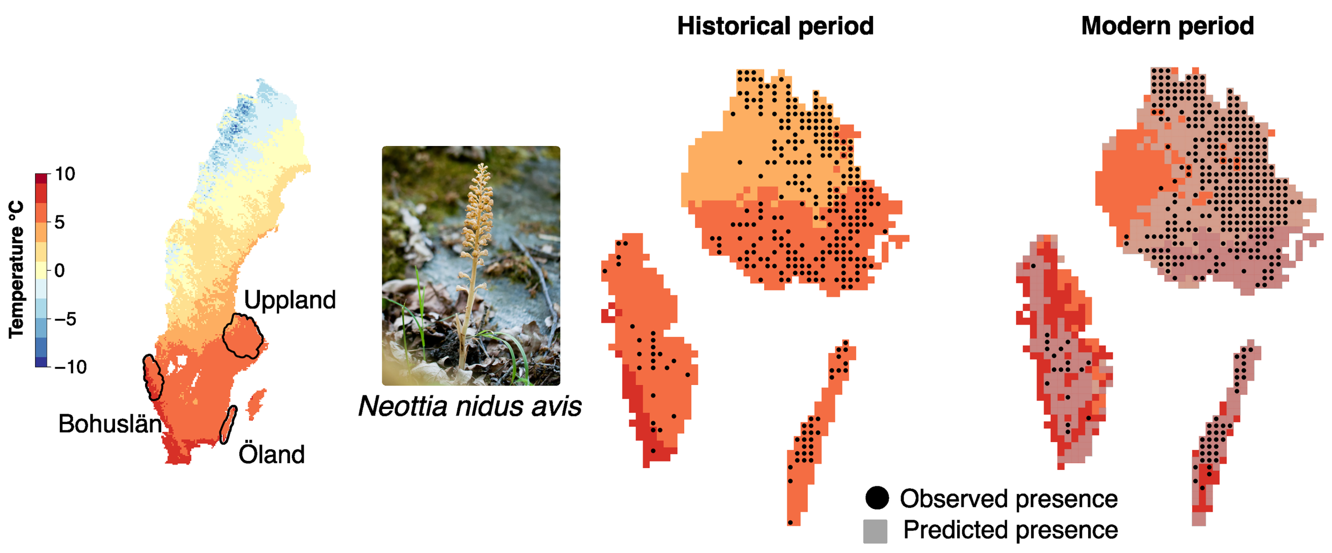

FIGURE 1 Illustration of study design, showing the location of the three provinces along Sweden's temperature gradient (mean annual temperature 1961–1990) and data for an example species *Neottia nidus-avis*. Ensemble species distribution models were built using species observations (black points) and environmental data from the historical period (early 20th century, mean annual temperature 1961–1970) and used to predict occurrences in the modern period (1990–2020, mean annual temperature 2001–2010; translucent grey squares) based on current environmental conditions. These were then compared to observations in the modern period.

2 | MATERIALS AND METHODS

2.1 | Data sources

2.1.1 | Species occurrence data

We used plant species occurrence data from the Swedish provinces of Bohuslän, Öland and Uppland (Figure 1). Historical data were extracted from plant atlases that were largely based on inventories from the early-mid 20th century (Almquist, 1929; Fries, 1945; Sterner, 1938), but exact dates for each observation are not known. Modern atlas data were based on inventories carried out since 1990 (Andersson & Gunnarsson, 2024; Blomgren et al., 2011; Jonsell, 2010). For the historical atlases, Öland and Uppland's observations were extracted from the 286 (Öland) and 438 (Uppland) species distribution maps using GIS software (Auffret & Thomas, 2019a; Maad et al., 2009). For Bohuslän, data were extracted from the database used to create the modern flora (Blomgren et al., 2011), containing georeferenced historical observations of 1460 species. All observations were then assigned to the 5 × 5 km Swedish national grid cell in which they were located, this being the same grid used for the historical maps and the inventory unit used for the modern inventories. After taxonomic harmonisation to the species level according to the nomenclature of the Swedish taxonomic database (https://namnochslaktskap.artfakta.se), using in the first hand Swedish names and in the second hand scientific names, 84 species were retained for analysis that were recorded in all three provinces in both time periods. For each species, we recorded both presences and 'absences' at the grid cell level, with absences defined where a species was not recorded in a grid cell in the plant atlas in a time period. Atlases from both periods were created to document the distributions of species within the provinces. Historical atlases had a lower recorder effort (often being the work of a single person), but we consider the presence data to be at least of a comparable quality to those used for species distribution modelling, with absences broadly likely to be true absences rather than non-detections. Modern atlas inventories are characterised by a high recording effort, with the aim of documenting each species within each 5 × 5 (and often each 2.5 × 2.5 km) grid square. Nonetheless, the number of unique species-grid-cell observations did not increase dramatically, with 26,409 recorded presences in 1055 grid squares in the historical period and 29,301 presences in 1074 grid squares in the modern period. Median change in frequency in the raw data was +30 grid cells, and ranged between −169 and +371 across all species.

2.1.2 | Environmental data

For environmental data, we took daily 4 × 4 km gridded climate data from 1961 to 2011 from the Swedish Institute for Hydrology and Meteorology's database *pthbv*, which we then aggregated to monthly values and resampled the grid to match the 5 × 5 km Swedish national grid used for the species occurrence data, and extracted a number of climatic variables (Table 1). For the historical period, we averaged values across the first available decade in the database 1961–1970, and for the modern period we used 2001–2010. Cover of four broad land-use categories (grassland, forest, arable fields and surface water) was derived for the historical period from maps created during 1940s to 1960s. Modern land-use data were taken from the 2018 national land-cover map *Nationellamarktäckedata* (Table 1). The historical environmental data represent a time towards the end of the

TABLE 1 Environmental variables used for building and evaluating species distribution models of 84 plant species across three provinces of Sweden, based on observations at 5 × 5 km grid cells.

Climate	*Variables*: Temperature (°C): Mean annual temperature; mean of monthly maximum temperatures; mean of monthly minimum temperatures. Precipitation (mm): Total annual precipitation; mean of monthly minimum precipitation, mean of monthly maximum precipitation *Source*: Swedish Meteorological and Hydrological Institute database of gridded daily values (4 km resolution, resampled to 5 × 5 km grid). Historical period 1961–1970; modern period 2001–2010
Land use	*Variables*: Fraction cover of grassland, forest, arable fields and surface water *Source*: Historical data from Economic maps published 1940s–1960s (1 m resolution, aggregated and resampled to 10 m; Auffret et al., 2017a). Grassland category mainly consists of grasslands, but also includes other open land cover, including wetlands. Because of difficulties in separating water and forest in the digitisation process, lakes and rivers were added to the digitisations using a modern map layer. Modern data from 2018 Swedish land-cover map (10 m resolution), with 25 categories re-classified to match the broad categories of the historical data
Soil	*Variables*: Fraction of peat, sand & gravel, bedrock, silt & clay, till and other soils *Source*: National soil maps. Original data in vector format at 1:25000 to 1:1000000 scales were harmonised to create a 50 m resolution layer (noting that the smallest features on the coarsest map are approximately 500 m across)
Distance to coast	*Variable*: Euclidean distance between the grid cell centroid and the Swedish coast

historical inventory periods, potentially several decades after some species observations. This temporal mismatch could affect the performance of our models. However, the rapid increase in mean annual temperature occurred in Sweden post-1970 (Schimanke et al., 2022), while the widespread abandonment and afforestation of grasslands in Sweden has been observed subsequent to the publications of the historical maps used here (Cousins, 2001; Johansson et al., 2008). Therefore, we consider the broad climatic and land use conditions of the grid cell to represent the time of the species observations.

