Species distribution models as a tool for forest management planning under climate change: risk evaluation of Abies alba in Bavaria

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Abstract

Questions: How can SDMs be adopted as a tool for forest management planning? Based on presence-absence data, which modelling techniques are appropriate to determine species potential distribution for forest management planning under climate change? Do species distribution models (SDMs) agree with expert knowledge about species distribution and species traits? How can forest researcher deal with distribution data of a species whose distribution is heavily affected by human impacts?

Location: Bavaria (Southern Germany).

Methods: We used SDMs based on the Second National Forest Inventory from 2002 (4 x 4 km grid) containing presence-absence data of tree species to identify species environment relationships (‘Grinnellian niche’). As an example, the distribution of silver fir (Abies alba Mill.) was modelled. Site condition data of the plots were derived from solar radiation, climate and soil maps. Models applied were boosted regression trees (BRT) and generalised additive models (GAM). Model predictions were compared with an expert based evaluation of the potential natural vegetation and were run with a climate change scenario (WETTREG B1) to project future distribution of silver fir.

Results: Both models discriminated well between presence and absence of silver fir but underestimated the potential distribution. The BRT model was more sensitive to local site conditions in the present data, but the GAM showed more generality. The truncated response curves and high uncertainties of predictions at the edge of the site spectrum indicated a low data density and that the data did not cover the whole niche space of silver fir. As indicated by validation with expert knowledge, the model output approached potential distribution by optimizing true positive predictions. The classification of SDMs output into risk classes allowed model evaluation and interpretation. Predictions of GAM and BRT under the climate change scenario showed high accordance and therefore, low uncertainty. Finally, large areas of Bavaria are described to have a high risk of silver fir cultivation in future.

Conclusions: SDMs are especially interesting as a decision basis for forest management because some of the general limitations of static modelling approaches are not relevant in this context. Limitations of forest inventory data can be partially overcome by using information on the potential distribution of species. The transferability of the models to future scenarios strongly depends on the spectrum and range of the training data sets and the depicted functional relationships. In order to improve the models and reduce the uncertainties, we need to improve the soil data and cover the whole niche space of silver fir.
Introduction

Successful forestry requires compliance between bioclimatic and chemo-physical site conditions and the ecological traits of a tree species growing on that site. Climate change induces considerable alterations in forest site conditions, and forest management must already prepare for them within the next rotation period as shifts in species distribution are likely to occur (Thuiller et al. 2005; Pompe et al. 2008). The risk in cultivating a tree species can only be limited if the requirements of the species are fulfilled by site conditions, e.g. precipitation and temperature regime, today and in future. Hence, we have to answer the question under which environmental conditions a successful cultivation of a species is possible. Therefore, we try to identify the potential distribution of tree species via species distribution models (SDMs, Guisan & Thuiller 2005).

As a way of risk handling, SDMs in forest management planning can be used to characterise the ecological traits of a species as a basis for species choice in order to replace species in the long run that are presumably less adapted to future site conditions with species that may be more adapted to changing environmental conditions (Haines 2004; Hane winkel et al. 2010). While most SDMs focus on changes in species distributions on the basis of natural dispersal mechanisms, until now, there are only a few papers dealing with SDMs as a forest management planning tool (Hane winkel et al. 2010 with focus on an economic evaluation of climate change impact on forestry; Mezquida et al. 2010).

We refer with the species environment relationship to the ‘Grinnellian niche’ as defined by Hirzel & Le Lay (2008): A positive population growth rate due to the local combination of environmental variables that can exist without immigration. We define the potential distribution of a species as all areas in which it can be grown with the help of forest management (e.g. planting, fencing, reducing competitors). Sites outside this potential distribution are not suitable for growing this particular species. In this sense, absences indicate an unspecific risk of mortality that often will be accompanied by low growth rate and yield. The realised distribution refers to the presences in our inventory data.

The reason for a high risk or a high mortality outside the potential distribution can either be linked more or less directly to climate (drought, frosts) or indirect via insects, diseases or competition arising from neighbouring trees (Monserud & Sterba 1999), however it can also be caused by soil pathogens (Packer & Clay 2000) which do not have a straight link to climate. We cannot specify the reasons for mortality and therefore describe the unspecific risk primarily with the help of climate data and determine an evaluation of risk under the assumption of climate change.

We chose the distribution of silver fir (Abies alba Mill.) in Bavaria as an example to evaluate SDMs for their support in forest management decisions on tree species suitability. The National Forest Inventory (BMELV 2005) provides an adequate data base for modelling as it covers a wide range of site conditions in which this mountainous species can and can not be grown. Thus, Bavarian climate and site data comprise the range margins at the cold and at the warm edge of silver fir’s distribution.

