

Comparing future shifts in tree species distributions across Europe projected by statistical and dynamic process-based models

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Abstract

Many tree species are predicted to shift their geographic ranges with changing climate, but the extents, timing, and magnitude of these shifts remain uncertain. Comparing various modeling strategies is crucial for reducing uncertainty related to these responses and for guiding the interpretation of model results. Here we compared outputs of a dynamic vegetation model (DVM) and an ensemble of statistical bioclimatic envelope models (BEMs) in predicting range shifts of 14 representative tree species in continental Europe. Expanding the number of species and geographic extent compared to previous model comparisons, we found that the DVM produced more conservative range shift estimates, even in long-term equilibrium simulations. The differences in range shift projections were greatest for Mediterranean species, whose expansion northwards was inhibited in the DVM by more competitive prevailing temperate species. In contrast to our expectation, competitive traits of the species studied did not consistently affect the differences. The agreement between BEM and DVM results was highest in boreal species, suggesting that BEMs are an efficient method for modeling species under strong control of abiotic factors. BEMs produced substantially larger range contractions at the southern edge of distribution, in contrary to the DVM, where contractions were more modest. Despite these differences, both approaches also yielded consistent northwards shifts of forest types, which may have substantial negative impacts on forest economy, and alter species composition in natural forest stands.

1. Introduction

Climate change may become a major threat to global biodiversity (Bellard et al. 2012; Thomas et al. 2004), and warming over past decades has already caused substantial range shifts and abundance changes in a wide range of species (Chen et al. 2011; Jump and Penuelas 2005; Parmesan and Yohe 2003). Substantial future range shifts and local extinctions have been projected for the future (Cheung et al. 2009; Lawler et al. 2009; Thuiller et al. 2008).

Assessing the potential impact of climate change on terrestrial ecosystems requires detailed estimates of vegetation responses, trees in particular, which also provide a variety of habitats and ecosystem services (Ellison et al. 2005; Linder et al. 2012). Many tree species have long generation times, and their genetic and phenotypic adaptive capacity may be exceeded by rapid climate change (Jump and Penuelas 2005; Lindner et al. 2010). These factors emphasize the importance of studying range shift potentials for many tree species.

Two modeling methodologies are commonly used for projecting climate change impacts on trees: statistical bioclimatic envelope models (hereafter BEMs), and process-based models, such as dynamic vegetation models (hereafter DVMs) and forest growth models (Landsberg 2003; Landsberg and Waring 1997; Schelhaas et al. 2007).

BEMs construct a statistical relationship between species' observed distributions and climatic variables, and this relationship may be used to predict species distributions in space and time (Elith and Leathwick 2009; Pearson and Dawson 2003). Applications include estimation of potential geographic distributions of species and projections into the past and/or future e.g. under climate change. Although biologically simplistic, BEMs have the advantage of relative ease of use, and data sets describing species distributions, and current and potential future climates have become increasingly available (Elith and Leathwick 2009). However, the reliability of future projections by BEMs has been questioned because the used underlying statistical relationships do not necessarily imply causation and may therefore not hold when extrapolated, e.g. under climate change (Dormann et al. 2012). Furthermore, various algorithms simulating current distributions similarly well have been observed to produce widely differing future projections (Araújo and Guisan 2006; Araújo and New 2007; Buisson et al. 2010).

Within the DVM category, forest growth models commonly focus on simulating tree growth and forest yields (Landsberg 2003), while other DVM approaches combine aspects of forest growth with competition for resources, population dynamics (succession), and range shifts. The latter include Dynamic Global Vegetation Models (DGVMs), which only use bioclimatic limits related to a particular physiological mechanism and are based on broadly defined Plant Functional Types (PFTs, Prentice et al. (2007)). Process-based models may be considered biologically more realistic, but they are also "data hungry" (Guisan and Thuiller 2005), requiring detailed input data, which is often available only for well-studied species or PFTs.

Despite both BEMs and process-based DVMs being widely applied in modeling tree species distributions (e.g. Benito Garzón et al. 2008; Hickler et al. 2012; Kramer et al. 2012; Snell et al. 2014; Thuiller et al. 2005), few studies have systematically compared these two approaches. Results comparisons from various modeling approaches, with the identification of results that are robust across model types and exploration of reasons for differences in the results is important to guide the interpretation of model projections. With limited sets of

species, various modeling approaches have yielded similar results under present-day conditions (Gritti et al. 2013). Under climate change, DVMs have projected more conservative range contractions compared to BEMs, because they also simulate additional processes such as the physiological effects of carbon dioxide (CO₂) (Cheaib et al. 2012; Hickler et al. 2015; Keenan et al. 2011) and phenotypic plasticity or local adaptation (Morin and Thuiller 2009). Kramer et al. (2010 and 2012) also found substantially smaller simulated range shifts for European beech (*Fagus sylvatica*) when using the DVM LPJ-GUESS platform, compared to projections with the BEM approach using the BIOMOD platform (Thuiller et al. 2009b). Generally, this result is expected because DVMs account for successional lags in range shifts, even if assuming unlimited dispersal (Hickler et al. 2012), while BEMs assume that species distributions are in climatic equilibrium and do not address the question of how long it will take for the species to establish viable populations in areas projected to be suitable in the future (but see Engler and Guisan 2009; Engler et al. 2009 for approaches that account for dispersal limitation). However, most comparisons have been conducted with limited geographic coverage, or with 1–3 species. Therefore, to fully understand the implications of using various approaches, we still lack comparisons in continental-scale Europe with a broad set of species with different characteristics in different biogeographic regions.

In our study, we compare current and future projections of a widely used DVM (LPJ-GUESS, Smith et al. 2001, parameterized for major European tree species, and PFTs for shrubs by Hickler et al. 2012) with a widely used BEM approach (BIOMOD platform, Thuiller et al. 2009b) for 14 common tree species across Europe. Thereby, we cover a larger geographic extent than earlier comparison studies, and more tree species. The large extent is important because model performance may depend on biogeographic region, as BEMs have high predictive performance when modeling species at range margins (Luoto et al. 2005). Cold tolerance imposes stricter control on species distributions compared to drought limits in the south (Normand et al. 2009), and thermal niches also tend to be more conserved in relation to cold tolerance (Pellissier et al. 2013). This means that abiotic control on geographic distribution may be stronger in cold boreal environments compared to that in the south, which may manifest as improved model predictive performance. Both the Mediterranean and Northern Europe are projected to be subjected to severe velocities of climate change (Giorgi and Coppola 2009; Giorgi and Lionello, 2008), and thus quantifying the model agreement by biogeographic region is important for pinpointing potential uncertainties.

