

Biotic and abiotic variables show little redundancy in explaining tree species distributions

Eliane S. Meier, Felix Kienast, Peter B. Pearman, Jens-Christian Svenning, Wilfried Thuiller, Miguel B. Araújo, Antoine Guisan and Niklaus E. Zimmermann

E. S. Meier (eliane.meier@wsl.ch), F. Kienast, P. B. Pearman and N. E. Zimmermann, Land Use Dynamics, Swiss Federal Research Inst. WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. – J.-C. Svenning, Ecoinformatics and Biodiversity Group, Dept of Biological Sciences, Aarhus Univ., Ny Munkegade 114, DK-8000 Aarhus C., Denmark. – W. Thuiller, Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Univ., Joseph Fourier, BP 53, FR-38041 Grenoble Cedex 9, France. – M. B. Araújo, Depto de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, I/José Gutiérrez Abascal, 2, ES-28006 Madrid, Spain, and 'Rui Nabeiro' Biodiversity Chair, CIBIO, Univ. de Évora, Largo dos Colegiais, PT-7000 Évora, Portugal. – A. Guisan, Dept of Ecology and Evolution, Inst. of Geology and Paleontology, Univ. of Lausanne, Biophore Building, CH-1015 Lausanne, Switzerland.

Abiotic factors such as climate and soil determine the species fundamental niche, which is further constrained by biotic interactions such as interspecific competition. To parameterize this realized niche, species distribution models (SDMs) most often relate species occurrence data to abiotic variables, but few SDM studies include biotic predictors to help explain species distributions. Therefore, most predictions of species distributions under future climates assume implicitly that biotic interactions remain constant or exert only minor influence on large-scale spatial distributions, which is also largely expected for species with high competitive ability. We examined the extent to which variance explained by SDMs can be attributed to abiotic or biotic predictors and how this depends on species traits. We fit generalized linear models for 11 common tree species in Switzerland using three different sets of predictor variables: biotic, abiotic, and the combination of both sets. We used variance partitioning to estimate the proportion of the variance explained by biotic and abiotic predictors, jointly and independently. Inclusion of biotic predictors improved the SDMs substantially. The joint contribution of biotic and abiotic predictors to explained deviance was relatively small (~9%) compared to the contribution of each predictor set individually (~20% each), indicating that the additional information on the realized niche brought by adding other species as predictors was largely independent of the abiotic (topo-climatic) predictors. The influence of biotic predictors was relatively high for species preferably growing under low disturbance and low abiotic stress, species with long seed dispersal distances, species with high shade tolerance as juveniles and adults, and species that occur frequently and are dominant across the landscape. The influence of biotic variables on SDM performance indicates that community composition and other local biotic factors or abiotic processes not included in the abiotic predictors strongly influence prediction of species distributions. Improved prediction of species' potential distributions in future climates and communities may assist strategies for sustainable forest management.

Effective nature management in the face of anthropogenic climate change challenges ecologists to improve predictions of how species distributions might respond to altered climate. Predictions of these responses are often generated with species distribution models (SDMs, Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006). SDMs most often relate presence/absence or abundance of species to abiotic variables such as climatic, topographic or edaphic factors, and are used to assess factors that potentially control species distributions and to predict the distribution of suitable habitat of species. Nonetheless, biotic interactions such as competition, mutualism, amensalism or commensalism also affect species distributions, in addition to the effects of abiotic factors (Connell 1961, Loehle 1998, Soberón 2007). The relative importance of

abiotic and biotic range determinants remains unclear. The tendency to omit biotic variables from models when predicting the effects of climate change does not eliminate the potential effects of biotic processes and adds an unknown amount of uncertainty to models used to predict climate change effect. Thus, we need to determine whether inclusion of biotic predictors can reduce uncertainty in models that are used to predict climate change impacts.

It remains unresolved whether SDMs can help to distinguish between environmental/physiological constraints that make up the fundamental niche and the biotic interactions that constrain species to occur within their realized niches (Hutchinson 1957). The relative importance of biotic and abiotic influences on species distributions has generated a variety of opinions. Some authors argue that

general species distribution patterns are not considerably influenced by biotic interactions (Huntley et al. 1995, Bakkenes et al. 2002) or only at small-scales (Pearson and Dawson 2003, Heikkinen et al. 2007), whereas others have argued for a strong role for biotic interactions, causing standard SDM predictions to be incomplete at best (Davis et al. 1998, Anderson et al. 2002, Araújo and Luoto 2007). Negative biotic interactions are often thought to mainly constrain species distributions at equatorial/lower limits, while positive biotic interactions and abiotic factors are expected being the dominant determinants of poleward/upper range limits (MacArthur 1972, Brown et al. 1996, Loehle 1998, Vetaas 2002, Normand et al. 2009). Furthermore, biotic interactions might lead to a high degree of indeterminacy in species range responses to changes in the abiotic environment (Davis et al. 1998, Case et al. 2005). Indirect evidence of biotic interactions affecting models for trees at the regional scale are also suggested by early-successional species being more difficult to model than dominant late-successional species, most likely due to the realized niche of the former depending on the degree of range filling of the latter (Guisan et al. 2007, Pearman et al. 2008).