According to Wolf (2003), silver fir is tolerant of a wide range of soil conditions, nutrient content and availability as well as pH levels and depends most on moisture availability and temperature. The species is very cold-hardy but sensitive to frost drought during mild winter periods with frozen soils and late frost during spring (Wolf 2003; Elling et al. 2009). The distribution of silver fir is limited mainly to the mountainous regions of Europe but the species can be found at elevations of 135 m a.s.l. in Poland and 325 m a.s.l. in the Italian Apennines (Wolf 2003). Walentowski (1998) investigated Bavarian silver fir plant communities. His stands covered a temperature range from 4.4 to 7.7 °C mean annual temperature and had a minimum annual precipitation sum of 650 mm in regions with temperatures between 6 and 7 °C. January temperature covered – 3.8 to – 1.8 °C. Silver fir can stand harsher conditions outside of silver fir plant communities: Walentowski (1998) states that there are silver fir trees in regions with annual temperatures between 7.5 and 9 °C with good condition. The climatic elevational limit in the Bavarian Alps is reached at a mean annual temperature of about 4 °C and a mean January temperature below – 5 °C.

The realized distribution of Silver fir has been reduced considerably due to the strong influence of human activities in the past few centuries. While silver fir is present on only 14% of the inventory plots, potential natural vegetation (PNV) estimates imply that 80% of these plots are suitable for this species. Thus, silver fir is a good example of how to deal with problems arising in modelling the potential distribution of a strongly human affected species.

Since natural silver fir sites (mixed mountain forests) have been mostly afforested with spruce (Picea abies [Karst.] L.) in the last one and a half centuries, silver fir is nowadays appreciated as a stand stabilising and structure-enriching element. Furthermore, silver fir is seen as an alternative to Norway spruce under climate change due to a higher drought, storm and bark beetle resistance on suitable sites (Elling et al. 2009).

We used boosted regression trees (BRTs) as a new non-parametric modelling approach and used semi-parametric generalised additive models (GAMs) as a well established reference technique in habitat modelling. We aimed at a
parsimonious modelling approach involving variable selection procedures for GAM (Mellert et al. 2011) and for BRT models (Elith et al. 2008).

We discuss our modelling techniques and results in the light of forest management planning. This involves the following questions:

- How can potential rather than realised distribution of silver fir be described?
- Are modelling technique, structure, results and performance adequate for our purpose?
- Can predicted probabilities be used for a risk assessment of silver fir cultivation under climate change?
- Do SDMs agree with expert knowledge?
- What are the strength and limitations of SDM approaches?

Based on the answers to these questions, we finally look for possibilities to improve SDMs as a tool for forest management planning.

**Methods**

**Study area**

Our study region comprises the entire forested area of the federal state of Bavaria in Germany (2.5 Mio hectares) which represents 36.5% of the state territory. Bavaria is comprised of temperate forests and entails 15 different so-called growing regions with varying site conditions. These range from nutrient poor acidic soils in palaeozoic mountains to nutrient rich loamy sites (e.g. periglacial loess) and also comprise large calcic landscapes in the Jura Mountains and the Northern Alps. The climate varies from subatlantic lowlands at the Main river in NE Bavaria (50°N, 9°E, 200 m a.s.l., mean annual temperature 8.5 °C, 750 mm annual precipitation sum) to the alpine in Southern Bavaria (47.5°N, 13°E, < 5.5 °C mean annual temperature, > 1500 mm annual precipitation sum) where the forest tree line approaches 1800–1900 m a.s.l.

**Occurrence and site condition data**

Our data on silver fir occurrence is based on a 4 × 4 km grid from the Second National Forest Inventory data plots (BMELV 2005), of which 2192 are located in Bavaria and have forest cover. Each inventory plot consists of up to four subplots located at the corners of a square with a side length of 150 m. For each of the 6103 subplots we transformed the proportions of silver fir into presence and absence values. Then, we selected only one subplot at each plot with a preference for presence data. Thus, an absence in the data means that there was no silver fir in four subplots. This led to a prevalence of 0.22 compared to 0.14 for all subplots. A preliminary study supported this approach: we found that disabling absences in short range distances (method ‘circular’ according to Thuiller et al. 2009) could improve model performance considerably.

We extracted site condition data at each subplot in a GIS-analysis based on a 50 m × 50 m digital elevation model. We calculated potential global radiation with the ESRI solar radiation tool (ESRI ArcGIS 9.2) and used interpolated monthly temperature and precipitation data from Germany’s National Meteorological Service (Zimmermann et al. 2007) at the plots. Soil data for all of Bavaria were only available in coarse resolution (1:200 000).