Furthermore, LPJ-GUESS simulates tree population dynamics, competition for resources, and succession at a higher level of detail than the other DVMs that have been the focus of earlier model comparisons (Cheaib et al. 2012; Gritti et al. 2013; Keenan et al. 2011; Morin and Thuiller 2009). Only this detail makes it possible to parameterize major tree species in a generalized modeling framework that can be applied with PFTs at the global scale (Hickler et al. 2012). LPJ-GUESS, for example, accounts for differences in shade tolerance (life history strategy) between tree species, which might be important for successional dynamics and lag times under climate change. Early successional species often have high growth rates, good dispersal abilities, but limited competitive power (Tilman 1994), suggesting that they would be able to track the shifting climate efficiently, but would later be outcompeted from suitable climatic areas by more competitive, late successional species, which often have higher competitive ability (Meier et al. 2012). LPJ-GUESS explicitly simulates these processes (except dispersal limitations, but assumes a higher establishment rate for pioneer tree

species after disturbance) while BEMs do not. Therefore, the BEM and DVM results are potentially most in agreement for the present climate and for species with high competitive ability (i.e. late successional species), and have lower agreement for early successional species. This trend may be reversed in the future, as early successional species would be first to reach dominance in a new climatically suitable habitat. Analyzing and understanding these differences between model results is crucial for interpreting the results. Following this reasoning, we hypothesized that

1. The BEM approach would project greater range shifts than DVM, but the differences would level out when the DVM projections are given more time to reach equilibrium with the changing climate
2. Late successional species with good competitive abilities (high individual longevity and high shade tolerance) will show higher agreement between the models (both in baseline climate and equilibrium scenario) than early successional species, as dominant competitors may outcompete early successional, inferior species from climatically suitable space
3. Early successional species with inferior competitive ability (low longevity and low shade tolerance) will show relatively higher agreement at the end of the century under climate change (non-equilibrium situation), as they will be able to become substantially abundant in climatically suitable areas more quickly in the DVM framework
4. The agreement between the two approaches will vary geographically and be higher for boreal species.

2. Material and Methods

2.1. Climate and species distribution data sets

Baseline and future climate data for Europe (described in Fronzek et al. 2012) were obtained from the EU project ALARM. The data set covers the years 1901–2100 with 10' x 10' spatial resolution and consists of monthly values for temperature, cloud cover, and precipitation. The climate data for 2001–2100 were derived from the HadCM3 model, driven by the SRES A2 emission scenario. Historical (1901–1998) atmospheric CO₂ concentrations for DVM were obtained from McGuire et al. (2001) and Keeling and Whorf (2009) for years 1999 and 2000. Projected (2001–2100) CO₂ concentrations were obtained from the Intergovernmental Panel on Climate Change (IPCC) (Prentice et al. 2001, Appendix II).

For BEM parameterization, five bioclimatic variables were used, determining vegetation distribution on a continental scale: total annual growing degree days (GDD₅) (Sykes et al. 1996; Woodward 1987), mean temperature of coldest month (MTC) (Prentice and Helmsaari 1991; Thuiller et al. 2005), annual thermal oscillation (García-López and Allué 2011), summer (JJA) precipitation (Benito Garzón et al. 2011; Czúcz et al. 2011; Ruiz-Labourdette et al. 2012), and the moisture index (Hobbins et al. 2001; Svenning and Skov 2004). For BEM modeling, averages for 1961–1990 (“baseline”), 2021–2050, and 2071–2100 were calculated from the climate data. A more detailed description of the variables is given in Table S1. The derivation of bioclimatic limits for the DVM is described in the model description of LPJ-GUESS (see below).

Distribution data of 14 common European tree species (*Abies alba*, *Betula pendula*, *Betula pubescens*, *Carpinus betulus*, *Juniperus oxycedrus*, *Pinus halepensis*, *Quercus pubescens*,

Quercus ilex, *Quercus coccifera*, *Corylus avellana*, *Quercus robur*, *Picea abies*, *Pinus sylvestris*, and *Fagus sylvatica*) were obtained from Atlas Florae Europaeae (hereafter AFE) on an approximately 50 x 50km grid. AFE is an ongoing project (began in 1965) mapping the distribution of vascular plants in Europe, coordinated by the Finnish Museum of Natural History (<http://luomus.fi/en/atlas-florae-europaeae-afe-distribution-vascular-plants-europe>), and maps of species distributions have been published in several volumes between 1972 and 2013. For our study, data sets of species' distributions were obtained in electric grid format from the AFE secretariat (see supplementary figures S7–S20 for visualization of distribution data).

2.2. Bioclimatic Envelope Models

We produced an ensemble of bioclimatic envelope models using seven modeling algorithms available in the BIOMOD platform (Thuiller et al. 2009b): generalized linear models, generalized additive models, classification tree analysis, flexible discriminant analysis, artificial neural networks, multiple adaptive regression splines, and random forests. These are models frequently utilized in BEM modeling studies (França and Cabral 2015; Heikkinen et al. 2012; Marmion et al. 2009; Meller et al. 2014).

We built a consensus projection from all individual model runs to account for variability in individual model projections (Araújo and New 2007; Ranjitkar et al. 2016) for our study area grid cells with the future climate data. Consensus (or ensemble) projections also perform better when modeling range-shifting species (Araújo et al. 2005; Araújo and New 2007). We used the consensus to project species' distributions in the current climate (1961–1990, “baseline”) and in two future time periods: 2021–2050 and 2071–2100 with A2 SRES scenario. We used the models built on the 50 x 50km resolution to project species distributions to the 10' x 10' grid (Meller et al. 2014; Thuiller et al. 2005). Variable importance in the BIOMOD consensus prediction was evaluated with a permutation procedure (see Thuiller et al. 2009b for details). Additional details of the BEM parameterization can be found in the electronic supplementary material.

2.3 Dynamic Vegetation Model: LPJ-GUESS

LPJ-GUESS (Smith et al. 2001) is a flexible modeling framework for simulating the distribution of PFTs or tree species, vegetation types and dynamics (succession adopting a forest gap model approach), and biogeochemical cycles (carbon, water and, recently for the global version with PFTs but not included here, nitrogen (Smith et al., 2014)). It is process-based, as the competition between trees (PFTs or species), shrubs, and grasses emerges from their functional traits (Hickler et al. 2012). It shares many ecophysiological process representations with the widely used Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM, Sitch et al. 2003), but vegetation dynamics and vegetation structure are simulated at a higher level of detail, which makes it possible to parameterize the model for particular tree species, at least in relatively species-poor temperate and boreal regions (Hickler et al. 2012, 2004).

Simulated plant-physiological processes include photosynthesis and plant respiration, and carbon allocation along with the exchange of carbon and water between the vegetation, soil, and atmosphere. The model also includes disturbances by fire and a generic patch-

destroying disturbance, representing, e.g., pest attacks and the effects of windstorms. To represent the vegetation of a model grid cell (homogenous climate and soil texture input), the results of a number of replicate patches (which differ from each other because of stochastic tree establishment, mortality, and patch-destroying disturbance; each 0.1 ha large) are averaged, here 200.