Predictions for any given location or for future and past climates are often based on the implicit assumption that biotic interactions remain constant, or are not important for the focal species (Guisan and Thuiller 2005). However, over large geographic ranges biotic interactions may not be constant, partly because of environment-dependant competitive abilities and partly because of spatial variation in the distribution of interacting species due to different environmentally constraining factors or due to anthropogenic influences. During climate change, biotic interactions may vary further, since species may shift their ranges individually as they migrate at different speeds and/or in differing directions (Davis and Shaw 2001, Suttle et al. 2007).

In this paper we approach the problem of identifying potential effects of biotic interactions on current large-scale distributions by including biotic predictors in SDMs. We address the following questions: 1) are SDM estimates of tree species distributions improved when data on other tree species are explicitly included as biotic predictors alongside abiotic (topographic and climatic) predictors? 2) What is the magnitude of the independent and joint contributions of abiotic and biotic predictors to reducing model variance? 3) Does the importance of biotic predictors for explaining species distributions depend on traits of the focal species, such as their response to disturbance and stress, seed dispersal distance, shade tolerance, or frequency and dominance in the landscape? In our study we examine correlations in species occurrences, which means that we cannot evaluate the direction of influence in interspecific interactions. Additional experiments would be required to disentangle the direction of influence in interspecific interactions. Further, we interpret the importance of biotic predictors on the performance of SDMs as an indication of the relevance of local biotic interactions (i.e. competition, mutualism, amensalism and commensalism) or local abiotic processes not included in the large-scale predictors for determining species distributions.

Material and methods

Study area

The study area (45°49'N-47°48'N, 5°57'E-10°29'E) in the central Alps encompassed 12 340 km² of forested area, half of which was located above 1000 m. The climate is moist and mildly maritime north of the Alps, but dry and more continental in the interior valleys. The Alps act as a barrier separating the climates of southern (Mediterranean) and central Europe (Zimmermann and Kienast 1999). Public forest accounted for 68%, the rest being privately owned. Two thirds of the forest are frequently managed, 18% infrequently managed and 14% remain unmanaged (Brassel et al. 1999). Forest management is primarily practiced at low elevations, and selection forestry is the predominant management scheme. Thus, no larger-scale clear-cutting is applied, and natural regeneration is often furthered by management activities. The major change in species composition due to forest management is expected for *Picea abies* at the cost of the otherwise dominant *Fagus sylvatica*. *Picea abies* has its major distribution at high elevation in the subalpine belt, but is partly planted at low elevations on the Plateau. However, palynological studies demonstrate, that *P. abies* occurs naturally at low elevations. It has been present long before intense human activities have occurred and under similar climatic conditions as today (Burga 1988, Burga and Hussendorfer 2001). A simulation of natural forest succession using a dynamic forest succession model also reveals that *P. abies* is expected to naturally occur at the Swiss Plateau (Bolliger et al. 2000).

Data sources and study species

Species data was extracted from the National Forest Inventory of Switzerland (NFI). The database contains data on individual trees in 200 m² circular sample plots. The first inventory (NFI_1, 1983–1985) was recorded on a 1-km regular grid, while NFI_2 (1993–1995) was on a 1.4-km grid. All grid points located in forest were sampled (Fig. 1). A total of 5236 plots were repeated during NFI_1 (n = 10 419) and NFI_2 (n = 6412). All trees with diameters at breast height (1.37 m above the ground; DBH) larger than 12 cm were measured for basal area.

We selected eleven target tree species out of approximately 50 common species. The selected species are sufficiently abundant to be modeled (> 100 observations), belong to two different functional groups (broadleaved deciduous and needleleaved evergreen), and combine to cover the full elevation gradient available in Switzerland, reaching from 180 m a.s.l. to the treeline situated at roughly 2450 m a.s.l. in the dry interior valleys. The seven broadleaved species included European beech *Fagus sylvatica* sycamore *Acer pseudoplatanus*, European ash *Fraxinus excelsior*, silver birch *Betula pendula*, pedunculate oak *Quercus robur*, sessile oak *Quercus petraea*, and common whitebeam *Sorbus aria*; while the four conifers included Norway spruce *Picea abies*, silver fir *Abies alba*, Scots pine *Pinus sylvestris*, and Swiss stone pine *Pinus cembra*. Eight of these species were also incorporated as biotic predictors (Table 1).