The selected explanatory variables can be divided into three categories of abiotic site characteristics accounting for the availability of water, energy and nutrients which determine silver fir growth and therefore limit its distribution. Spring and summer temperature, potential radiation from May till September as well as the type of base saturation of the soils (Kölling et al. 1996) were dropped by the selection of variables procedure (see below). Thus, the models account for the categories water and energy:

- **Water**
  - Aridity-Index (De Martonne 1926) \[ i = P / (T + 10) \]
  - with \( P \) = annual sum of precipitation (mm) and \( T \) = mean annual temperature (°C)
  - Precipitation sum June to August (mm)
  - Precipitation sum May to September (mm)
  - Available water capacity to 1 m soil depth (mm)

- **Energy (radiation, temperature)**
  - Temperature in January (°C)
  - Mean temperature May to September (°C)
  - Growing degree days with a baseline of 5 °C (dimensionless heat unit)
  - Potential radiation March to April (kWh · m⁻²)
  - Potential radiation June to August (kWh · m⁻²)

**SDM techniques**

SDM techniques which attempt to model the Grinnell’s niche can be divided into three groups with respect to the underlying calibration data (Soberón & Nakamura 2009). If absence data is not available, e.g. data from animal observations or floristic archives, either presence-only methods or presence-background techniques (Soberón & Nakamura 2009) are adequate. As we examined presence-absence data, we conducted the presence-absence version of SDMs and used potential natural vegetation (PNV) for validation to check for the ability of our models to predict the ecological potential of silver fir. Although PNV has been criticised (e.g. Chiarucci et al. 2010), we believe that the post glacial migration history and the potential distribution of silver fir and its plant communities in Bavaria are well studied (Walentowski 1998; Walentowski et al. 2006) and is therefore rather reliable for the estimation of the potential distribution.
We calibrated and tested models in two steps in order to assess possibilities for the further development of SDMs. First, we calibrated SDM to our presence-absence data set and evaluated models on training data by 10-fold cross validation. Additionally, we tested how models perform for predicting potential distribution depicted by PNV. Second, we constructed SDMs out of a presence-absence data set that pooled the PNV data and the inventory data with preference to presences (set union: a presence in one data set resulted in a presence in the combined data set). Building up a set union of observations means also to remove fallacious absences from observations as suggest by some authors (Hirzel & Le Lay 2008; Zarnetzke et al. 2007). Such a model serves as a reference which is assumed to be closer to the potential distribution of silver fir as a model only based on one data set.

We used boosted regression trees (BRT), as this SDM technique was described to be superior in describing distributions and discriminating between presences and absences over other predictive modelling techniques (Elith et al. 2006; Guisan et al. 2007). Data mining methods such as BRT are capable of fitting robust models to ecological data because they are well suited for modelling interactions of predictors (Ridgeway 2006) and can handle sharp discontinuities. We included up to three-fold interactions and although the training rules of these nonparametric models are too complex for scrutiny, species response can be plotted. We checked the influence of the variables on the distribution of silver fir in accordance with our physiological hypotheses. We used BRTs as implemented in the R (R Development Core Team, R Foundation for Statistical Computing, Vienna, AT) package gbm (Ridgeway 2006).

As a second method we used generalised additive models (GAMs) (Hastie & Tibshirani 1990; Wood 2006). GAMs are semi-parametric extensions of generalised linear models (GLMs) and allow fitting of response curves with a non-parametric smoothing function instead of parametric terms. This improves the exploration of species responses to environmental gradients and allows the fitting of statistical models in better agreement with ecological theory compared to GLMs (Lehmann et al. 2002). We chose GAMs as implemented in the R package mgcv (Wood 2009) as this software provides an automated choice of smooth terms (Wood 2006). We omitted interaction terms in GAMs because the number of potential parameters to be estimated increases exponentially with the number of predictors in such a model and would thus violate our intension of parsimonious model building.

Selection of variables and parameter estimation

We focused on making our models parsimonious by selecting the most important environmental variables out of our predefined categories water, energy and nutrient supply and prevent overfitting as well as an estimation of a too generalised model (bias-variance tradeoff). GAMs were fitted using the GCV-score, checking response curves for ecological plausibility (Austin et al. 2006) and avoidance of collinearity in the final model. We conducted a stepwise backward variable selection procedure for the ranking of candidate variables in which the covariate with the highest P-value was removed at each step until the GCV increased (elbow-criterion). GCV is based on the leave-one-out cross-validation criterion, which is calculated with the sum of the squared prediction errors, when each observation is predicted by a model assessed by the rest of the data (Wood 2006). We checked response curves and removed high collinear predictor from the final model (criterion Spearman’s r < 0.7, Fielding & Haworth 1995). We set the basis functions of natural cubic splines to three degrees of freedom allowing cubic polynomial splines.

For calibration of BRTs, we used the gbm.step and gbm.simplify procedure from Elith et al. (2008). These procedures involve a 10-fold cross-validation which estimates the optimal number of trees and variables by minimizing the predictive deviance of the model. Variables were left out when they had a relative influence below 3%. Tree complexity was set to 5 and learning rate to 0.01 which resulted in a model with 800 trees resp. 1750 for the pooled data of PNV and inventory data.