We used the results from a version parameterized for major European tree species and PFTs by Hickler et al. (2012), who provide details about the model version and setup used here. Bioclimatic limits determine which species can occur in a model grid cell (environmental filtering), and these were fitted by visually comparing continental-scale species distributions with the geographic variation in the bioclimatic variables (Hickler et al. 2012). The following limits were used: minimum growing degree day sum above 5°C (GDD) for establishment (the effective GDD for broadleaved species is also affected by delayed budburst to avoid spring frosts), the minimum mean monthly temperature for survival, and the minimum growing season average fraction of plant-available soil moisture in the upper soil layer for establishment.

If tree species can coexist based on their bioclimatic limits, competition between trees, shrubs, and herbaceous vegetation is simulated adopting a forest gap model approach. Main plant traits that determine the competition between tree species in this model version are e.g. the shade-tolerance class, phenology (evergreen *versus* summergreen), root distribution across the two soil layers, and the maximum non-stressed longevity. There is a trade-off between high establishment under favorable conditions at the forest floor (such as after disturbance) and high growth rates for shade-intolerant species (such as *B. pubescens*) on one hand and establishment under conditions of low light availability and survival with low growth rates (such as *P. abies*) on the other. Tree dispersal was unlimited in the model, but transient responses of tree succession are captured (Hickler et al. 2012).

The modeling protocol is fully described in Hickler et al. (2012), and followed a standard setup for LPJ-GUESS. In short, the simulation began from bare ground, and the model was spun up for 400 years to reach approximate equilibrium with the climate and CO₂ concentration at the beginning of the 20th century, before using historical and future climate scenarios and CO₂ data as model input. For this spin-up period, historical climate data from the first 30 years of the century were used repeatedly, detrended for temperature. The same approach was used for the long-term equilibrium simulation, repeatedly using the last 30 years of the climate model output (2071–2100) and the average CO₂ concentration of that period for 400 additional years after 2100.

2. 4. Model comparison

We compared the model predictions in four different time frames: “baseline” (1961–1990), and two time windows in the future: 2021–2050 and 2071–2100. In addition to these, DVM end-of century projections were compared to equilibrium simulation results to assess how much of the potential differences during the 21st century were caused by successional processes, modeled in the DVM but not in the BEMs.

2.4.1. Overall agreement

The predictive performances of both approaches under baseline climate were estimated against AFE distribution data. Next, a general agreement for all time periods and species was estimated by comparing leaf area index (LAI) values from LPJ-GUESS with occurrence probability from the BEMs. Finally, a general agreement for all time periods was estimated by comparing the summed presence-absence projections of all species. The magnitude of projected range shifts was compared by calculating latitudinal range centroids and shifts in their distribution. These analyses are detailed below.

Model predictive performance under baseline climate was evaluated with True Skill Statistic (TSS), sensitivity and specificity against AFE data. Sensitivity is the proportion of correctly predicted presences, and specificity is the proportion of correctly predicted absences. TSS is defined as sensitivity + specificity - 1, and, contrary to Cohen's Kappa, is independent of the prevalence of presence observations in the input data (Allouche et al. 2006). For calculating validation statistics, the BEM ensemble was used to project species distributions to the AFE grid. The predicted probabilities of species occurrence in a grid cell were converted to presence-absence predictions using cut-off levels maximizing ensemble performance when evaluated using the TSS score (Supporting information, section 1.5). To assess DVM performance, LAI values were scaled to 0–1 (see below) and transferred to the AFE grid by taking the maximum LAI for each species in each grid cell. Subsequently, the cut-off threshold maximizing TSS was defined for each species, and using this threshold, the LAI predictions were converted to presence-absence. Species-specific cut-off levels were used, as different species tend to have very different LAI values (Supporting information, section 1.5.2.).

We investigated the overall agreement between the models by comparing the occurrence probabilities from the BEMs to LAI values from LPJ-GUESS, as these two may be interpreted as surrogates of abundance, reflecting relative suitability of each grid cell for a particular species. Occurrence probability is a reasonable proxy of local abundance (Thuiller et al. 2014; Weber et al. 2016), although not for population growth rate or site carrying capacity (Thuiller et al. 2014). LAI describes the ratio of one-sided leaf surface area to ground surface area, and has been used as a successful proxy for the distribution of potential natural vegetation on undisturbed sites (Hickler et al. 2012; Sitch et al. 2003) and species distributions (Gritti et al. 2013; Kramer et al. 2012, 2010). LAI values were averaged from annual LPJ-GUESS LAI outputs for the study periods for each species.

We compared the projected abundances during the different time periods by calculating Spearman correlation scores for each species. A single correlation score was calculated for a species to represent “overall agreement” between the two models. Spearman's rank correlation was applied as the LAI, and occurrence probabilities did not show linear relationship under graphical inspection (data not shown). As the BEM probability values range from 0 to 1, for comparison purposes we also scaled LAI values to range from 0 to 1 for each species, so that LAI was scaled between 0 and the maximum species-specific LAI value in all grid cells.

We calculated the summed agreement of presence-absence predictions for all 14 species in all four time frames to highlight the spatial distribution of agreement or disagreement of BEMs and DVMs. If both models predicted presence or absence, a cell was designated a value of 1. If model predictions differed, the cell was given a value of 0. These values were

summed across all species, consequently a score of 14 indicating high agreement between BEM and DVM, and 0 a very low agreement.

To compare the magnitude of projected range shifts, we calculated the range centroids projected by both models with Equation (1.), following Cheung et al. (2009):

$$ML = \frac{\sum_{i=1}^N A_i \times Lat_i}{\sum_{i=1}^N A_i} \text{ (Equation 1)}$$

where ML is the calculated range centroid, A_i is the predicted abundance (probability of occurrence or LAI value) in the i th grid cell and Lat_i is the latitude of the i th grid cell, where predicted abundance > 0. The magnitude of the projected range shift in each time frame was calculated as the difference between the latitude of future and baseline range centroids for each species. Significance of the differences in the range shifts projected by the two models was analyzed with the Wilcoxon signed-rank test, as the range shift values were not normally distributed. Pairwise comparisons were performed because we considered reasonable that the two modeling approaches applied for each species should be considered as two related samples.

2.4.2. Assessing model agreement by species traits and ecosystems

We tested whether the correlations between BEM and DVM projected abundances in the different time frames would depend on species-specific competitive traits (shade tolerance and longevity) or geographic distribution (Table S3) with ANOVA, following backwards stepwise model selection, with a p-value of 0.05 as the acceptance threshold for the variable into the model. Residual patterns were visually investigated to identify heteroscedasticity. In such cases, residual variance structures were applied with generalized least squares regression using Restricted Maximum Likelihood (REML) estimation (Zuur et al. 2007). Model improvement was investigated with likelihood ratio tests (Zuur et al. 2009), but as none of the residual variance structures significantly increased model performance, ANOVA analyses was applied.