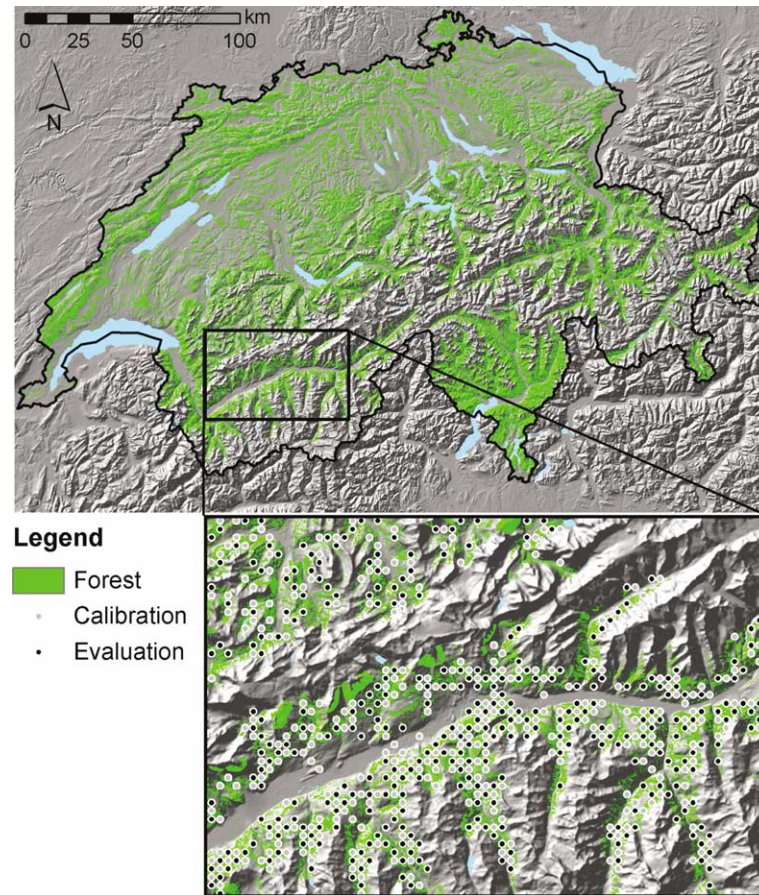


Figure 1. Distribution of study plots (circles of 200 m² represented by black and grey dots) within the forest of the central Alps (45°49'N-47°48'N, 5°57'E-10°29'E). Black dots represent the plots used for model calibration (n = 5236), grey dots represent plots used for external model evaluation (n = 5183).

Response variables

We analyzed two response variables: 1) presence-absence data (PA), where presence was recorded when a tree of a target species was present on the sample plot. This is frequently used in studies that model species distributions. 2) Basal area (BA), the basal area of a target species as a proportion of the total basal area recorded on the sample plot. Since basal area is a surrogate of biomass, it can also be used as a measure of competition in the stand (Waring and Running 2007).

Biotic predictor variables

We evaluated three species-specific variables to describe the influence of predictor species on the occurrence of a target species: 1) relative abundance (AB), defined as the number of stems of a predictor species as a proportion of total number of stems recorded in a sample. 2) Relative abundance of large individuals (AB_L), defined as the number of stems of large individuals of a target species as a proportion of the total number of stems on the sample plot. An individual was considered large (L) if it was taller than the median height of the target species in a stand. Height is indicative of competitive ability for light because taller plants shade shorter plants. Competitive advantage can

depend on relative rather than the absolute height (Falster and Westoby 2003). 3) Total shading by large individuals (LAI_L), defined by the cumulative leaf area index (*CumLAI*) of all large trees. Biotic predictors were all correlated <|0.5|.

In order to identify species heights for deriving AB_L and LAI_L, we first estimated actual tree height (H_a ; [cm]) according to Bugmann (1994):

$$H_a = 137 + b_1 \times D_a + b_2 \times D_a^2 \quad (1)$$

where D_a [cm] is the actual diameter of the individual trees as taken from NFI, and b_1 and b_2 are species-specific parameters derived as follows (eq. 2 and 3):

$$b_1 = \frac{2(H_{\max} - 137)}{D_{\max}} \quad (2)$$

$$b_2 = -\frac{b_1}{2 \times D_{\max}} \quad (3)$$

where H_{\max} is the maximum possible height of a tree species in cm, and D_{\max} the maximum possible DBH (i.e. at 137 cm above ground), also in cm (Supplementary material Appendix 1). For a target species, we first calculated median tree height in each plot and then calculated the fraction of individuals of the relevant predictor species larger than the

Table 1. Species traits of the selected species for modeling and analyses.