Model evaluation

For evaluating the predictive performance of models we examined the area under a receiver-operating characteristic curve, AUC. This criterion is threshold independent since it summarises overall model performance over all possible thresholds (e.g. Elith et al. 2008) and it is widely used to compare model accuracy (e.g. Elith et al. 2006; Guisan et al. 2007). Predictions of both model approaches were examined by 10-fold cross validation using AUC. There are different suggestions how to interpret AUC values. Hosmer & Lemeshow (2000) suggest a threshold of 0.7 for models to be adequate, while Harrell (2001) recommends a threshold of 0.8. Additionally, we checked the accuracy of the predicted probabilities with calibration plots (Freeman & Moisen 2008b).

Spatial dependence

Ignoring spatial dependence of grid points may lead to inflated significance levels and bias parameter estimates (Dormann et al. 2007; Kühn 2007). On the other hand purely statistical criteria are not sufficient to answer the question if the inclusion of space is appropriate in species-environment regression models (Lichstein et al. 2002).
The inclusion of space may even cause scale shifts in the coefficients’ estimates and generate complex patterns of collinearity between space and the independent predictor variables (Hawkins et al. 2007). Additionally, models which include spatial information loose their ability to be transferred in space and time (Guisan & Thuiller 2005). Nevertheless, we tested GAMs with a spatial effect in order to account for spatial dependence and unobserved confounders (Paciorek 2009). As a result, we applied a model without any spatial term as we found that models involving a spatial effect led to misleading projections for silver fir. In North-Eastern Bavaria (‘Fichtelgebirge’) for example, spatial models predicted absences whereas silver fir is present in this region and has a high potential due to mountainous climate.

Interpretation and classification of model predictions

The outputs of the models are probabilities of occurrence on a continuous scale from 0 to 1 (0–100% probability). We followed Freeman & Moisen (2008a) in choosing an adequate way to individually interpret the probability surface of our models in maps. The likelihood was translated into three risk classes by choosing two thresholds which was done in order to use ‘full’ information of the predicted probabilities and facilitate forestry planning. As a standard threshold we used the prevalence as suggested by Cramer (1999) and Liu et al. (2005) which is usually used to convert probabilities into presences and absences. We classified sites with probabilities above the prevalence as sites with a low risk of growing silver fir because these sites were highlighted by the majority of presences. A second threshold was chosen by a sensitivity value of 0.95 so that 95% of all presences in the data set are correctly classified by the model (only 5% omission error, discussed by Jiménez-Valverde & Lobo 2007; Lobo et al. 2008) in order to come closer to the potential distribution of silver fir. Probabilities below this sensitivity are regarded as high risk due to the numerous absences, whereas values between the prevalence and the sensitivity threshold are treated as medium risk. We averaged risk classifications from the models GAM and BRT which led to five classes, the three former classes and two transitional ones. Accordance, or lack of accordance between the models, was used for uncertainty considerations. The resulting medium risk class is formulated from the two combinations low/high (high uncertainty) and medium/medium (low uncertainty).

Validation based on expert classification

Models were compared with an expert classification of the potential natural vegetation (PNV) at the inventory sub-plots. For the Second National Forest Inventory in Germany, PNV was defined as an exemplary perception of a maximum developed plant community that would grow on a specific site when direct human influence would abruptly cease (Walentowski et al. 2006). Plant communities were forecasted via forest site maps and maps of forest regions in Bavaria and checked in the field by species occurrence and Ellenberg indicator values during the inventory. We transferred the plant communities that include silver fir into presences and the remaining sites into absences.

Projections with a climate change scenario

We used a climate change scenario (B1, IPCC 2000) based on the atmospheric general circulation model ECHAM5 downscaled with the statistical model WETTREG (Spekat et al. 2007, mean realisation), recalculated climate data for the period 2071–2100 at the inventory plots and reran SDMs with these data. The B1 scenario family is the most optimistic in matters of global warming (IPCC 2000). It projects an increase of mean annual temperature of about 1.9 °C and a decrease of mean annual precipitation sum of about 4.4 percent for Bavaria. According to WETTREG B1, the precipitation sum will increase slightly in the dry and warm Northwest of Bavaria and decrease in the other regions. Warming is described to occur mostly in winter: mean temperature of the growing season (Mai to September) will increase about 1.5 °C in Bavaria, whereas January temperature is projected to increase about 3.2 °C as compared to the period 1971–2000.

Results

Calibration

Final model design, response curves and calibration plots

GAM and BRT models are mainly driven by radiation and climate parameters (Fig. 1 and Table 1). Soil characteristics were of minor relevance and soil water capacity is only included in the BRT model. Variable selection of BRT and GAM resulted in different models but the variables of the latter were also selected for the former. The response curves of growing season temperature differ between the two SDMs, whereas the ones of growing season precipitation show the same effect. The response curves of spring radiation are comparable in both models.