In addition to climate and land-use data, we collected two additional sets of data to help build the species distribution models. First, we calculated distance to coast as the distance between the centroid of each grid cell and the nearest section of coastline, because there are a number of species that are associated with coastal habitats. Second, we used the Swedish Geological Survey's collection of soil maps that cover Sweden to create a national map of continuous coverage using the highest-resolution data available for each location, before we calculated the fraction cover of broad soil type within each 5 × 5 km grid cell (Table 1).

2.1.3 | Species' climate and habitat associations

Associations of all 84 species to habitat and climate were taken from Tyler et al. (2021) and Auffret and Thomas (2019b), respectively. We calculated broad grassland specialisation on a scale from 0 to 10, according to the total proportion of the Swedish population estimated by the authors to reside in heath, meadow and fen habitats, with forest specialisation calculated on the same scale across different forest habitats. That is, a species with a grassland specialisation of 10 is considered to only be present in grassland habitats. For climate associations, species mean temperature index is the average temperature experienced by a species across its Swedish range (higher values indicating warmer-associated, southerly distributed species), while species temperature range index is the difference between the warmest and coolest observation across its range (higher values indicating more climatically widespread species). These values are based on the time and location of all observations of each species from modern regional plant atlas inventories across the majority of Sweden that have been carried out since 1975 (i.e. not only the three study provinces; Auffret & Thomas, 2019a).

2.2 | Species distribution models (SDM)

Species distribution models allow us to correlate environmental conditions hypothesised to influence the presence of a certain species in a given area to estimate where it is more likely to occur (environmental suitability). We fitted SDMs for each species based on historical data (species observations and environmental variables in their original units) using the BIOMOD2 package in the R software (R Core Team, 2021; Thuiller et al., 2009), including 5 commonly used algorithms that have been shown to have good performance (Polaina et al., 2021; Valavi et al., 2022; Wisz et al., 2008): generalised linear model, GLM; generalised additive model, GAM; flexible discriminant analysis, FDA; generalised boosting model, GBM; and maximum entropy, MAXENT. Algorithms were run using default settings, apart from GAM, where we specified a smoothing term (k) of 3 – a relatively low value to limit overfitting (so-called ‘wiggliness’). We applied four runs per algorithm, to allow cross validation (each run selects a different subset of 70% of data to fit the model). Only non-correlated environmental predictors (VIF ≤ 4) were kept for the modelling, including maximum monthly temperature and precipitation, fractions of arable, open and forest land (all from the historical period), as well as distance to the coast, and proportions of peat, sand/gravel, rock and silt/clay soil types.

A total of 20 individual candidate models were fitted per species (4 runs × 5 algorithms), providing continuous predictions of occurrence (in the historical period) between zero and one. These were converted into a binary classification using a threshold value (specific for that species and model) that was automatically selected to maximise the model's TSS score, based on the 30% subset of observations not used to build each candidate model (Liu et al., 2013). TSS is the sum of a model's sensitivity (proportion of presences in the 30% subset of observations withheld from model building that were correctly predicted by the model) and its specificity (proportion of correctly-predicted absences), minus one (Allouche et al., 2006; Peirce, 1884). We then used a committee averaging process to choose the candidate models of high predictive performance that would be included in the single ensemble model per species. Candidate models were included in the ensemble if they had a TSS score of ≥0.7. When fewer than 10 candidate models matched this criterion, the models with a TSS score above the median for that species were included. The ensemble model prediction is then the average of the binary predictions of the candidate models, which is then automatically converted into binary values to maximise TSS.

In addition to carrying out traditional internal cross-validation by calculating TSS of modelled and observed occurrences within the historical time period (Araújo & New, 2007; Hirzel et al., 2006), we also implemented an independent, temporal validation. The ensemble models above were used to forecast occurrence probability in the modern period (again subsequently converted into a binary prediction) according to modern environmental data. Then, to validate how well these models were able to predict observed changes in species distributions, these predictions were then compared with modern occurrences (instead of the 30% subset of past occurrences) and both TSS scores and AUC (area under curve) values were calculated. For a more specific analysis of predictive accuracy at the species level, we also calculated the fraction of grid squares in which persistences (observed as present in historical and modern), extirpations (observed as present in grid cell in historical, not recorded in modern observations) and colonisations (not recorded in historical, present in modern) were correctly predicted. This approach allows us to look more carefully at the prediction accuracy of turnover over time, because high TSS values can occur largely due to correctly-predicted continued absence in a grid square. At the grid-square level, we calculated the fraction of persistences, extirpations and colonisations that occurred in the grid square that were correctly predicted by the species distribution models.

2.3 | Model performance in relation to species associations and environmental change

First, to assess the agreement between validation methods, we regressed TSS scores for each species' ensemble model against each other using a linear model, with TSS scores from the traditional cross-validation as the response variable and TSS scores from the independent temporal validation as the predictor variable. To analyse whether accurate prediction of turnover using SDMs was related to species' associations to climate and habitat, we built a suite of binomial general linear models, using a quasi-binomial correction due to overdispersion. The response variables were the fraction of grid cells in which each species was observed to persist, be extirpated from or colonise, that were correctly predicted by the SDMs. Predictor variables were grassland specialisation, forest specialisation, species mean temperature index and species temperature range index. Because of the high correlation (>0.7) between species mean temperature index and species temperature range index, separate models were created, each containing habitat specialisation and one of the temperature indices (total 6 models: 3 responses × 2 temperature indices). Because the responses were fractions, models contained weights corresponding to the total number of observed extirpations, persistences, colonisations for each species.

We then built three additional binomial generalised linear models analysing turnover at the grid-cell level in relation to observed environmental change. The fraction of persistences, extirpations and colonisations that were observed in each grid cell and that were correctly predicted by the SDMs were response variables, while the change in mean annual temperature that had occurred in the grid square, grassland abandonment (fraction of pixels in each grid cell that were classified as grassland in the historical period and forest in the modern period) were predictor variables. We also included three 'control' predictors: [1] microclimatic variation, in terms of the standard deviation of the 50 m resolution mean annual temperature data within the grid cell (Meineri & Hylander, 2017), which is known to affect responses to environmental change (Suggitt et al., 2018) and predictive accuracy of SDMs (Maclean & Early, 2023); [2] latitude, which incorporates a number of environmental variables relevant to global environmental change (De Frenne et al., 2013) was added following a sequential regression approach (Dormann et al., 2013), to include the effect of latitude that does not relate to mean annual temperature (which was one of our focal predictors); [3] spatial autocorrelation, which was controlled for by including as predictors the first two eigenvectors of an analysis of the principal coordinates of neighbour matrices, based on the centroids of each grid cell (Borcard & Legendre, 2002). Weights were included corresponding to the total number of persistences, extirpations and colonisations observed within each grid cell.