Species	Number of occurrences		Predictor species	CSR strategy	Seed dispersal	Shade tolerance		Freq.- domin. group
	NFL_1c	NFL_1e				Juv.	Ad.	
<i>Abies alba</i>	1520	1610	x	CS	100	3	1	FD
<i>Acer pseudoplatanus</i>	752	737	x	C	100	2	4	IS
<i>Betula pendula</i>	218	178	x	R	200	7	9	ID
<i>Fagus sylvatica</i>	2114	2096	x	CS	25	3	1	FD
<i>Fraxinus excelsior</i>	684	645	x	C	100	4	6	ID
<i>Picea abies</i>	3387	3322	x	CS	100	5	5	FD
<i>Pinus cembra</i>	123	114		S	25	6	5	ID
<i>Pinus sylvestris</i>	436	431	x	CSR	100	7	9	ID
<i>Quercus petraea</i>	226	233		CS	25	6	7	ID
<i>Quercus robur</i>	171	159	x	CS	25	7	9	IS
<i>Sorbus aria</i>	167	150		SR	25	6	7	IS

Notes: NFL_1c are forest plots for calibration and NFL_1e for external evaluation; seed dispersal shows the avg. seed dispersal distances [m]; predictor species (x) are species used as predictors in the models; shade tolerance of juveniles and adults indicate low values for high shade tolerance; freq.-domin. group indicates "F" for species with a frequent occurring in the landscape and "I" for infrequent occurring species, while "D" indicates high local abundance (i.e. dominant) and "S" low local abundance (i.e. subordinate).

median (AB_L). Formulas for estimating LAI_L are found in Supplementary material Appendix 2.

Species traits

We selected several species traits to group the species accordingly and test whether the contributions of the biotic and abiotic sets of predictors differ as a function of species traits. We formulate hypotheses regarding effects of biotic variables on species that differ in their traits (Table 1, 2). We base our hypotheses on the general expectation that more competitive species are associated with higher effects from biotic variables, since we cannot evaluate the direction of the influence when using correlative methods.

CSR strategies: species were grouped according to their strategies in response to disturbance (factors reducing biomass) and stress (factors restricting productivity, Grime 1979). According to the stress gradient hypothesis (Bertness and Callaway 1994) species occurring in undisturbed, low-stress environments (C strategy) should be involved in intense exclusionary biotic interactions (i.e. interspecific competition) compared to species adapted to frequent disturbances (R strategy) or high stress (S strategy) that may be involved in mutualistic biotic interactions. We expected exclusionary biotic interactions to be strongest compared to other types of biotic interactions, and thus, two groups were considered, one with species with R, S or

SR strategies and one with C strategy species. Due to unequal number of species assigned to the two groups, the results must be considered with care. CSR strategies were assigned according to Brzeziecki and Kienast (1994).

Seed dispersal distances: consideration of seed dispersal distance leads to contrasting predictions regarding the importance of biotic predictors. On the one hand, we expect that models for species with longer seed dispersal distances are more influenced by biotic predictors than models for species with shorter seed dispersal distances. Intra-specific biotic interactions with parent trees are replaced with increased separation by interspecific interactions (Howe and Smallwood 1982), resulting in increasing contribution of biotic predictors with increasing seed dispersal distance. On the other hand, seed dispersal is an essential mechanism for plants to tackle temporal and spatial habitat changes (Gleason 1926, Cain et al. 2000). Seed dispersal distance is closely linked to successional stage on which a species is dominant. Early-successional plant species typically have fat tailed dispersal kernels (i.e. a larger proportion of long-distance movements) and rapid growth rates that enable them to respond quickly to disturbance. Late-successional species usually demonstrate contrasting tendencies (Tilman 1994). In the absence of disturbance in high-resource environments, late-successional species generally competitively exclude early-successional species due to better resource use efficiency (Rees et al. 2001). Accordingly, species with shorter seed dispersal distances tend to occur in late-successional environments with strong biotic interactions, and thus, may have models with higher contributions of biotic predictors. However, we expect that this effect is weak compared to the effect from the transition from intra to interspecific interactions with distance to parent. To examine these alternatives, we grouped species according to Lischke et al. (2004) into species with short seed dispersal distances (25 m) and species with long seed dispersal distances (100–200 m).

Shade tolerance: forest succession is driven largely by interspecific differences in shade tolerance (Kobe et al. 1995). Shade-tolerant species are evolutionarily better adapted for photosynthesis in low light than are shade-intolerant species

Table 2. Species traits in relation to the expected effect of biotic predictors on species distributions. For definitions of the traits see text.

Trait	Weak effect expected	Strong effect expected
CSR strategy	R and S strategy	C strategy
Seed dispersal distance	Short distance	Long distance
Shade tolerance	Shade tolerant	Shade intolerant
Frequency-dominance group	Frequent-dominant species	Infrequent-subordinate species

(Boardman 1977, Kobe et al. 1995). Therefore, shade-tolerant species have an advantage over similar-sized species during competition for moisture and nutrients (Kimmins 2004). Since the degree of shade tolerance also varies by age (Ellenberg 1992), we tested whether models for species with differing juvenile and adult shade tolerance are differentially affected by biotic predictor variables. We derived species-specific shade-tolerance values from Bugmann (1994). We expect stronger effects for shade-intolerant species (values > 5) than for shade-tolerant (values < 5) because species with higher shade tolerance are unlikely outcompeted for light, and thus, may occur in many abiotically suitable habitats. We also expect stronger biotic effects for juveniles than for adults, because tall adults of shade intolerant species may still reach the canopy and thus sufficient light, which may not be the case for juveniles.