The response curves of the most important predictors of the BRT model are presented in Fig. 1d–h. The response curve of the aridity index according to De Martonne (1926) shows that a warm-dry climate (i.e. lower values) is less suitable for silver fir. For higher probabilities of the overall model, a minimum summer precipitation sum of more than 250 mm is needed. The response curve of January temperature shows that silver fir is a
mountainous species which is more often found at colder sites. The Bavarian data contain distribution limits not only towards the warm but also towards the cold end of climate suitability. This is described by the response curves of growing season temperature and growing degree days (not shown).

The GAM (Fig. 1a–c) describes a relation between probability of occurrence and precipitation sum in the growing season (strong increase of probability between 300 and 450 mm). The response of silver fir to growing season temperature has the shape of an optimum curve, indicating that there is a distribution limit both at the cold and at the warm edge. The response curves show high uncertainties at their edges, indicated by the confidence intervals (grey bands in Fig. 1a–c). Spearman’s rank correlation coefficient of the temperature and precipitation variable is $-0.43$.

Models that were calculated with the pooled data of PNV and inventory data differed slightly in variable importance and therefore in selected variables and in shape of some response curves (not shown but see Fig. 2 for the different data sources). Summer precipitation and spring temperature determine the BRT model and therefore the aridity index loses predictive power. The response curves of the GAM describe a limitation towards higher temperature and lower precipitation.

The calibration plots (not shown) show a high agreement between predicted probabilities of occurrence based on the training data set and observed proportions of sites occupied by silver fir. Only the predictions of BRT tend to be underconfident (Schröder et al. 2009) above a probability of 0.5.

**Evaluation and plausibility**

**Model performance**

One aspect of model evaluation is the model’s ability to distinguish between presence and absence, also called
discrimination. AUC values of our models were acceptable for all variants. The AUC was 0.79 for the GAM model based on the inventory data and 0.84 for the model based on PNV combined with the inventory data. With an AUC of 0.90 for the inventory data and 0.98 for PNV combined with the inventory data, BRT showed a better ability to discriminate.

Table 1. Response variables of the two models GAM and BRT built upon inventory data. Relative importance of GAM is due to P-values in model output. Hypotheses and response curves and their accordance are described verbally.

<table>
<thead>
<tr>
<th>SDM</th>
<th>Variable</th>
<th>Relative importance</th>
<th>Hypothesised distribution limit</th>
<th>Limit indicated by response</th>
<th>Accordance with hypothesised limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>GAM</td>
<td>Precipitation May–September</td>
<td>Most</td>
<td>Water availability during growing season</td>
<td>Minimum of 300 mm</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>Radiation March–April</td>
<td>Second</td>
<td>Length of vegetation period</td>
<td>Pessimum between 190 and 230 kW · h · m⁻²</td>
<td>Partly; interaction with temperature variables</td>
</tr>
<tr>
<td></td>
<td>Temperature May–September</td>
<td>Third</td>
<td>Energy in growing season, heat</td>
<td>Optimum between 10 and 15 °C</td>
<td>Yes</td>
</tr>
<tr>
<td>BRT</td>
<td>Aridity index (de Martonne)</td>
<td>35.2%</td>
<td>Water availability</td>
<td>Threshold at index of 70</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>Precipitation June–August</td>
<td>13.7%</td>
<td>Water availability, drought</td>
<td>Minimum of 240 mm</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>Temperature January</td>
<td>13.1%</td>
<td>Winter frost and winter dormancy</td>
<td>The colder the better, maximum of −1 °C</td>
<td>Partly; interaction with temperature variables</td>
</tr>
<tr>
<td></td>
<td>Radiation March–April</td>
<td>8.3%</td>
<td>Length of vegetation period</td>
<td>Pessimum between 190 and 230 kW · h · m⁻²</td>
<td>Partly; interaction with temperature variables</td>
</tr>
<tr>
<td></td>
<td>Available water capacity</td>
<td>7.2%</td>
<td>Water availability</td>
<td>Threshold of 200 mm</td>
<td>No; high values are bogs (not suitable)</td>
</tr>
<tr>
<td></td>
<td>Temperature May–September</td>
<td>6.6%</td>
<td>Energy in growing season</td>
<td>The warmer the better</td>
<td>Partly; interaction with temperature variables</td>
</tr>
<tr>
<td></td>
<td>Precipitation May–September</td>
<td>5.5%</td>
<td>Water availability during growing season</td>
<td>The higher the better</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>Radiation June–August</td>
<td>5.3%</td>
<td>Energy in growing season, heat</td>
<td>Threshold at 430 kW · h · m⁻², above lower probabilities</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>Growing degree days</td>
<td>5.1%</td>
<td>Energy, length of vegetation period, heat</td>
<td>Optimum curve</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Fig. 2. Presences and absences according to inventory and potential natural vegetation (PNV) data.
Maps of predicted probabilities versus expert based PNV