2.4 | Potential sources of SDM uncertainty

2.4.1 | Sensitivity analysis of presence-absence thresholds

Choice of threshold value for converting probability of occurrence to a binary measure is a source of variation in predictions of turnover at the grid-cell level (Nenzén & Araújo, 2011). Therefore, we performed a sensitivity analysis in which we re-ran the above analyses of prediction accuracy at both the species level and grid-cell level, but with a lower (TSS-chosen threshold minus 0.1 on the 0–1 scale) and higher (TSS-chosen threshold plus 0.1) threshold for converting probability of occurrence into predicted presence from the ensemble forecasts.

2.4.2 | Extrapolation into novel environments

An additional source of potential error in SDM predictions is that models are expected to perform badly when predicting species occurrences in environments that do not exist in the data used for fitting the model (Elith et al., 2010). As such, we conducted a multivariate similarity surface (MESS) analysis to identify where novel environments exist in the modern data, and which predictor variables are responsible. We used the MESS implementation of the ecospat package (Di Cola et al., 2017), on the variables that changed over time and that were included in the SDMs: maximum monthly temperature and precipitation, fractions of arable, open and forest land.

2.4.3 | Niche overlap with changing distributions

It is possible that it is not (only) species' habitat and climate associations that affect the predictive ability of SDMs, but that species can occupy different niches over time. To investigate this possibility, we calculated Schoener's D for each species, according to Broennimann et al. (2012) and using the R packages ade4 and ecospat (Di Cola et al., 2017; Dray & Dufour, 2007). Niches were characterised using all climate, land use and soil variables described in Table 1. Values range between zero and one, where zero indicates random overlap while one indicates complete overlap. Significant differences from random overlap were determined using 999 replications. Values of Schoener's D were then added to the models evaluating SDM performance (TSS-chosen presence-absence thresholds only) in relation to species climate and habitat associations to examine whether extent of niche overlap over time affected the ability of our SDMs to predict colonisations, extirpations and persistences.

3 | RESULTS

3.1 | SDM performance

Performance of SDMs among species was highly variable. Using the traditional (70:30) cross-validation method, TSS varied between 0.42 and 0.87, with a mean value of 0.65. This indicates that all models can be judged as reasonable; TSS values of 0.2–0.6 can be considered fair to moderate (de Luis et al., 2020), while 0.5 has also been stated as acceptable. Model performance according to the independent temporal (using past to predict present) validation method was much poorer, with TSS values of between 0 and 0.72, with an average value of 0.28. Equivalent AUC values ranged from 0.54 to 0.91, and had a mean value of 0.75. Nonetheless, performance was still reasonable for many species, especially considering that above TSS values for what constitutes a fair or moderate model are generally applied to models evaluated using traditional internal cross-validation methods. There was also a generally good agreement between TSS values between validation methods for each species (Parameter estimate: 0.75, Standard error: 0.23, *t*-value: 3.12, *p*: .02, Model R^2 = .11; Figure 2; Table S1 in the Data S1).

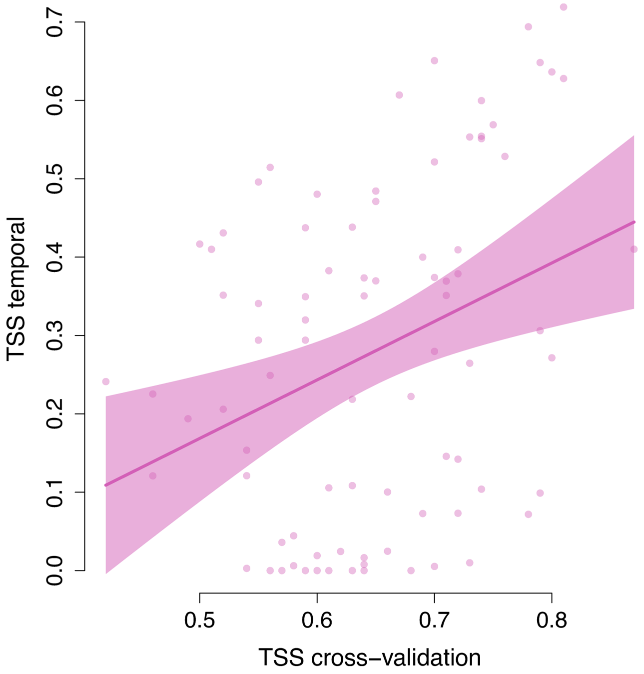

FIGURE 2 Modelled relationship between Species Distribution Models' (SDM) True Skill Statistic (TSS: fraction correctly predicted absences plus correctly predicted presences minus one) calculated using traditional cross-validation validation method within the same time period, by which models are built using 70% of the study area and validated in the remaining 30%, and an independent temporal validation method, by which models from a historical time period are used to predict modern observations based on modern environmental conditions. Points correspond to 84 Swedish plant species, the line indicates the modelled relationship, surrounded by 95% confidence bands. Note differences in axis extent. Model R^2 = .11. Figure created using the visreg package (Breheny & Burchett, 2017).

3.2 | Prediction accuracy of species turnover

Across all species, extirpation was most under-predicted, with a mean of 27% observed extirpations of each species being predicted as such by the SDMs, the remainder being incorrectly predicted as persistences (median: 13%; interquartile range: 0%–48%). Prediction accuracy was better for colonisations (mean: 67%; median: 78%; interquartile range: 35%–99%), and best for persistences (mean: 82%; median: 93%; interquartile range 71%–100%). The accuracy of SDMs in predicting turnover was related to the characteristics of the species being predicted. Persistence and colonisation were better predicted in species that were less-associated with forest habitats (low forest specialisation), and in species with warmer (high species mean temperature index) and relatively more restricted Swedish ranges (low species temperature range index). On the other hand, such species were less well predicted in terms of extirpations, which were more accurately predicted for forest specialists, species with overall cooler and wider climatic ranges (Figure 3; Table S2). In other words, for a species that was associated with (for example) forest habitat, many of the grid cells that were observed presences in the modern