In addition, we investigated whether the successional lags in the DVM framework (differences in projected range centroids (latitudes) between 2071–2100 and equilibrium) would be greater for late successional species with good competitive abilities (i.e. high shade tolerance). To investigate this, we analyzed successional lag as a function of shade tolerance for each species with ANOVA, however, as in this case REML estimation indicated substantial ($p < 0.01$) improvement in model performance, variance structures for each shade tolerance classes were applied. The significance of the main effects (shade tolerance) was investigated with likelihood ratio tests.

2.4.3. Comparing climatic niche width

To investigate how the models describe the species' climatic tolerances, and how severely the species would be subjected to possibly adverse climatic conditions in the future, we quantified the projected bioclimatic niches under baseline and future climate, consisting of two of the input variables known to control the northward and high altitude tree distributions at a continental scale (Prentice and Helmisaari 1991; Woodward 1987): annual GDD₅ and mean temperature of the coldest month, and examined the climatic niche width

along with the potential shift in climatic niche under future climate change (see supplementary information section 2.3. and 2.4. for details).

3. Results

3.1. Model agreement under baseline (1961-1990) climate

The BEMs had higher predictive performance (TSS score) than the DVM (LPJ-GUESS) when validated against the AFE distribution data (Table 1), rising mostly from higher sensitivity values in the BEMs. This was caused by the DVM generally producing more restricted geographic distributions than the BEMs (Figs S7–S20, Table S3).

BEM and DVM projections under baseline climate diverged most for *A. alba* and *Q. robur* (Table S3), which were also species with low predictive performance in the DVM (Table 1). Annual GDD₅ and mean temperature of the coldest month were the variables with the highest importance across all species in the BEMs (Supplementary information section 1.3).

Table 1. TSS, sensitivity, and specificity of BEMs and the DVM under baseline climate (1961-1990). *Abi_alb* = *Abies alba*, *Bet_pen* = *Betula pendula*, *Bet_pub* = *Betula pubescens*, *Car_bet* = *Carpinus betulus*, *Jun_oxy* = *Juniperus oxycedrus*, *Pin_hal* = *Pinus halepensis*, *Que_pub* = *Quercus pubescens*, *Que_ile* = *Quercus ilex*, *Que_coc* = *Quercus coccifera*, *Cor_ave* = *Corylus avellana*, *Que_rob* = *Quercus robur*, *Pic_abi* = *Picea abies*, *Pin_syl* = *Pinus sylvestris*, *Fag_syl* = *Fagus sylvatica*. BEMs: Bioclimatic Envelope Models, DVM: Dynamic Vegetation Model (LPJ-GUESS).

Species	BEM			DVM		
	Sensitivity	Specificity	TSS	Sensitivity	Specificity	TSS
<i>Abi_alb</i>	0.949	0.827	0.776	0.578	0.85	0.429
<i>Bet_pen</i>	0.965	0.765	0.730	0.877	0.781	0.658
<i>Bet_pub</i>	0.972	0.696	0.669	0.862	0.69	0.551
<i>Car_bet</i>	0.963	0.798	0.762	0.922	0.669	0.592
<i>Jun_oxy</i>	0.968	0.786	0.754	0.859	0.799	0.658
<i>Pin_hal</i>	0.990	0.816	0.806	0.903	0.835	0.737
<i>Que_pub</i>	0.972	0.735	0.707	0.867	0.618	0.486
<i>Que_ile</i>	0.990	0.775	0.765	0.932	0.723	0.655
<i>Que_coc</i>	0.973	0.845	0.818	0.951	0.795	0.746
<i>Cor_ave</i>	0.917	0.763	0.680	0.906	0.592	0.498
<i>Que_rob</i>	0.976	0.724	0.700	0.879	0.508	0.387
<i>Pic_abi</i>	0.989	0.825	0.814	0.945	0.839	0.784
<i>Pin_syl</i>	0.949	0.835	0.784	0.889	0.763	0.652
<i>Fag_syl</i>	0.970	0.830	0.800	0.727	0.841	0.568

The more restricted geographic distributions predicted by the DVM may also have contributed to the BEM range centroids averaging higher projected latitudes under baseline climate (Table 2), although the range margin latitudes were similar (Fig. S7–20). Under baseline climate, the boreal conifer *Pinus sylvestris* had the highest divergence in predicted latitude of range centroid (Table 2). After this, the highest divergence occurred for *Quercus ilex* and two of the Mediterranean species: *Pinus halepensis* and *Juniperus oxycedrus* (Table 2).

Table 2. Differences (BEMs - DVM, in latitudes) of projected range centroids for baseline (1961–1990) and equilibrium. Explanations of abbreviations of species names are given in the caption of Table 1. BEMs: Bioclimatic Envelope Models, DVM: Dynamic Vegetation Model (LPJ-GUESS).

	Abi_alb	Bet_pen	Bet_pub	Car_bet	Cor_ave	Fag_syl	Jun_oxy	Pic_abi	Pin_hal	Pin_syl	Que_coc	Que_ile	Que_pub	Que_rob
Baseline (1961 – 1990)	0.24	0.92	3.17	0.46	0.82	0.44	4.66	2.58	3.95	7.79	3.03	4.40	1.68	2.09
Equilibrium	4.75	1.41	1.28	0.49	2.25	3.18	7.63	2.45	8.34	6.60	5.89	7.11	2.14	4.95

3.2. Magnitude of the projected range shifts

The BEMs produced significantly greater latitudinal range shifts in the two future time periods, 2021–2050 and 2071–2100 (Wilcoxon signed rank sum test, $W = 188$, $p = 1.95 * 10^{-5}$ and $W = 186$, $p = 2.89 * 10^{-5}$, $n=14$, Fig.1a, b). The BEMs produced greater range shifts also in the equilibrium situation ($W = 159$, $p = 0.0027$, $n=14$), although overall the differences leveled out (Fig. 1c). Mediterranean species showed the highest disagreement in projected range centroids between the models in equilibrium (Table 2), which arose mainly due to the BEMs predicting larger range expansions along with contractions, whereas contractions were much more modest in the DVM (Figs S13, S15, S17–19). The range centroid divergence of *P. sylvestris* (Table 2) arose from low LAI values predicted by the DVM in Central Europe (Fig. S21). Despite this, the presence-absence projections between the models were rather consistent (Fig. S16).

The estimated range shift magnitudes for individual BEM models within the ensemble were quite consistent, and no similarities or dissimilarities between individual BEM algorithms and the DVM projection could be seen across species (Fig. S2). This indicates that differences between the two approaches were not caused by averaging the models within the BEM approach.