Frequency-dominance groups: species can be classified according their frequency in the landscape and their local dominance (Collins et al. 1993, Zimmermann et al. 2007). Here, we classified species as “frequent” when occurring in >25% of all forest plots. Species were classified as “dominant” if the average relative abundance (AB) per plot among all NFI plots was >25% in plots where the species was present. Because frequency of occurrence of species may depend on local abundance (Hanski 1982, Collins et al. 1993), we predict that locally dominant species due to their competitiveness occur more frequently in suitable habitats than do subordinate species. Thus, we expect greater model improvement from adding biotic predictors to models of less dominant and less frequent species than when modeling dominant, frequent species. Several previous studies have indeed shown that tree species frequency in forested landscapes increases with the key competitive trait, shade-tolerance (Pacala et al. 1996, Svenning et al. 2004).

Abiotic predictor variables

We chose a comprehensive set of topo-climatic variables as abiotic predictors on the basis of their relevance to plant physiology and for explaining spatial patterns. The topo-climatic data were generated at a 25-m spatial resolution following Zimmermann and Kienast (1999) and Guisan et al. (2007). We selected only predictors with correlations <|0.5| to avoid problems with multicollinearity. This left seven topo-climatic predictors: 1) degree-days with a 5.56°C threshold (DDEG556, [°C × d]), 2) summer frost frequency (SFROYY, [d]) expressing the sum of frost events during the frost-sensitive time of the year, 3) moisture index from March to August (MIND38, [mm d⁻¹]) as a measure of the water balance of an area in terms of gains from precipitation and losses from potential evapotranspiration, 4) precipitation days (PDAY, [ndays]) as the number of days per year with precipitation higher than 1 mm, 5) potential yearly global radiation (SRADYY, [kJ m⁻² d⁻¹]) expressing the potential amount of direct and indirect solar energy irradiated to the surface, 6) topographic position (TOPOS, [range]) as the difference between the average elevation in a circular moving window applied to a 25-m digital elevation model (DEM) and the centre cell of the

window (representing soil properties such as soil depth and nutrient availability), and 7) slope (SLP, [°]) expressing the slope angle in degrees derived from the DEM (subsuming gravitational disturbance processes such as rock fall, solifluction, and avalanches).

Data analysis

We used a variance partitioning approach (Mood 1971, Borcard et al. 1992, Fig. 2) by fitting generalized linear models (GLM, McCullagh and Nelder 1989) using three different combinations of predictors for each tree species: just the abiotic (ABIOT) or just the biotic (BIOT) predictor variables, or the abiotic and biotic predictor sets combined (FULL). Each model was calibrated using different types of species responses (PA and BA) and BIOT and FULL models using different biotic predictors (AB, AB_L and LAI_L).

We built GLMs with logit links (assuming a binomial distribution) followed by both backward and forward stepwise variable selection based on AIC (Akaike’s information criterion, Akaike 1974) and BIC (Bayesian information criterion, Schwarz 1978). Here, we only report AIC-based results because both criteria led to the same models, likely because of the large sample sizes. For proportional response variables (BA- and AB-models) we used weighted GLMs to account for the total number of tree individuals and stand basal area of all trees per plot, respectively (Dalgaard 2002). For binary response variables (PA-models) no weights were used. Predictors were entered both as linear and quadratic terms to allow for nonlinear responses. For model calibration we used tree species data from NFI_1 from plots intersecting with NFI_2 (i.e. NFI_1 \cap).

Model fit was evaluated by the adjusted D^2 ($adj.D^2$) following Weisberg (1980) for each of the selected species, a measure that adjusts the deviance explained (“deviance” is the variance in likelihood methods; D^2) by the number of fitted regression parameters and the number of observations. To partial out the deviance explained by the abiotic and biotic predictor sets, we followed earlier work using GLMs (Lobo et al. 2001, Zimmermann et al. 2007). The

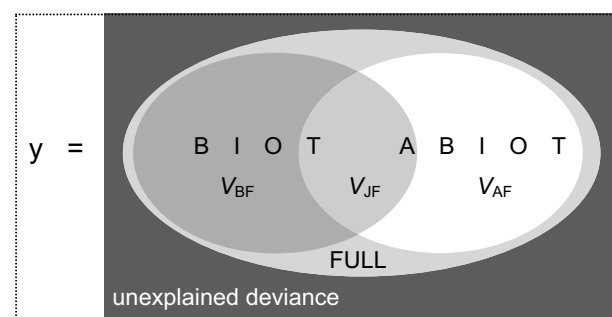


Figure 2. Variance partitioning concept. BIOT: deviance explained by biotic predictor set; ABIOT: deviance explained by abiotic predictor set; FULL: deviance explained by both biotic and abiotic predictor sets; V_{BF} : alone contribution to deviance explained by biotic predictor set; V_{JF} : joint contribution of both predictor sets; and V_{AF} : alone contribution of the abiotic predictor set. Adapted from Legendre (1993).