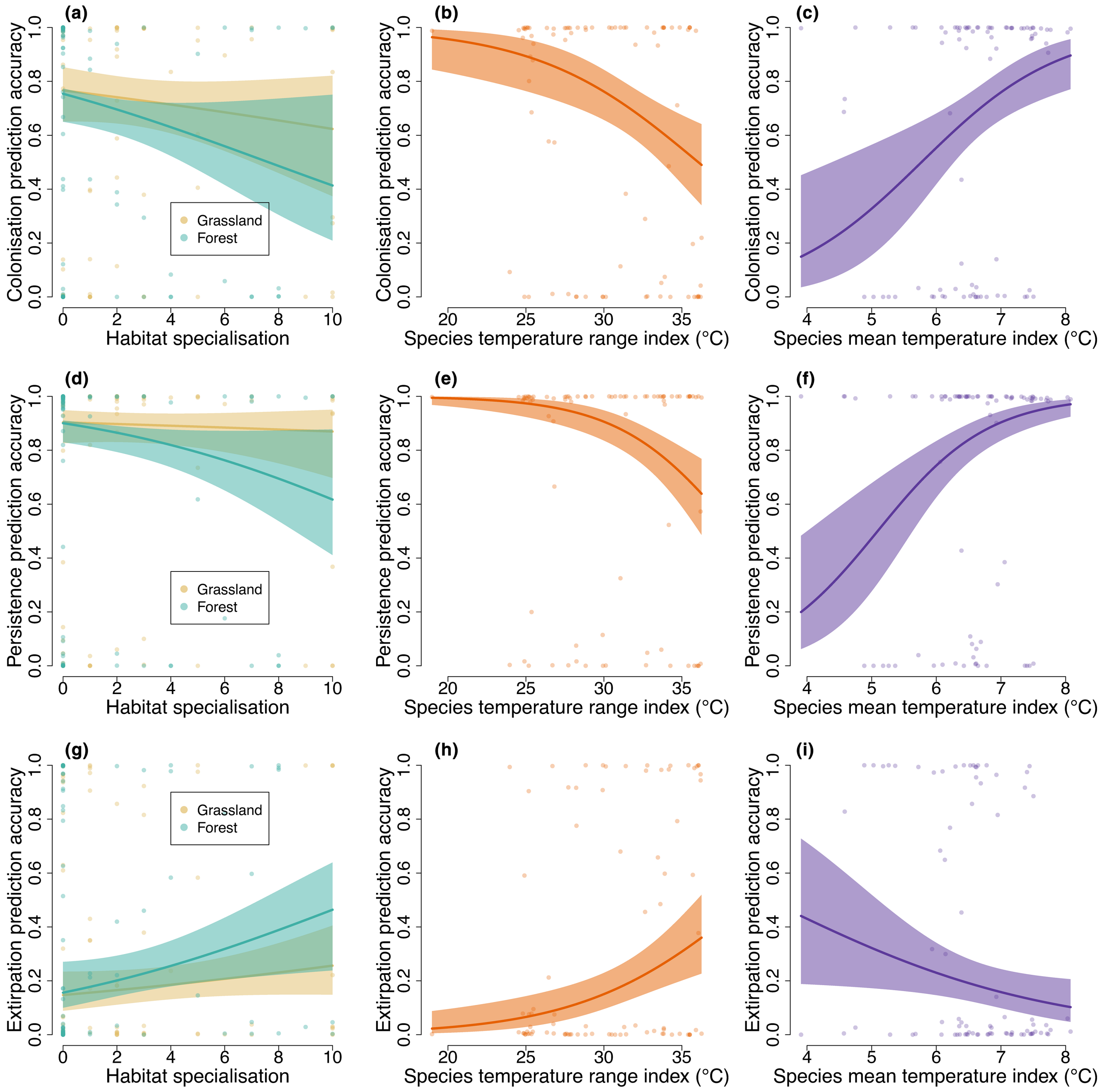

FIGURE 3 Modelled relationships between species' habitat specialisation (a, d, g; where 0 indicates that the species is never, and 10 that it is only found in that habitat type) and climate associations (b, c, e, f, h, i) and predictive accuracy of species distribution models in terms of fraction of grid cells that were colonised (top row), persisted in (middle row) or were extirpated from (bottom row), that were correctly predicted by SDMs. Points correspond to 84 Swedish plant species, coloured lines indicate the modelled relationships, surrounded by 95% confidence bands. Collinearity between species temperature range index and species mean temperature index means that each response variable was modelled separately, containing one of the species' temperature indices. Models containing species temperature range index as a covariate performed better (higher R^2: colonisation 0.21 compared to 0.2; persistence 0.35 and 0.35; extirpation 0.26 and 0.17), and therefore figure panels showing habitat specialisation are derived from those models (Table S2).

period (either as persistences or colonisations), were predicted as absences using the models parameterised using the historical environmental data (Figure 3a,d). On the other hand, species with wide climatic ranges in Sweden were more likely to be correctly-predicted to be extirpated from a grid square than species with narrow climatic ranges. That is, such narrow-ranged species were more likely than wide-ranged species to persist when the SDMs predicted them to disappear (Figure 3h).

Despite these clear associations between species characteristics and SDM prediction accuracy, model ability to predict species' persistences, extirpations and colonisations was in many cases still poor. For example, for even the most forest-specialised and climatically cool and widespread species, extirpation prediction accuracy was only around 0.5 on average (Figure 3g–i), meaning that around half of all SDM-predicted persistences (species observed in grid cells in the historical period and predicted to be present in the modern period) actually ended up being extirpations (no observation in the grid cell in the modern period).

Niche overlap between species' historical and modern observed ranges was generally quite high, but variable, ranging from 0.1 to 0.56 (Figure S1). Sixty percent of all species showed a niche overlap significantly different from zero. Values of Schoener's D were not shown to affect the ability of SDMs to predict colonisations, persistences or extirpations (Table S3).

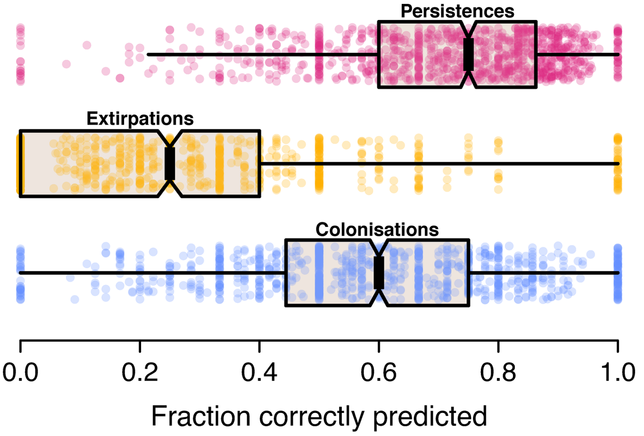

FIGURE 4 Predictions of persistences, extirpations and colonisations at the 5 × 5 km grid-cell level. For colonisations ($n = 1032$ grid cells), persistences ($n = 1022$) and extirpations ($n = 969$). Points represent the fraction of the different elements of species turnover that were observed within a grid cell that were correctly predicted by species distribution models. Boxes show median and interquartile range, and whiskers indicate range (excluding outliers). Notches represent 95% confidence intervals around the median.

3.3 | Prediction accuracy of grid-square turnover

Broad underprediction of extirpations was also evident at the grid-cell level, where predictive accuracy of the SDMs was again highly variable. Specifically, in many grid cells, around 75% of all species that were not recorded in the modern period despite being present in the historical period were incorrectly predicted to be present (i.e. were predicted persistences). The fraction of observed colonisations was generally better predicted than extirpations, while observed persistences were better predicted still (Figure 4; non-overlapping confidence intervals). Our models identified no clear correlates of predictive accuracy of extirpations or colonisations in terms of the climate and land-use change that had occurred in a grid cell (Table S4). However, observed persistences were more likely to have been predicted by the SDMs in grid cells that experienced less environmental change in terms of temperature warming and grassland abandonment (Figure 5). In other words, grid cells that experienced a higher magnitude of land use and climate change contained relatively more species that were predicted to have gone locally extinct, but still persisted, compared to grid cells where more moderate environmental change had occurred.