The range shift estimates were less species-specific in the BEMs, whereas responses were more variable in the DVM (Fig. 1a, b). Range shifts projected by the BEMs straightforwardly reflect the shift in climatic variable values that the models were fitted to, whereas responses were more divergent in the DVM, reflecting the combined effects of climatic shift, competition, and successional lags (Fig. 1d). Differences between the models were somewhat reduced at equilibrium conditions (Fig. 1c), showing that differences in the two preceding time periods (2021–2050 and 2071–2100) were partly caused by successional time lags influencing DVM projections. Especially late-successional, shade-tolerant species showed long delays in their responses in the DVM (Fig. 1d), but this was not statistically significant ($L = 3.549$, $p = 0.169$, $n = 14$). The temperate *Abies alba* showed particularly pronounced northwards shifts between the end of the century and the equilibrium run. *A. alba*, which is relatively sensitive to low minimum winter temperatures, could expand its range northward, as it benefited from warmer winters, but as a shade-tolerant species, the response was delayed (Fig. 1b, d). Although the shift in mean latitude of this species was

more pronounced in the DVM prediction, both models predicted the presence of *A. alba* at the Baltic Sea coast (Fig. S7), and the BEMs also predicted presence in high-elevation areas of Central Europe, whereas the DVM did not (Fig. S7).

3.3. Overall agreement between BEM and DVM results

When examining the correlation scores between species abundances, the overall agreement between the two approaches was highest under baseline climate, declined towards the end of the century, and subsequently increased in the equilibrium (Fig. 2a, b). Highest agreement was attained in boreal species (Fig. 2a), which showed a consistent pattern through the different time frames. The low agreement on *Q. robur* and *C. avellana* was caused by BEMs projecting higher range expansions and contractions, and the DVM projecting absence of the species in the Alps and in high-elevation areas of Scandinavia (Fig. S11, S20).

When summed presence-absence predictions were examined, the models reached highest agreement in boreal areas (Fig. 3a), arising from relatively high agreement for boreal species present in these areas (Fig. 2a). With proceeding climate change, model agreement declined (Fig. 3b–c), but was again somewhat higher in the equilibrium situation (Fig. 3d). Also, the models showed low agreement in mountainous areas such as the Alps. During 2071–2100, notable uncertainty was also observable in the transition zones between temperate and boreal ecosystems (Fig. 3c), mainly in southern Sweden and Finland, which also persisted in the equilibrium scenario (Fig. 3d).

3.4. The effects of competitive traits and geographic range on model agreement

The competitive traits (shade tolerance and individual longevity) did not have an effect on overall model agreement during any time period when assessed with correlation scores (Fig. 4a–b, table S4). However, boreal species had significantly higher correlation scores in 2071–2100 ($p=0.025$) and marginally significant scores ($p=0.08$) in the equilibrium (Fig. 4c, Table S4). In general, the agreement was higher for boreal species ($n=3$) for all time scales (Fig. 4c). This pattern was also confirmed by analyzing presence-absence predictions, which yielded similar results (Fig. S4).

3.5. Predicted shifts in biogeographic regions

Both modeling approaches predicted substantial contraction of the southern distribution of the boreal species studied (Fig. 5a–c). *B. pendula*, classified as a temperate species in our study, exhibited a similar pattern (Fig. S8). Both models also predicted northward shifts in temperate and Mediterranean ecoregions (Fig. 5e–f, 5h–i), although responses were more heterogeneous at the species level. Both models predicted temperate species to shift towards areas around the Baltic Sea, and experience range contractions in southern parts of their distributions. Range contractions for temperate and Mediterranean species were greater in BEMs than in the DVM (Fig. 5e–f, 5h–i).

4. Discussion

Comparison of the two approaches yielded important insights, which can help to guide the interpretation of results from the two applied modeling approaches in other studies. Although the BEMs performed better in modeling distributions under baseline climate, as observed by earlier comparison studies (Cheaib et al. 2012; Kramer et al. 2010), future predictions showed divergent patterns, with some consistent features.

4.1. Magnitude of projected range shifts and successional processes

As hypothesized (hypothesis 1), the BEMs projected larger northward range shifts than the DVM, which is in agreement with results from earlier comparison studies (Cheaib et al. 2012; Kramer et al. 2012, 2010; Morin and Thuiller 2009). This pattern was consistent for all time periods, including the equilibrium scenario. The BEMs projecting generally larger range contractions at the southern distribution edge was a main driver behind the pattern in equilibrium. As suggested by Kramer et al. (2012), this may be caused by the BEMs assuming an equilibrium with baseline geographic distributions and climatic variables, which, when extrapolated into the future, may in certain cases yield predicted abundance declines with no clear biological causal mechanism (see section 4.3.).

The increase of model agreement in the equilibrium scenario compared to the end of the century highlights the importance of successional processes. Results here suggest that time lags are particularly important for late-successional species, which are often important ecosystem engineers, and have high numbers of associated species (Ellison et al. 2005). Similar slower responses of late-successional species have previously been found by Meier et al. (2012), caused by slower growth rates and poorer dispersal abilities than early-successional species.

Successional lags are not the only important difference between the two approaches when interpreting the simulated range shift magnitudes, because the DVM simulated smaller range shifts even during the equilibrium run. These results suggest that complex competitive interactions, which are more fully covered in the DVM, may reduce range shifts compared to those expected from statistical approaches that relate occurrences to climate alone. Physiological CO₂ effects are one such potentially important factor (Cheaib et al. 2012; Keenan et al. 2011; Reyer 2015), which are only accounted for in the DVM. CO₂-driven increases in photosynthesis, NPP, and canopy density, for example, disfavor pioneer species. However, we did not analyze these effects in detail because their magnitude is uncertain (Hickler et al. 2015). In addition, the simulated geographic distributions are rather insensitive to physiological CO₂ effects in this model version (Hickler et al. 2009). Also, the model may not capture between-species differences in its response, as observed in certain cases (e.g. Dawes et al. 2010), and how and why tree species differ in their responses is not known. (See also section 4.2 below).

4.2. Effects of competition

We observed no overall consistent effect of competition on the agreement between the two modeling approaches, thus our hypotheses 2 and 3, related to the effects of competitive traits on model agreement, were not confirmed. However, effects of competition were very evident, particularly for shade-intolerant species. The high divergence in the latitudes of baseline range centroids in the boreal conifer *Pinus sylvestris* was caused by the DVM