contribution of each set of predictors was estimated by subtracting the $adj. D^2$ of the opposite set of predictors from the FULL model, so that $V_{BF} = V_{FULL} - V_{ABIOT}$, and $V_{AF} = V_{FULL} - V_{BIOT}$. V_{BF} and V_{AF} are the pure contributions of the biotic and abiotic predictor sets to the total deviance explained, while the joint contribution (V_{JF}) of the two predictor sets was calculated as $V_{JF} = V_{FULL} - (V_{ABIOT} + V_{BIOT})$. In rare cases, V_{JF} may become negative as a result of opposing effects of the two sets of predictors in the FULL model (Legendre 1998).

Partial $adj. D^2$ values were then further evaluated to test whether the pure and joint contributions to the $adj. D^2$ followed patterns that matched species groups according to their traits. We used the Mann–Whitney U test and the Kruskal–Wallis test to compare the effect of traits classified into two and three groups, respectively.

In addition to the variance partitioning, we evaluated model accuracy internally by 10-fold cross-validation (Venables et al. 2002) and externally by testing the models against the NFI_1 plots that were not part of NFI_2 (i.e. NFI_1e). We used Cohen's kappa (Cohen 1960) and area under the receiver characteristic curve (ROC) (AUC; Fielding and Bell 1997) for models calibrated with binary response variables (PA-models). For models calibrating proportional responses (BA-models) we used mean absolute error (MAE, Voltz and Webster 1990), root mean square error (RMSE, Voltz and Webster 1990) and the coefficient of determination, R^2 (Menard 2002). All data was prepared and analyzed using R (R Development Core Team 2008) and ArcGIS 9.2 (ESRI 2006).

Results

Model qualities using different types of biotic variables

The explicit inclusion of biotic predictors improved model fit (Table 3). However, model quality varied among tree species, chosen response variable and selected biotic predictors. Since the amount of shade (LAI_L) was never significant, we did not consider it further. The explained deviance was significantly lower for presence-absence models (PA) than for proportional basal-area models (BA, paired t-test, $p < 0.001$; Table 3).

For presence-absence models the accuracies of the two partial models (ABIOT and BIOT) were similar, but significantly exceeded by the FULL model (paired t-test, $p < 0.001$ and see Table 4). Further, model accuracies as estimated with 10-fold cross validation and external validation on NFI_1 data not used for model calibration (NFI_1e) did not differ significantly, which indicates that we obtained stable models with low bias (Supplementary material Appendix 3). For the proportional basal-area models MAE was similar for the two partial models, but significantly smaller for the FULL model (paired t-test, $p < 0.001$ and see Table 6). However, for most modeled tree species MAE and RMSE differed substantially, indicating large variance in individual errors in the sample (Supplementary material Appendix 4). Likewise, model quality (R^2) was similar for the two partial models, but higher for the FULL model. For these proportional models, accuracies

Table 3. Deviance explained ($adj. D^2$) for ABIOT, BIOT and FULL models for PA and BA responses and species-specific relative abundances as biotic predictors. Bold face indicates the model with the highest fit.

Species	ABIOT		BIOT		FULL	
	PA	BA	PA	BA	PA	BA
<i>Abies alba</i>	0.18	0.19	0.23	0.40	0.40	0.61
<i>Acer pseudoplatanus</i>	0.11	0.10	0.15	0.25	0.26	0.41
<i>Betula pendula</i>	0.25	0.36	0.20	0.34	0.35	0.51
<i>Fagus sylvatica</i>	0.26	0.26	0.27	0.48	0.47	0.65
<i>Fraxinus excelsior</i>	0.18	0.20	0.19	0.32	0.34	0.49
<i>Picea abies</i>	0.19	0.25	0.20	0.44	0.36	0.59
<i>Pinus cembra</i>	0.62	0.71	0.38	0.51	0.65	0.75
<i>Pinus sylvestris</i>	0.19	0.25	0.14	0.29	0.31	0.48
<i>Quercus petraea</i>	0.23	0.29	0.20	0.33	0.37	0.54
<i>Quercus robur</i>	0.24	0.28	0.12	0.21	0.31	0.41
<i>Sorbus aria</i>	0.12	0.15	0.09	0.16	0.17	0.29
Mean	0.23	0.28	0.20	0.34	0.36	0.52
Stdv	0.14	0.16	0.08	0.11	0.12	0.13

estimated by 10-fold cross validation and by external validation using NFI_1e data did not differ significantly.