3.4 | Sensitivity and MESS analyses

Using higher or lower threshold values for predicted presences in the modern period had no marked effect on the direction and clarity of predictor variables relating to species' climate and habitat associations, nor grid-cell level environmental change (Tables S5–S8). This indicates that any effect that a change in threshold value might have on predictive accuracy was not biased towards any particular species or locations. Interestingly, using the stricter threshold for predicted presences resulted in lower model R^2 values, further indicating that the TSS-based threshold choices are ecologically meaningful. The

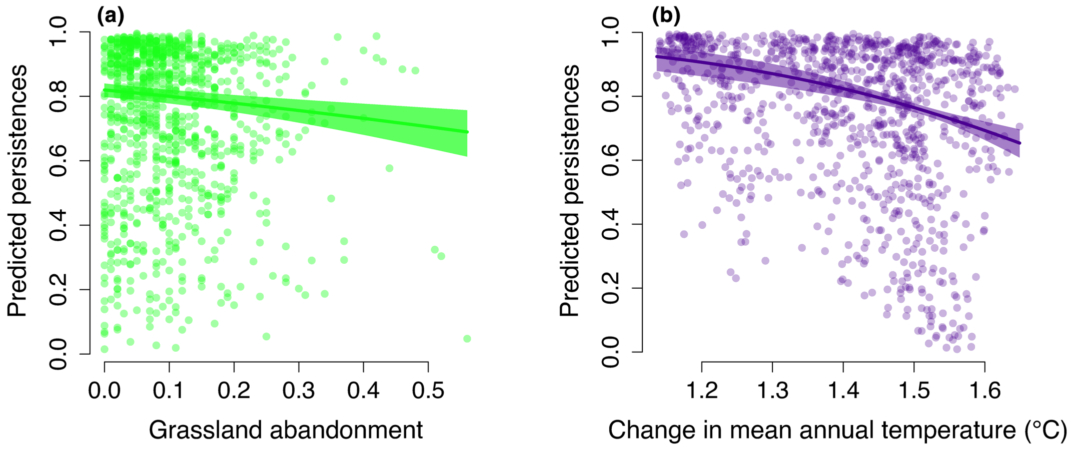

FIGURE 5 Modelled relationships between the fraction of persistences that were correctly predicted by species distribution models, and levels of environmental change: (a) fraction of grid cell containing abandoned grassland, (b) change in grid cell's mean annual temperature between 1961–1970 and 2001–2010. Points correspond to 84 Swedish plant species, coloured lines indicate the modelled relationships, surrounded by 95% confidence bands. High values of predicted persistence indicate that the majority of a grid cell's observed persistences were correctly predicted, while low values show that species were incorrectly predicted to have been extirpated. Model $R^2 = 0.19$.

MESS analyses showed that extrapolation occurred within all grid cells. In 98% of cases this was due solely to the temperature variable (mean of monthly maximum temperatures), which showed no overlap between 1961–1970 and 2001–2010 (Figure S2). That is, the highest value in the lowest period was lower than the lowest value in the highest period.

4 | DISCUSSION

Our study used long-term species observation data together with information regarding recorded changes in climate and land use to examine the predictive accuracy and temporal transferability of species distribution models. Our results indicate that in many cases, traditional cross-validation methods of model evaluation that use the same data for calibration as validation are likely overestimating the accuracy of models that are then used to predict future responses to potential climate-change scenarios. Such limitations in species distribution models are well known, with validating using independent data having previously found to result in lower-accuracy predictions compared to cross-validation (Araújo et al., 2005; Rapacciuolo et al., 2012; Santini et al., 2021). Our analyses go a step further, revealing also the types of species and landscapes that may specifically be better or worse predicted.

4.1 | Prediction of species-level turnover

Ideally, predictions of turnover from species distribution models would be equally good, regardless of species' habitat and climate associations. We found that models predicting occurrences of relatively warm-associated species performed better in terms of presence (colonisation and persistence), than cool-associated species. Warm-adapted species are expected to, and have been observed to, expand their distributions with warming climate (Auffret & Svenning, 2022; Lenoir et al., 2008). As such, our results do not support previous warnings of difficulties in predicting expansions of successful species in future climates based on observed climatic niche shifts in between species' native and non-native ranges (Atwater et al., 2018; Early & Sax, 2014). Some of our species did exhibit apparent niche shifts (low niche overlap over time), but overall we found high niche overlap between historical and modern ranges, while niche overlap did not explain predictive ability of our SDMs at the species level. Instead, we found that it was species that could have benefitted from non-climatic anthropogenic change that were less well-predicted. Species with larger geographic ranges, that are in many cases associated with ruderal life-histories, have increased throughout Europe at the expense of more range-restricted species (Geppert et al., 2020; Staude et al., 2022), while the ongoing trend of grazing abandonment has led to secondary succession and woody regrowth and an increase in shade-tolerant species (Auffret & Svenning, 2022; Buitenwerf et al., 2018). For these species, whose expansions are less-directly related to climate warming, and more related to opportunistic range-filling due to land use and other changes, many modern-day observed occurrences were not predicted by the species distribution models. Therefore, while model predictions of species-level shifts at cool, expanding range edges might in many cases be reasonably accurate, species distribution models may be less accurate at predicting observed local increases in plant species richness and biotic homogenization (Keith et al., 2009; Vellend et al., 2017).

Extirpations were in general poorly predicted compared to persistences and colonisations at the species level (Figure 3d–f). This means that in many cases, species that were predicted to persist are likely to have gone locally extinct. Particularly concerning is that extirpation accuracy was very low in all species with any level of grassland association, because it is these species that have been most threatened by land-use change in the 20th century in Europe (Auffret et al., 2018; Gerstner et al., 2014). Range-restricted species, which are another threatened group, were also poorly predicted in terms of extirpations. This is probably because species that have small geographic ranges (with the exception of alpine species) are restricted by other environmental factors than climate. On the other hand, it appears that in terms of species' average thermal associations, predictions of turnover were relatively accurate. Like with colonisations of warm-associated species, extirpations of cool-associated species – which might be expected to suffer from warming temperatures (Lynn et al., 2021; Wiens, 2016) – were better-predicted. However, extirpations of warm-associated species were poorly predicted. While increases in these species have been observed following climate warming, local losses are likely to have been driven by non-climatic factors, and factors other than changes in our broad land use classification.

4.2 | Prediction of assemblage-level turnover

The underprediction of extirpations at the species level also translated to generally poor performance at the grid-cell level (Figure 4). Persistences were generally better predicted, but we nonetheless found that in grid cells undergoing the highest magnitude of climate and land use changes, there was a larger fraction of cases where the fraction of prediction of persistence within a grid square was lower, because models predicted higher levels of extirpation within a grid square than were observed to occur. This result shows how extirpations can also be overpredicted by SDMs, although it should not distract from the large proportion of extirpation events that were incorrectly predicted as persistences in the majority of grid cells (Figure 4). The poor performance of our models in predicting extirpations is in contrast to results reported by Illán et al. (2014), whose hindcasting study in North American birds found that local extinctions were better predicted than colonisations. We do not know whether this is due to differences in taxa, system or modelling approach. Nonetheless, it is a potential worry that our forecasting study has severely underestimated observed local species losses, as it suggests that the many studies that predict dire ecological futures with continuing environmental change (Thomas et al., 2004; Thuiller et al., 2005; Warren et al., 2018) might even be representing conservative scenarios.