predicting low LAI values for *P. sylvestris* in Central Europe (Fig. S21), where it was outcompeted by more shade-tolerant broad-leaved species. This pattern is consistent with the potential natural vegetation of the area (Bohn et al. 2000; Hickler et al. 2012). The divergence in Mediterranean species increased in the future, with BEMs predicting distribution shifts towards Central Europe, while shifts predicted by the DVM were very moderate, which we interpret to arise from competition from prevailing temperate species (Fig. 5h–i). Competition also explains the decrease in latitudinal range shift in the DVM prediction for *P. sylvestris* during the 2071–2100 period and in the long-term equilibrium results. As a fast-growing species with high colonization potential, *P. sylvestris* could initially expand its range at the northern range margin, but, in the long term, *Picea abies*, which is shade-tolerant, increasingly outcompeted *P. sylvestris*. *P. abies* reached the highest agreement between the BEM and DVM results of all species in all of the studied time periods, because it was simulated to have highly competitive traits, and thus may be considered a dominant competitor compared to other species throughout most of its potential range. In the DVM (LPJ-GUESS) simulations, other shade-intolerant species, such as *Betula pendula*, also suffered from competition from more shade-tolerant species in the long term (equilibrium run), as net primary productivity (NPP) and forest cover increased in a warmer climate and because of CO₂ fertilization effects. However, as the applied model version does not account for nutrient limitations, the real magnitude of the CO₂ effect, which is highly debated (e.g. Hickler et al. 2015), will be lower than in the model. Elevated CO₂ did not affect the growth of *P. abies* in a highly nutrient-limited stand in northern Sweden (Kostiainen et al. 2009), and CO₂ levels only had a minor effect on the range contraction magnitude of *P. sylvestris* in France (Cheaib et al. 2012). On the other hand, NPP will probably increase in many northern forests as nitrogen mineralization rates increase with elevated temperature (e.g. Wårlind et al. 2014), and the nutrient status in the soil is also one main factor determining the competition between *P. abies* and *P. sylvestris*, which is not accounted for in the model version applied here. Accounting for nutrient dynamics in the model could increase the competitive ability of *P. sylvestris*, but implementing the competition between the two species for nitrogen in a process-based framework would be very challenging. The high agreement of both approaches on *P. abies* suggests that especially on dominant species, both models are able to capture ecologically relevant processes which exert climatic control on geographic distributions.

Both modeling approaches applied here model the “realized” environmental niche of the species; however, competitive processes are explicitly described in the DVM approach, whereas variation due to competitive (and other) effects potentially affecting the present distribution will be attributed to climatic factors (the assumption of climatic equilibrium in the BEMs, Guisan and Thuiller 2005), which may cause unexpected consequences when extrapolating to the future. In this sense, the DVM approach may be considered more realistic. However, despite the DVM only relying on bioclimatic tolerance limits based on physiological mechanisms thought to be important for absolute range limits, these were also calibrated with observed distributions, thus partly suffering from similar limitations.

4.3. Bioclimatic tolerance limits as possible causes for differences

The way in which the relationship to climatic factors is quantified in each approach is one reason for the projection differences between the two models. Bioclimatic limits only define absolute limits in LPJ-GUESS. For example, minimum GDD₅ for establishment constrains the

distribution at the northern range limit and at high altitudes (together with the minimum temperature for survival). GDD_5 is not used to constrain the distribution southwards, which instead is constrained by the maximum winter temperature (chilling requirement) for northern species and the simulated available soil water content as a proxy for drought. In addition, competition from species that are better adapted to a warmer climate in terms of their photosynthetic optima and respiration rates is accounted for. Contrastingly, the BEMs estimate species' tolerances between the current distribution of species and climate (e.g. GDD_5 values), potentially using each variable to constrain the entire range. At a continental scale, growing season length mainly controls the northern distribution edge of species, as flowering and seed ripening may be dependent on sufficient accumulated GDD days (Woodward 1987, but see Körner 2003). However, as the growing seasons lengthens in the future, the BEMs may project the species' southern distribution edge to contract, as the GDD values move out of the climatic niche that was quantified in the model calibration phase, thus causing extensive contractions in the southern distribution edge without linking this contraction to a specific mechanism (Kramer et al. 2012). Together with competitive interactions in the DVM discussed earlier, these differences caused the major discrepancies between the models for Mediterranean species. The extrapolation of BEMs into future conditions is one of the major uncertainties within this method (Buisson et al. 2010; Pearson et al. 2006). In this sense, the DVM projections, which rely on descriptions of specific physiological processes, may yield more accurate estimates of causal processes defining population dynamics at the contracting edge (Kramer et al. 2012).

It is interesting that the projections in both modelling approaches were very similar for *P. abies*. Several studies have identified *P. abies* to highly sensitive to drought and storm damage (Altman et al., 2017; Schurman et al., 2018; Vitali et al., 2017). At low elevations, *P. abies* stands are vulnerable to drought, especially when stand age is high (Primicia et al., 2015; Schurman et al., 2018). The high agreement between BEMs and the DVM arose from the two models projecting similar contractions at the southern distribution edge of *P. abies*. This suggests that vulnerability to drought is the major factor controlling the southern distribution edge on the continental scale, and that both approaches were able to capture this response into the projections, which is in agreement with other projections for *P. abies* under climate change (Dyderski et al., 2018; Hanewinkel et al., 2013).

Under future climate change, the more conservative geographic range shifts projected by the DVM caused the climatic factors to shift in relation to the projected species distributions (Fig. S5). This was caused by climatic conditions shifting more rapidly than simulated species abundances in the DVM framework, indicating a "climatic debt" (Devictor et al. 2012). As the DVM includes a component of population establishment in the predictions, it can yield temporally more accurate projections compared to the BEMs, which model instantaneous shifts. This means that in the future, local populations will be subjected to climatic conditions they are not adapted for, before they have time to migrate to areas of suitable climate. It is important to note that although unlimited dispersal was assumed in the DVM, because of successional processes, projected distributions still lagged behind the shifting climate, causing large shifts in bioclimatic niches. In reality, geographic distribution shifts are likely to be even slower due to the time required for dispersal, influenced by dispersal barriers such as habitat fragmentation (Meier et al. 2012). Because of this, the bioclimatic shifts that European tree species will likely be exposed to in the future are probably even larger than estimated here.

4.4. Effect of geographic range on model agreement

Model agreement varied geographically and agreed best on the three boreal species studied, confirming hypothesis 4. This higher agreement can be caused by species distributions being more strongly under control by abiotic factors in harsher conditions, and on the contrary, the competitive biotic interactions to be more important in favorable conditions in the south. As BEMs have been shown to be very effective in modeling species distributions at the margins of their ranges (Luoto et al. 2005), and on species with restricted distributions, i.e. species with distributions strictly controlled by climatic factors (Marmion et al. 2009), the higher agreement concerning boreal species could arise from better BEM performance. In our study, the BEMs built on boreal species tended to have higher TSS scores than for temperate or Mediterranean species.

Species in boreal ecosystems have limited capability to migrate polewards, as the land mass slips into the Arctic Ocean. The geographic ranges of all three boreal species in our study extend very far into the Arctic under the baseline and future climate, and thus extensive range shifts are not possible. Thus the models would reach reasonable agreement regarding the future projections by just quantifying similarly processes at the southern edge of the distribution (contracting edge), which explains the higher agreement between the BEMs and the DVM on these species during all time periods (Fig. 4c). A similar strong agreement by various models on the range shifts of boreal trees has also been reported from the eastern United States (Iverson et al. 2017), confirming this interpretation.