The modelled distribution is presented in Fig. 3, showing the results for GAM and BRT separately. The BRT model accentuates the areas with low suitability a little bit stronger than the GAM. The models reflect today’s distribution of silver fir and therefore differ from our reference expert classification (PNV): only 26.5% of the PNV presences are also presences in the inventory data whereas 95.5% of the absences in PNV data are also absences in the inventory data. If we compare the modelled areas of low risk (predictions higher than prevalence) with the pooled PNV and inventory data, we find 43 (GAM) resp. 41% (BRT) of the PNV plus inventory data presences modelled as presences and 87 resp. 96% of the absences classified as absences.

With a sensitivity of 0.95 as threshold, the amount of accordance of presences increases to 85 resp. 67% whereas the accordance in absences decreases to 52 resp. 85%.

Figure 4a shows the risk assessment based on the combined PNV and inventory data. The output of the two models GAM and BRT was transformed into two risk classes with prevalence as threshold and combined to one map resulting in three classes. The same combination was done for the model output of GAM and BRT that were built upon the inventory data which resulted in five risk classes (not shown, cf. Methods). The combined risk maps of the two different data bases matched in 41% of the cases. If a tolerance of one risk class was accepted, the matching rate was 67%. Thus, the risk maps differed on 33% of the

Fig. 3. Predicted probabilities transformed to risk. Predictions of GAM (a) and BRT (b) at the inventory plots. Output is classified in three risk categories. Climate data is from the period 1971–2000. Lines represent borders of 15 physical forest regions according to the Bavarian State Institute of Forestry.

Fig. 4. Predicted probabilities and scenario of future distribution. Models built with synthetic data. Combined predictions of GAM and BRT with today’s climate (a) and a scenario of future distribution (b) at the inventory plots. Output is classified in three risk categories. Climate data in (b) according to WETTREG B1 scenario 2071–2100, plots beyond today’s growing season temperature are removed in the projection. Lines represent borders of 15 physical forest regions according to the Bavarian State Institute of Forestry.
Projection

Scenario of future distribution

Running the models with future climate scenarios gives a first glance of future challenges in forestry. Figures 4b and 5 show the risk for cultivating silver fir with climate data for 2071–2100 under the assumption of the WETTREG B1 scenario and thus, the number of low probability sites increases. Only on mountainous sites with higher elevation and precipitation is a low or medium risk for silver fir cultivation expected (Bavarian Alps, Bavarian Forest). Especially BRTs predict a strong decrease in the suitability for cultivating silver fir in Bavaria compared to the modelled situation in 1971–2000 (Fig. 3). This is due to the very strong effect of January temperature on habitat suitability. According to scenario B1, most of the warming in southern Germany is projected to occur in winter. Therefore, the January temperature shift is very strong and affects predictions more than any other parameter.

The models based on inventory data for today’s climate underestimate distribution compared to PNV-based models, whereas future projections based on two different data bases do not differ very much (82% accordance with a tolerance of one risk class and only 6% opposing risk estimates). We excluded 348 plots from Figs 4b and 5 that are projected to be warmer in the growing season than today in order to avoid extrapolation into non-analogous climate (cf. Discussion).

Discussion

Model evaluation

Most of the response curves followed our expectations (Fig. 1, Table 1). The sum of summer radiation (not shown) for example has a negative effect on the probability of occurrence in the BRT model. This is in accordance with silver fir’s tolerance to shade, mountainous distribution (Wolf 2003) and drought sensitivity (Lebourgeois et al. 2010).

The influence of temperature in January indicated that silver fir is most frequent in mountainous and colder regions in Bavaria (Table 1). The January temperature response obviously does not depict the low temperature limits and the risk of frost damages as suggested by our hypothesis. A physiological reason for this result may be that the distribution and growth in the Alps is predominantly limited by a very short vegetation period in cold Alpine regions and not primarily by frost temperatures in January (Walentowski 1998; Shi et al. 2008; Lebourgeois et al. 2010).

Within model calibration, a major source of uncertainty is the quality of input data. The fact that soil data were only available at a coarse resolution (1:200 000) did not allow us to adequately specify edaphic resources at each site. The diffuse description may be partly responsible for the weak explanation by soil parameters.

Both modelling techniques, GAM and BRT, showed that the data of extreme sites were insufficient to cover the whole niche of silver fir as indicated by truncated shape of response curves. For example the probability of occurrence along the temperature gradient (Fig. 1f: Average temperatures in January) remains high at the lower end of that gradient. Additionally, high uncertainties of predictions at the edge of environmental space indicated...
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by the GAM response (Fig. 1b) show that the edge of the gradient is sparsely covered with data.