The occasional overprediction of extirpations, as well as the underprediction of colonisation events at both the species and grid-cell level, could be related to the spatial scale of the study, because plant populations respond to environmental factors at scales smaller than the grid cells used in most SDM exercises (Chauvier et al., 2022). Populations can persist in small remnant habitats and in microclimatic refugia despite broad-scale changes at the grid-cell level (Eriksson, 1996; Suggitt et al., 2018), while a single individual can establish despite the grid cell as a whole being judged as unsuitable by the model. However, the larger proportion of overpredicted extirpations in grid cells that have experienced the largest changes temperature and land use (compared to those where changes were more moderate) may indicate time-lagged extinctions, whereby the unexpected persistences are only temporary due to the generally slow responses that plants can exhibit to environmental change, for example due to the long life-histories and persistence in soil seed banks (Honnay & Bossuyt, 2005; Plue et al., 2021).

4.3 | Sources of uncertainty

Should we trust the predictions made by species distribution models? Our results showed that some species are better predicted than others. While the broadly expected (and observed) increases in warm-associated species and declines in cool-associated species were predicted to a reasonable extent, changes in other groups of species such as habitat specialists that have exhibited quite considerable distribution changes over time (both in terms of expansions and retractions) were largely underestimated. Therefore, our findings warn against placing too much faith in models based on common indices of climate and land use that might not always capture the breadth and spatial scale of species' niche requirements. Nonetheless, models can always be improved.

Our goal was to follow general rules of good practice when building our SDMs, rather than create the perfect models. We included several aspects of fine tuning and high standards for SDMs, for example including only one occurrence per grid cell, including only non-correlated predictors, using committee averaging and to create binary predictions and then applying sensitivity analysis on these results, and calculating multiple evaluation metrics (Araújo et al., 2019; Araújo & New, 2007; Fourcade, 2021). Our species data also included what we describe as true absences, which should result in more robust model predictions than presence-only datasets. However, long-term data do often suffer from spatially and temporally variable and unknown observer effort (Isaac & Pocock, 2015), while our historical species and environmental data are also less-well temporally matched compared to our modern data. Because sampling effort is usually higher in modern datasets, it is the underprediction of colonisations in our results that are likely to be most affected, whereby present species may have been missed in historical surveys. Additional uncertainty exists in our results due to extrapolation into novel environments. The MESS analysis revealed that novel climates existed across the entirety of our study area. As well as serving as a reminder of the rapidity of global climate warming, it may help to explain some of the overall poor prediction of extirpations in our study. Species – regardless of their temperature associations – may have gone locally extinct in part due to a warming climate, but the models would not have known how such novel climates might affect their occurrences. This highlights difficulties of predicting biodiversity responses in the future, especially at higher emission scenarios.

Further to identifying and trying to reduce bias in commonly used modelling techniques such as ours, work is taking place to improve and refine SDMs in other ways. Individual models can incorporate factors such as biotic interactions (Kissling et al., 2012), dispersal (Shipley et al., 2022), ecological assembly rules (D'Amen et al., 2015), physiology (Kearney & Porter, 2009; Talluto et al., 2016) and detection probability (Guillera-Arroita, 2017), while the ensemble process can also be improved to optimise predictive ability (Valavi et al., 2022). Where more detailed time series of occurrences are available, colonisation-extinction modelling (also known as dynamic occupancy models) can offer a more powerful way of modelling and predicting species dynamics under environmental change (Briscoe et al., 2021; Nordén et al., 2020).

4.4 | Concluding remarks

While predictive models can always be improved, the largely dire ecological futures that have been predicted are in line with observations that anthropogenic environmental change is negatively affecting many plant species across Europe (Auffret & Svenning, 2022; Eichenberg et al., 2021; Stroh et al., 2023). On the other hand, local plant richness can increase (Vellend et al., 2017), probably due to the success of a subset of already widespread generalists, as well as new species to a region, whose temporal trends are therefore not tracked. We think that on balance, despite an underprediction of colonisation of successful species, our broad findings of strong underprediction of extirpation at the species and grid cell level mean that we should take warnings of future biodiversity loss from species distribution models very seriously. However, some unexpected persistences following large environmental changes gives hope that targeted conservation actions could still be effective at reducing biodiversity loss at landscape scales.

ACKNOWLEDGEMENTS

This work was funded by the Swedish Research Councils Formas (2015-1065) and VR (2020-04276), as well as Stiftelsen Konung Carl XVI Gustafs 50-årsfond för vetenskap, teknik och miljö. Many thanks to two anonymous referees whose comments improved the robustness and clarity of the study. Finally, we are very grateful to the many Swedish botanists from the 20th and 21st centuries who

have spent their time recording plant species, mostly in their free time. Such research would not be possible without them.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13834.

DATA AVAILABILITY STATEMENT

Processed datasets and code used for analysis presented here are published at the Swedish National Data Centre (https://doi.org/10.5878/xt40-pv58; Auffret et al., 2024). For raw data, historical and modern species observations are available from the Swedish species observation system ArtPortalen (https://artportalen.se). Species temperature indices were taken from Auffret and Thomas (2019b), while habitat specialisation information was extracted from the supplementary information of Tyler et al. (2021). Climate data are free to access from https://www.smhi.se/data/ladda-ner-data/griddade-nederbord-och-temperaturdata-pthbv. Historical land-cover data are available (Auffret et al., 2017b), while modern land cover is published by the Swedish Environmental Protection Agency at https://www.naturvardsverket.se/verktyg-och-tjanster/kartor-och-karttjanster/nationella-marktackedata/ladda-ner-nationella-marktackedata/.

ORCID

Alistair G. Auffret https://orcid.org/0000-0002-4190-4423
Hedvig Nenzén https://orcid.org/0000-0002-0189-4283
Ester Polaina https://orcid.org/0000-0002-5064-5881

REFERENCES

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*, 1223–1232.

Almquist, E. (1929). Upplands vegetation och flora. *Acta Phytogeographica Suecica*, *1*, 1–622.

Andersson, U.-B., & Gunnarsson, T. (2024). *Ölands Flora*. SBF-förlag.

Antão, L. H., Bates, A. E., Blowes, S. A., Waldock, C., Supp, S. R., Magurran, A. E., Dornelas, M., & Schipper, A. M. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology & Evolution*, *4*, 927–933.

Araújo, M. B., Anderson, R. P., Márcia Barbosa, A., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*, eaat4858.

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, *22*, 42–47.

Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, *11*, 1504–1513.

Asamoah, E. F., Beaumont, L. J., & Maina, J. M. (2021). Climate and land-use changes reduce the benefits of terrestrial protected areas. *Nature Climatic Change*, *11*, 1105–1110.