Our study also revealed that model agreement was consistently low under baseline and future climate in mountainous areas such as the Alps. Despite model agreement generally increasing in the equilibrium scenario, the agreement remained very low in this area. This indicates the high uncertainty related to modeling species distributions in such areas, which may arise from variable climatic conditions within a small geographic distance along an elevation gradient (Huntley et al. 1995). Certain species in mountainous areas, such as *A. alba*, may also be limited by post-glacial dispersal limitation, and are thus presently filling only part of their potential climatic niches (Svenning and Skov 2004), making modeling efforts challenging. Both our models, especially BEMs, predicted wider potential geographic distribution under baseline climate compared to observed distribution (Fig. S7), while also predicting a potentially suitable area in Scandinavia.

4.5. Robust results inferred from model comparison

Despite differences, several coherent patterns emerged across both models. Both approaches projected conifer species to mostly disappear from lowland areas of Central Europe. This is in agreement with similar results of substantial range contraction of *P. sylvestris* found by Cheaib et al. (2012) for France. Here, the range contraction applies to all boreal species in our study throughout Central Europe, indicating a substantial northward shift in the southern range of the boreal forest biome. The disappearance of boreal species, which are often important for the timber industry, may lead to major economic losses, as the more productive species are replaced by southern species with lower timber yields (Hanewinkel et al. 2013). Our results support this conclusion for future European forests.

Although projections regarding distribution shifts with temperate and Mediterranean species were more variable, both approaches consistently projected declines of temperate

species in Western Europe (southern Britain and France), and their subsequent displacement by Mediterranean species, a pattern also identified by Cheaib et al. (2012). Temperate species shifted their distributions northeast to Scandinavia and the eastern Baltic Sea, which is in agreement with previous studies utilizing BEMs (Hanewinkel et al. 2013) and indicating that the structure and functioning of forest vegetation in these areas will be substantially altered in the future, with likewise substantial negative impacts on forest economy. However, strong climate mitigation policies may result in less intensive climate change than what our simulations project (see Hickler et al. 2012 for more details).

The projections from either approaches or their combinations should not be treated as predictions, as both have intrinsic strengths and weaknesses. The model results can nevertheless guide adaptive management activities (Meineri et al. 2015), if managers are fully aware of the model assumptions and shortcomings (Dormann et al. 2012). Given the contrasting background assumptions of the two approaches (Dormann et al. 2012; Meineri et al. 2015), common patterns or disagreement may help evaluate the robustness of the projections and create more realistic models for particular applications (Connolly et al. 2017). Thus model comparisons are an important tool for highlighting the differences between model types and understanding their implications for future projections and their interpretation.

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Figure legends

Fig. 1. Projected range centroid shifts, compared to range centroids in baseline (1961-1990) a): BEMs, (b): DVM; (c): difference of projected shifts between the two approaches (BEM - DVM); (d): successional lag in the DVM (difference in latitudes between 2071–2100 and equilibrium) by shade-tolerance class. Explanations of abbreviations of species names are given in the caption of Table 1. BEMs: Bioclimatic Envelope Models, DVM: Dynamic Vegetation Model (LPJ-GUESS).

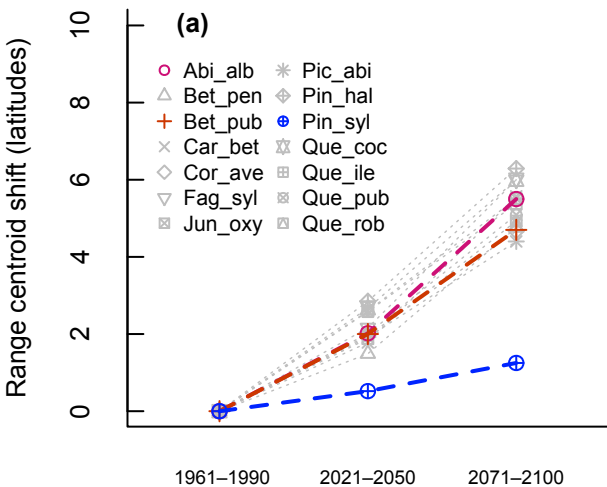
Fig. 2. Spearman correlation scores between LAI (Leaf Area Index) and probability of occurrence, projected for each species (a) and across all species (b). Explanations of abbreviations of species names are given in the caption of Table 1.

Fig 3. Summed agreement of BEMs and DVM presence-absence predictions across all species during the different time periods. BEMs: Bioclimatic Envelope Models, DVM: Dynamic Vegetation Model (LPJ-GUESS).

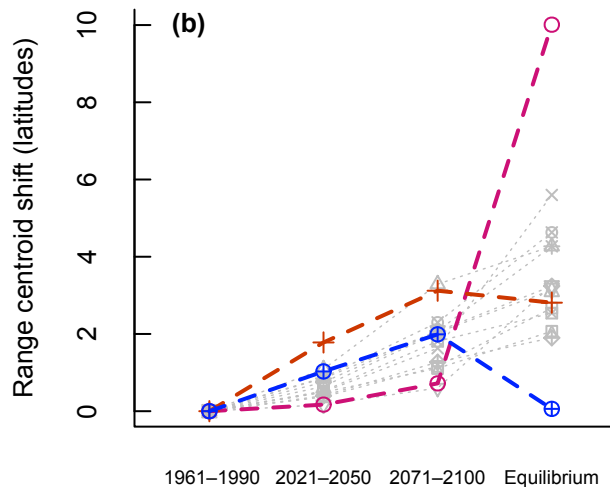
Fig. 4. Shade tolerance (a), individual longevity (b), and geographic range (c) plotted against model agreement (Spearman correlation score) in the baseline (1961-1990), future (2071–2100) and equilibrium scenarios.

Fig. 5. Shifts in biogeographical regions (species classified to a specific biogeographic region, Table S3) in the equilibrium scenario predicted by the two models (middle: BEM = Bioclimatic Envelope Models, right: DVM = Dynamic Vegetation Model, LPJ-GUESS) together with the baseline (1961 – 1990) observed distributions (left). Top row: boreal (N = 3), middle: temperate (N = 6), bottom: Mediterranean (N = 5). Color scale indicates the number of species in each grid cell.