**GAM versus BRT**

BRT and GAM are based on reasonable habitat-environment relationships (Fig. 1, Table 1). BRTs are strongly data driven and can model particular features. Therefore, BRT performs well in modelling today's distribution (high AUC). The response curves of BRT emphasise on the characteristic of this approach: BRT as a data driven machine-learning method allows the identification of harsh limits and uses more and different predictors and therefore discriminates better. In contrast, GAM is a method that suits continuum theory quite well (Austin 2002) and gives a generalised picture of how the distribution of silver fir is determined by precipitation, solar radiation and temperature (Fig. 1a–c). In principle, more generalised approaches are better for the purpose of projection into time and space. Indeed, we found that the potential distribution (PNV) could be better predicted by GAM. This is in accordance with Randin et al. (2006) who concluded from a comparison of GLMs and GAMs that overfitting may reduce transferability (though in their study GAMs tended to be overfitted). As demonstrated with our examples, a synthesis of both approaches could combine strength of both techniques but also show uncertainty in SDMs. Finding the appropriate method for merging the two model outputs would be optimized by using an independent test data set which we do not have at the moment.

**Potential versus realized distribution**

We used common presence-absence techniques as the underlying inventory data were presence-absence data. However, there are some alternatives that should be discussed in the case of an anthropogenic reduced distribution of a species as silver fir. Our overall approach of using calibration data and validation techniques is based on considerations of this particular issue.

It is common that presence-absence techniques are applied if presence-absence data are available (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Thuiller et al. 2009). Some authors (Hirzel & Le Lay 2008) argue that it is preferable to use presence-only (e.g. envelopes like ENFA) techniques if absences may be obscure. Fallacious absences infer the risk of misspecification of models (Hirzel & Le Lay 2008). Other authors (Engler et al. 2004; Zarnetzke et al. 2007) suggest the introduction of prior knowledge by ecological motivated selection of pseudo-absences for calibrating presence-background techniques.

As preliminary tests of presence-only approaches were dissatisfying (Surface range envelope, Thuiller et al. 2008; Mahalanobis distance, Faber & Kadmon 2003), we used presence-absence models that represent the standard technique but integrated potential distributions (PNV) and models calibrated on synthesised data (set union of observations and potential distribution) for validation purposes.

Thus, it could be demonstrated that optimisation of the true positive forecast of the models (sensitivity) could be a proper measure to approach potential distribution (PNV) of silver fir. On the other hand, regional differences of silver fir detraction can introduce a bias into the habitat environment relationship and thus, it is important to be aware of historic impacts when interpreting predictions. Our approach with models based on synthesised data (PNV and observations) reveals that calibrating models on potential distribution data could be an alternative if reliable absences are missing. The other type of errors, i.e. ‘spurious’ presences outside the natural range, are not relevant in the case of silver fir. Overabundant species like _Picea abies_ which had been introduced to sites where this species would hardly be present without forestry have to be handled differently. Predicting distributions of such a species would involve the risk to overestimate habitat suitability than to underestimate it.

**Projections under climate change**

One major aim of modelling in ecology – and thus for the use of SDMs – is to predict in either space or time (Peterson 2006). With the focus on the consequences of climate change on forestry, the aim is a prediction of species distribution in time in which adaptations to predicted changes can be made. But there are several limitations when using SDMs for predicting distributions in time with changing environmental conditions (Guisan & Thuiller 2005; Dormann 2007). Strictly speaking, predictions are not allowed for a non-analogous climate (Fitzpatrick & Hargrove 2009). That means, if combinations of future precipitation and temperature predicted in Bavaria did not exist within the calibration period, extrapolations of SDMs will be unreliable. Because test data of analogous regions outside of Bavaria was not available in comparable quality, our only possibility to judge the model transferability is a validation based on response curves (Mellert et al. 2011) and the predictive performance of models via cross validation. Using European distribution data will improve our approach and reduce uncertainty.

An import precondition for our approach is that Bavaria, our calibration area, contains an analogous climate in the warm-dry region in the Northwest where silver fir is already today beyond its suitability and is correctly described by the models. Although, only a small portion of our sites represent analogous warm-dry climates both SDM methods show comparably well defined limits at
the warm and dry edge of silver fir distribution as indicated by response curves (Fig. 1a, c–e). Under projections of B1, 17.5% of our sites will be warmer in the growing season than today’s maximum of 16.9 °C with a projected maximum of 18.2 °C. Therefore, we omitted to extrapolate beyond today's maximum and removed these plots from the Figs 4b and 5. This is certainly a simplification as we are using multiple variables in our models but temperature is expected to change much stronger than precipitation. Figures 4b and 5 show that models predict probabilities far below the threshold value (prevalence). This result is in accordance with shape of response and reasonable: sites that are too dry (warm) for growing silver fir today will be even less suitable under a predicted warming.