Atwater, D. Z., Ervine, C., & Barney, J. N. (2018). Climatic niche shifts are common in introduced plants. *Nature Ecology & Evolution*, *2*, 34–43.

Auffret, A. G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., Wennbom, M., Wood, H., Bullock, J. M., Cousins, S. A. O., Gartz, M., Hooftman, D. A. P., & Tränk, L. (2017a). HistMapR: Rapid digitization of historical land-use maps in R. *Methods in Ecology and Evolution*, *8*, 1453–1457.

Auffret, A. G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., Wennbom, M., Wood, H., Bullock, J. M., Cousins, S. A. O., Gartz, M., Hooftman, D. A. P., & Tränk, L. (2017b). *Data from: HistMapR: Rapid digitization of historical land-use maps in R* [Data set]. Stockholm University. https://doi.org/10.17045/STHLMUNI.4649854.V2

Auffret, A. G., Kimberley, A., Plue, J., & Waldén, E. (2018). Super-regional land-use change and effects on the grassland specialist flora. *Nature Communications*, *9*, 3464.

Auffret, A. G., Nenzén, H., & Polaina, E. (2024). *Data for: Underprediction of extirpation and colonisation following climate and land-use change using species distribution models* [Data set]. Swedish University of Agricultural Sciences. https://doi.org/10.5878/xt40-pv58

Auffret, A. G., & Svenning, J.-C. (2022). Climate warming has compounded plant responses to habitat conversion in northern Europe. *Nature Communications*, *13*, 7818.

Auffret, A. G., & Thomas, C. D. (2019a). Synergistic and antagonistic effects of land use and non-native species on community responses to climate change. *Global Change Biology*, *25*, 4303–4314.

Auffret, A. G., & Thomas, C. D. (2019b). *Data for: Synergistic and antagonistic effects of land use and non-native species on community responses to climate change* [Data set]. figshare. https://doi.org/10.6084/M9.FIGSHARE.8845832.V1

Blomgren, E., Falk, E., & Herloff, B. (2011). *Bohusläns Flora*. Föreningen Bohusläns Flora.

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, *153*, 51–68.

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*, *9*, 57–71.

Briscoe, N. J., Zurell, D., Elith, J., König, C., Fandos, G., Malchow, A.-K., Kéry, M., Schmid, H., & Guillera-Arroita, G. (2021). Can dynamic occupancy models improve predictions of species' range dynamics? A test using Swiss birds. *Global Change Biology*, *27*, 4269–4282.

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H., & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*, 481–497.

Buitenwerf, R., Sandel, B., Normand, S., Mimet, A., & Svenning, J.-C. (2018). Land surface greening suggests vigorous woody regrowth throughout European semi-natural vegetation. *Global Change Biology*, *24*, 5789–5801.

Chauvier, Y., Descombes, P., Guéguen, M., Boulangeat, L., Thuiller, W., & Zimmermann, N. E. (2022). Resolution in species distribution models shapes spatial patterns of plant multifaceted diversity. *Ecography*, *2022*, e05973.

Cousins, S. A. O. (2001). Analysis of land-cover transitions based on 17th and 18th century cadastral maps and aerial photographs. *Landscape Ecology*, *16*, 41–54.

D'Amen, M., Dubuis, A., Fernandes, R. F., Pottier, J., Pellissier, L., & Guisan, A. (2015). Using species richness and functional traits predictions to constrain assemblage predictions from stacked species distribution models. *Journal of Biogeography*, *42*, 1255–1266.

De Frenne, P., Graae, B. J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D. A., & Verheyen, K. (2013). Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, *101*, 784–795.

de Luis, M., Álvarez-Jiménez, J., Rejos, F. J., & Bartolomé, C. (2020). Using species distribution models to locate the potential cradles of the allopolyploid Gypsophila bermejoi G. López (Caryophyllaceae). *PLoS One*, *15*, e0232736.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R. G., Hordijk, W., Salamin, N., & Guisan, A. (2017). Ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*, 774–787.

Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., Safford, H. D., Mynsberge, A. R., Crimmins, S. M., & Swanson, A. K. (2011). Modeling plant ranges over 75 years of climate change in California, USA: Temporal transferability and species traits. *Ecological Monographs*, *81*, 241–257.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46.

Dray, S., & Dufour, A.-B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Early, R., & Sax, D. F. (2014). Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography*, *23*, 1356–1365.

Eichenberg, D., Bowler, D. E., Bonn, A., Bruelheide, H., Grescho, V., Harter, D., Jandt, U., May, R., Winter, M., & Jansen, F. (2021). Widespread decline in central European plant diversity across six decades. *Global Change Biology*, *27*, 1097–1110.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*, 330–342.

Eriksson, O. (1996). Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. *Oikos*, *77*, 248–258.

Fourcade, Y. (2021). Fine-tuning niche models matters in invasion ecology. A lesson from the land planarian *Obama nungara*. *Ecological Modelling*, *457*, 109686.

Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, *27*, 245–256.

Fries, H. (1945). *Göteborgs och Bohus Läns Fanerogamer och Ormbunkar*. Elanders Boktryckeri.

Geppert, C., Perazza, G., Wilson, R. J., Bertolli, A., Prosser, F., Melchiori, G., & Marini, L. (2020). Consistent population declines but idiosyncratic range shifts in alpine orchids under global change. *Nature Communications*, *11*, 5835.

Gerstner, K., Dormann, C. F., Stein, A., Manceur, A. M., & Seppelt, R. (2014). Effects of land use on plant diversity – A global meta-analysis. *Journal of Applied Ecology*, *51*, 1690–1700.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. *Ecography*, *40*, 281–295.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, *199*, 142–152.

Honnay, O., & Bossuyt, B. (2005). Prolonged clonal growth: Escape route or route to extinction? *Oikos*, *108*, 427–432.

Illán, J. G., Thomas, C. D., Jones, J. A., Wong, W.-K., Shirley, S. M., & Betts, M. G. (2014). Precipitation and winter temperature predict long-term range-scale abundance changes in Western north American birds. *Global Change Biology*, *20*, 3351–3364.

IPBES. (2019). *Global assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services* (E. S. Brondízio, J. Settele, S. Díaz, and H. T. Ngo, Eds.). IPBES Secretariat.

Isaac, N. J. B., & Pocock, M. J. O. (2015). Bias and information in biological records. *Biological Journal of the Linnean Society*, *115*, 522–531.

Johansson, L. J., Hall, K., Prentice, H. C., Ihse, M., Reitalu, T., Sykes, M. T., & Kindström, M. (2008). Semi-natural grassland continuity, long-term land-use change and plant species richness in an agricultural landscape on Öland, Sweden. *Landscape and Urban Planning*, *84*, 200–211.

Jonsell, L. (2010). *Upplands flora*. SBF Förlaget.

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*, 334–350.

Keith, S. A., Newton, A. C., Morecroft, M. D., Bealey, C. E., & Bullock, J. M. (2009). Taxonomic homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society of London. Series B*, *276*, 3539–3544.

Kissling, W. D., Dormann, C. F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G. J., Montoya, J. M., Römermann, C., Schiffers, K., Schurr, F. M., Singer, A., Svenning, J.-C., Zimmermann, N. E., & O'Hara, R. B. (2012). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, *39*, 2163–2178.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*, 551–556.