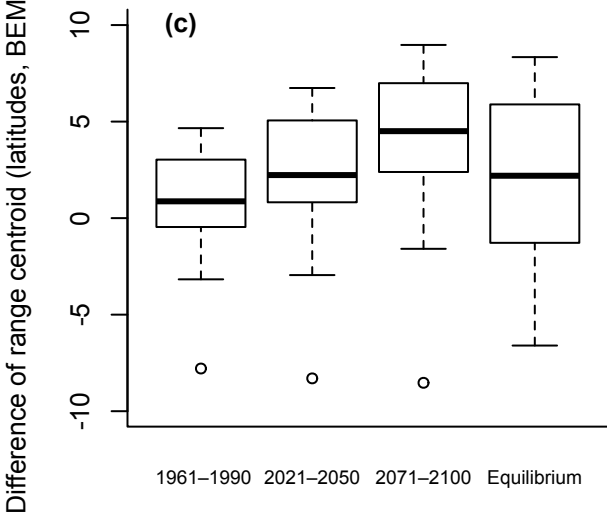
BEM-projected range shift



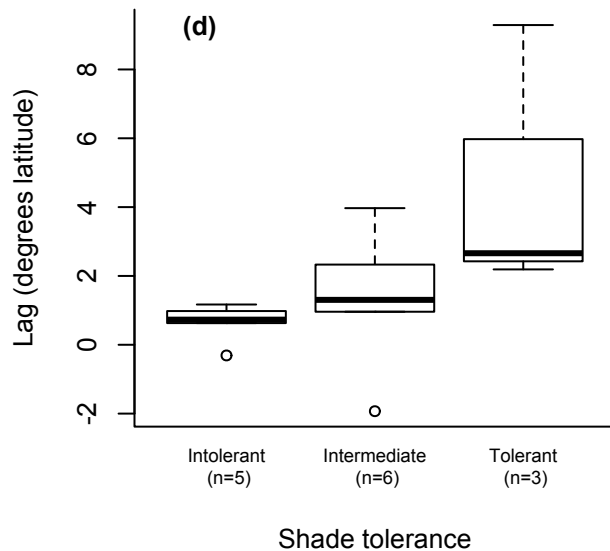
DVM-projected range shift



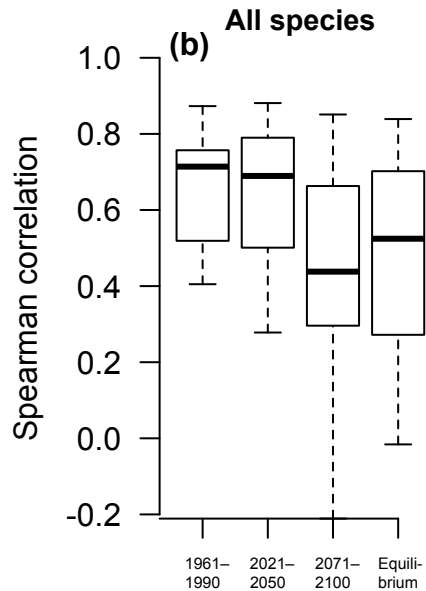
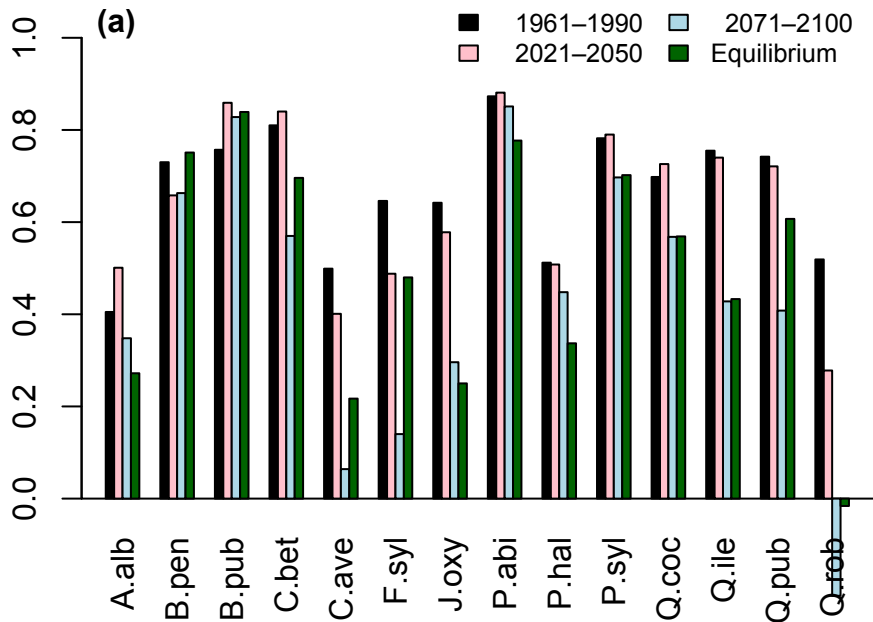
Differences in projections

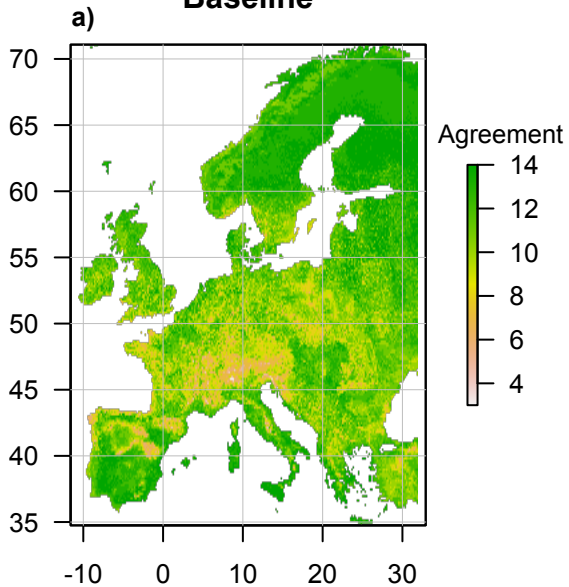
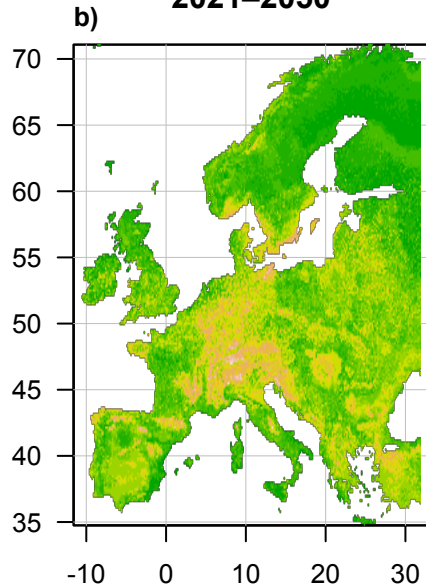
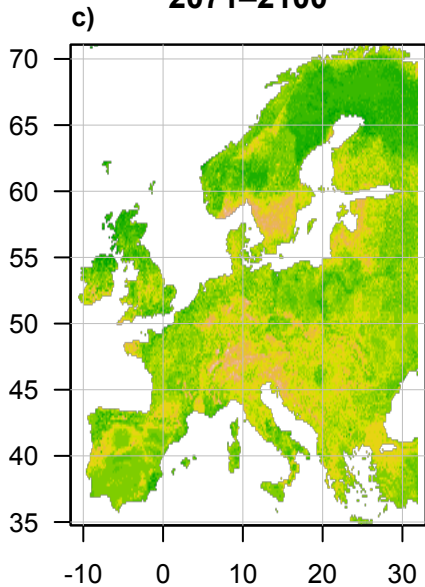


Lag by shade tolerance



Spearman correlation



Baseline**2021–2050****2071–2100****Equilibrium**