Nevertheless, we stress the uncertainties at the response edge showing that models are not sufficiently calibrated for extrapolation beyond the calibration space. For silver fir this is true especially for the low temperature limit. Therefore, predictions under climate scenarios have to be regarded with caution. It has to be kept in mind that climate scenarios are a major source of uncertainty in risk estimation for forest tree species (Dormann 2007) but this imponderability cannot truly be solved by SDMs as decision support for forest management planning.

**Forest risk assessment and risk management**

The aim of our work was to model the distribution of silver fir in relation to environmental parameters and to use model predictions for risk assessment. Tools for forest management planning under climate change are necessary since decisions have to be made today for a rotation period of about 60–100 years. SDMs, as a widely used tool to model species distribution (Guisan & Thuiller 2005), are especially interesting for forestry because some of the limitations of this technique (Hampe 2004; Guisan & Thuiller 2005) do not apply for silvicultural questions. In particular, there is no need to incorporate mechanistic dispersal or migration models into the statistical SDM (hybrid models, Gallien et al. 2010) since natural barriers are irrelevant for forest management (e.g. planting of North American *Pseudotsuga menziesii* in Europe). Also, competition between tree species is strongly reduced by forest management and in certain special situations fencing, pest control, liming or fertilization are auxiliary methods for regeneration and conversion of stands.

However, it is unknown how biotic interaction with pests will develop and if any new pests will invade Bavaria in the future. Therefore, we focus on current abiotic species/environment relationships (Grinnellian niche, analysed with noninteractive, nonconsumable *scenopoetic* variables, Soberón & Nakamura 2009) and we try to provide some of our experiences with that approach. The state of SDMs presented here is our basis for further improvement of models in order to use them as a tool for forest management practices.

We use the term ‘risk’ as an unspecific risk of mortality which occurs at the niche edge where the presence of silver fir in the geographical space decreases. We cannot specify the reasons for mortality because our models are mainly driven by 30 year means of climate variables. Our risk estimation therefore has a blur, however areas with high or low risk are well justified by either a high amount of absences or a high amount of presences in the inventory data, whereas uncertainty is higher in areas that are classified as medium risk sites. The risk estimation of BRT and GAM differed at some plots in respect to the risk class regardless of which data base was used (observations or synthesised data). This is because of the differences of the SDM techniques and of our calibrations described above. However, maps could at least give a semi quantitative view of regional risks of cultivating silver fir.

A conclusion of the risk assessment is that silver fir should not be introduced at sites where presently a high risk is calculated. Generally, risk handling can be done in different ways. At sites with a high risk in the future but low risk today, the rotation period can be shortened and risk can be spread by introducing different species with different risk assessments (transformation into stable mixed stands). For example, if drought is the cause for high risk, the competition about this resource can be reduced by thinning (Kohler et al. 2010) or combining trees with different root systems and/or need for water (Pretzsch et al. 2010). Quantitative estimation can only be established by collation with observed rates of forest damages.

**Conclusions and Perspective**

It could be demonstrated that SDMs provide useful information for forest management planning even for strongly anthropogenic affected distributions of tree species like silver fir. The maps produced give at least a semi quantitative view of the regional risks for cultivating silver fir. Additionally, we could identify the limitations of our approach. The truncated response curves and high uncertainties of predictions at the edge of the site spectrum indicated that the data were sparse at the distribution edge and did not cover the whole ‘Grinnellian niche’ space of silver fir. Additionally, absences have to be handled with caution because they might be fallacious and therefore misleading. Optimizing true positive predictions and using expert knowledge like PNV data (e.g. Walentowski et al. 2006) or vegetation maps (e.g. Bohn et al. 2003) improved the models ability to describe the potential distribution of the species. We argue that well
established expert data enhance applicability of SDMs as they provide functional descriptions of species environment relationships. The two presence/absence techniques we used (GAM and BRT) proved to be appropriate tools and allowed for the scrutiny of ecological reasonability (i.e. response curves in accordance with ecological knowledge). The translation of model output into risk classes was an important step towards better interpretability and usability of SDMs and also helped to handle the problems which arise from species not at equilibrium with environment (e.g. the anthropogenic affected distribution of silver fir).

In all, the use of SDMs improves forest management planning because the models provide a harmonised, comprehensible, reproducible and transferable decision basis. The results encourage us to further develop our SDMs as a regular decision support tool for forest management planning.

Acknowledgements

The project is funded via the initiative ‘Klimaprogramm Bayern 2020’. We thank the Bavarian State Ministry for Food, Agriculture and Forestry for their support. We further thank Ute Bachmann, Christian Kölling, Tobias Mette, Daniel Morovitz and Erik Settles for their support and/or help on linguistic improvements and two unknown reviewers for their comments which helped enormously to improve the manuscript.

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257: 1175–1187.


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