When comparing the three types of biotic predictor variables, we found that species-specific relative abundances (AB) explained the most deviance in fitted models (Table 5). Relative abundances of large individuals (AB_L) explained considerably less deviance (paired t-test, $p = 0.001$; Table 5) and the amount of shade as measured by LAI (LAI_L) failed to explain patterns. Model accuracies for models with relative abundances were similar to models with relative abundances of large individuals in terms of errors (MAE, RMSE), but were higher in terms of model quality (R^2 , Table 6). In general, models with relative abundances of large individuals had similar MAE for the two partial models and the FULL model. However, their RMSE was highest for the BIOT model, lower for the FULL model, and lowest for the ABIOT model, indicating large variance in individual model errors (Table 6). Model quality (R^2) was highest for the FULL model, lower for the ABIOT model and lowest for the BIOT model. Model accuracies taken from 10-fold cross validation were not significantly different from external validation using NFI_1e data.

When proportional basal area was the response, the deviance explained by individual predictors within the ABIOT and BIOT groups varied considerably among species. Degree-days was generally the strongest ABIOT predictor, while *Picea abies* had similar strength and was the strongest BIOT predictor (Table 7). The other tree species generally declined with increasing abundance of *Picea abies*,

Table 4. Mean model accuracy among species (Kappa, AUC) of ABIOT, BIOT and FULL models calibrated with PA data as species response and species-specific relative abundances as biotic predictors. Model accuracy was derived by 10-fold cross validation (CV) and external validation on NFI_1e.

	10-fold CV		External validation	
	Kappa	AUC	Kappa	AUC
ABIOT	0.24 ± 0.12	0.82 ± 0.07	0.23 ± 0.12	0.81 ± 0.07
BIOT	0.22 ± 0.14	0.80 ± 0.05	0.22 ± 0.13	0.81 ± 0.05
FULL	0.36 ± 0.18	0.89 ± 0.05	0.35 ± 0.18	0.89 ± 0.04

Table 5. Deviance explained ($adj.D^2$) for ABIOT, BIOT and FULL models for BA responses and species-specific relative abundances (AB) and species-specific relative abundances of large trees (AB_L) as biotic predictors. Bold face indicates the model with the highest fit.

Species	ABIOT	BIOT		FULL	
		AB	AB_L	AB	AB_L
<i>Abies alba</i>	0.19	0.40	0.11	0.61	0.33
<i>Acer pseudoplatanus</i>	0.10	0.25	0.06	0.41	0.15
<i>Betula pendula</i>	0.36	0.34	0.24	0.51	0.44
<i>Fagus sylvatica</i>	0.26	0.48	0.11	0.65	0.36
<i>Fraxinus excelsior</i>	0.20	0.32	0.10	0.49	0.31
<i>Picea abies</i>	0.25	0.44	0.31	0.59	0.44
<i>Pinus cembra</i>	0.71	0.51	0.38	0.75	0.72
<i>Pinus sylvestris</i>	0.25	0.29	0.30	0.48	0.53
<i>Quercus petraea</i>	0.29	0.33	0.12	0.54	0.36
<i>Quercus robur</i>	0.28	0.21	0.09	0.41	0.33
<i>Sorbus aria</i>	0.15	0.16	0.14	0.29	0.26
Mean	0.28	0.34	0.18	0.52	0.39
Stdv	0.16	0.11	0.11	0.13	0.15

although the relationship was unimodal for *Abies alba* and *Pinus sylvestris* (Table 7).

Variance partitioning of biotic and abiotic predictors

We report variance partitioning as applied to models with proportional basal areas as response and topo-climatic and/or relative abundance as abiotic and biotic predictor sets, respectively, because these were the predictors that best describe tree distributions. The pure contribution of abiotic (V_{AF}) and of biotic (V_{BF}) predictors to explanation of model deviance differed among species (Fig. 3A). Across species, the biotic contribution (0.25 ± 0.12) was larger than the abiotic contribution (0.18 ± 0.03), and the joint contribution (V_{JF}) was comparably small (0.09 ± 0.14). When accounting for species traits, species adapted to undisturbed low-stress environments (C, CS, CR, CSR) showed significantly higher contributions to explained deviance from biotic predictors than do species adapted to disturbed or stressful environments (R, S, SR; Mann–Whitney U test, $p = 0.04$; Fig. 3B). Further, species with medium to long seed dispersal distances (avg. = 100–200 m) tended to have larger contributions to explained deviance from biotic predictors than species with short seed dispersal distances (avg. < 25 m; Mann–Whitney U test, $p = 0.17$; Fig. 3B). Models of species with shade-tolerant

juveniles had significantly larger contributions from biotic predictors than did models of species with shade intolerant juveniles (Mann–Whitney U test, $p = 0.004$; Fig. 3B). A similar, but non-significant tendency was found from analyzing the effect of adult shade tolerance (Mann–Whitney U test, $p = 0.12$). Further, models of dominant species that occur frequently in a landscape showed significantly higher contributions to the deviance explained from biotic predictors than did models of dominant and subordinate species that demonstrate infrequent occurrence (Kruskal–Wallis test, $p = 0.04$; Fig. 3B). Abiotic and joint contributions did not differ significantly within characteristic species groups (Mann–Whitney U test and Kruskal–Wallis test, all $p > 0.27$).