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*, 1768–1771.

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*, 778–789.

Lynn, J. S., Klanderud, K., Telford, R. J., Goldberg, D. E., & Vandvik, V. (2021). Macroecological context predicts species' responses to climate warming. *Global Change Biology*, *27*, 2088–2101.

Maad, J., Sundberg, S., Stolpe, P., & Jonsell, L. (2009). Floraförändringar i Uppland under 1900-talet — En analys från Projekt Upplands flora [floristic changes during the 20th century in Uppland, east central Sweden; with English summary]. *Svensk Botanisk Tidskrift*, *103*, 67–104.

Maclean, I. M. D., & Early, R. (2023). Macroclimate data overestimate range shifts of plants in response to climate change. *Nature Climatic Change*, *13*, 484–490.

Mair, L., Hill, J. K., Fox, R., Botham, M., Brereton, T., & Thomas, C. D. (2014). Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change*, *4*, 127–131.

McCune, J. L., Rosner-Katz, H., Bennett, J. R., Schuster, R., & Kharouba, H. M. (2020). Do traits of plant species predict the efficacy of species distribution models for finding new occurrences? *Ecology and Evolution*, *10*, 5001–5014.

Meineri, E., & Hylander, K. (2017). Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography*, *40*, 1003–1013.

Nenzén, H. K., & Araújo, M. B. (2011). Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling*, *222*, 3346–3354.

Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., Palma, A. D., Ferrier, S., Hill, S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C. W. T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B. I., … Purvis, A. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, *353*, 288–291.

Nordén, J., Harrison, P. J., Mair, L., Siitonen, J., Lundström, A., Kindvall, O., & Snäll, T. (2020). Occupancy versus colonization–extinction models for projecting population trends at different spatial scales. *Ecology and Evolution*, *10*, 3079–3089.

Peirce, C. S. (1884). The numerical measure of the success of predictions. *Science*, *NS-4*, 453–454.

Platts, P. J., Mason, S. C., Palmer, G., Hill, J. K., Oliver, T. H., Powney, G. D., Fox, R., & Thomas, C. D. (2019). Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports*, *9*, 1–10.

Plue, J., Calster, H. V., Auestad, I., Basto, S., Bekker, R. M., Bruun, H. H., Chevalier, R., Decocq, G., Grandin, U., Hermy, M., Jacquemyn, H., Jakobsson, A., Jankowska-Błaszczuk, M., Kalamees, R., Koch, M. A., Marrs, R. H., Marteinsdóttir, B., Milberg, P., Måren, I. E., … Auffret, A. G. (2021). Buffering effects of soil seed banks on plant community composition in response to land use and climate. *Global Ecology and Biogeography*, *30*, 128–139.

Polaina, E., Soultan, A., Pärt, T., & Recio, M. R. (2021). The future of invasive terrestrial vertebrates in Europe under climate and land-use change. *Environmental Research Letters*, *16*, 44004.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rapacciuolo, G., Roy, D. B., Gillings, S., Fox, R., Walker, K., & Purvis, A. (2012). Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. *PLoS One*, *7*, e40212.

Santini, L., Benítez-López, A., Maiorano, L., Čengić, M., & Huijbregts, M. A. J. (2021). Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions*, *27*, 1035–1050.

Schimanke, S., Joelsson, M., Andersson, S., Carlund, T., Wern, L., Hellström, S., & Kjellström, E. (2022). *Observerad klimatförändring i Sverige 1860–2021 | SMHI* (p. 69). SMHI Klimatologi.

Shipley, B. R., Bach, R., Do, Y., Strathearn, H., McGuire, J. L., & Dilkina, B. (2022). megaSDM: Integrating dispersal and time-step analyses into species distribution models. *Ecography*, *2022*, e05450.

Soultan, A., Pavón-Jordán, D., Bradter, U., Sandercock, B. K., Hochachka, W. M., Johnston, A., Brommer, J., Gaget, E., Keller, V., Knaus, P., Aghababyan, K., Maxhuni, Q., Vintchevski, A., Nagy, K., Raudonikis, L., Balmer, D., Noble, D., Leitão, D., Øien, I. J., … Pärt, T. (2022). The future distribution of wetland birds breeding in Europe validated against observed changes in distribution. *Environmental Research Letters*, *17*, 24025.

Staude, I. R., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., Pauli, H., Van Calster, H., Vellend, M., Bjorkman, A. D., Brunet, J., De Frenne, P., Hédl, R., Jandt, U., Lenoir, J., Myers-Smith, I. H., Verheyen, K., Wipf, S., Wulf, M., Andrews, C., … Baeten, L. (2022). Directional turnover towards larger-ranged plants over time and across habitats. *Ecology Letters*, *25*, 466–482.

Sterner, R. (1938). *Flora der insel Öland*. Almqvist & Wiksells.

Stroh, P. A., Walker, K. J., Humphrey, T. A., Pescott, O. L., & Burkmar, R. J. (2023). *Plant atlas 2020: Mapping changes in the distribution of the British and Irish Flora*.

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J., Crick, H. Q. P., Duffield, S. J., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*, 713–717.

Syphard, A. D., & Franklin, J. (2010). Species traits affect the performance of species distribution models for plants in southern California. *Journal of Vegetation Science*, *21*, 177–189.

Talluto, M. V., Boulangeat, I., Ameztegui, A., Aubin, I., Berteaux, D., Butler, A., Doyon, F., Drever, C. R., Fortin, M.-J., Franceschini, T., Liénard, J., McKenney, D., Solarik, K. A., Strigul, N., Thuiller, W., & Gravel, D. (2016). Cross-scale integration of knowledge for predicting species ranges: A metamodelling framework. *Global Ecology and Biogeography*, *25*, 238–249.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*, 145–148.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, *32*, 369–373.

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 8245–8250.

Tyler, T., Herbertsson, L., Olofsson, J., & Olsson, P. A. (2021). Ecological indicator and traits values for Swedish vascular plants. *Ecological Indicators*, *120*, 106923.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*, 571–573.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J., & Elith, J. (2022). Predictive performance of presence-only species distribution models: A benchmark study with reproducible code. *Ecological Monographs*, *92*, e01486.

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J. L., Messier, J., Myers-Smith, I. H., & Sax, D. F. (2017). Plant biodiversity change across scales during the Anthropocene. *Annual Review of Plant Biology*, *68*, 563–586.

Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science*, *360*, 791–795.

Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology*, *14*, e2001104.

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., & NCEAS Predicting Species Distributions Working Group. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, *14*, 763–773.

BIOSKETCHES

In this study, the three authors have combined their respective interests regarding historical data, climate and land-use change and species distribution modelling.

Author contributions: A.G.A. and E.P. designed the study and analysed data. A.G.A. wrote the manuscript together with H.N. and E.P.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Auffret, A. G., Nenzén, H., & Polaina, E. (2024). Underprediction of extirpation and colonisation following climate and land-use change using species distribution models. *Diversity and Distributions*, *30*, e13834. https://doi.org/10.1111/ddi.13834