Discussion

Biotic predictors and model quality

We find that biotic variables considerably improved predictions of tree species distributions in Switzerland, with their effect being largely independent of abiotic topoclimatic factors. Several previous studies have extended SDMs by including biotic predictors (Rouget et al. 2001, Leathwick 2002, Araújo and Luoto 2007, Heikkinen et al. 2007, Sutherst et al. 2007). Similar to our findings, these studies generally demonstrate improved predictions when adding biotic predictors. For instance, the abundance of *Nothofagus* species in New Zealand is dependent on the presence or absence of their congeners (Leathwick 2002), while presence of host plant species is an important occurrence predictor for butterfly species in Europe (Araújo and Luoto 2007). Some owl species appear to facilitate the presence of other owl species in Finland (Heikkinen et al. 2007). In our study, we specifically demonstrate that the statistical contribution of the biotic predictors, which we assume reflect biotic interactions, small-scale information on species co-occurrence and local abiotic conditions (e.g. soil, nitrogen content), is largely independent of the contribution of macro-climatic factors. Our results also show that different ways of expressing biotic variables can have a large influence on model quality. Overall, biotic predictors have the potential to elucidate important aspects of species distribution patterns that are not easily represented by large-scale abiotic predictors.

Table 6. Mean model accuracy (MAE, RMSE, R^2) of ABIOT, BIOT and FULL models calibrated with BA data as species response and species-specific relative abundances (AB) and species-specific relative abundances of large trees (AB_L) as biotic predictors. Model accuracy was derived by 10-fold cross validation (CV) and external validation on NFI_1e.

	10-fold CV			External validation		
	MAE	RMSE	R^2	MAE	RMSE	R^2
ABIOT	0.08 ± 0.09	0.57 ± 0.87	12.52 ± 11.06	0.08 ± 0.09	0.47 ± 0.91	11.21 ± 9.44
BIOT _{AB}	0.07 ± 0.07	0.86 ± 1.35	14.09 ± 13.72	0.07 ± 0.07	0.89 ± 1.47	13.22 ± 13.51
BIOT _{AB_L}	0.08 ± 0.09	0.96 ± 1.56	6.25 ± 7.46	0.08 ± 0.10	0.97 ± 1.76	5.16 ± 6.69
FULL _{AB}	0.05 ± 0.05	0.75 ± 1.11	30.13 ± 20.77	0.05 ± 0.05	0.71 ± 1.13	28.98 ± 20.99
FULL _{AB_L}	0.07 ± 0.08	0.86 ± 1.33	19.22 ± 14.01	0.07 ± 0.08	0.85 ± 1.42	17.54 ± 12.16

Table 7. Deviance explained ($adj.D^2$) by individual predictors, derived from single variable GLMs with proportions of basal areas (BA) as response variable and abiotic and biotic predictors (only AB predictors are shown). Acronyms for the modeled species: first letter of genus plus two first letters of species epithet. Numbers indicate the $adj.D^2$ explained by the predictor. The direction of the trend between the predictor and the response species is indicated in parenthesis as positive linear "+", negative linear "-", positive unimodal "∩", negative unimodal "∪", or with no clear trend "N". Bold-face indicate $adj.D^2 > 0.10$.

Predictor	Aal	Aps	Bpe	Fsy	Fex	Pab	Pce	Fsy	Qpe	Qro	Sar	Mean	Stdv
SLP25	0.01	0.01∩	0.04+	0.00	0.02	0.00	0.06H	0.01U	0.05U	0.09	0.04+	0.03	0.03
MIND38	0.01∩	0.00∩	0.01+	0.02	0.07	0.06+	0.09I	0.16	0.20	0.19	0.01∩	0.08	0.07
SFROY	0.02	0.02	0.05	0.03	0.03U	0.03∩	0.43 +	0.01	0.02	0.02	0.01	0.06	0.12
DDEG556	0.15 ∩	0.05∩	0.08I	0.20 ∩	0.17 ∩	0.16	0.58	0.05I	0.20 ∩	0.23 ∩	0.04I	0.17	0.15
PDAY	0.03∩	0.03∩	0.17 ∩	0.01∩	0.01∩	0.08+	0.04	0.06	0.12 ∩	0.07I	0.00I	0.06	0.05
SRADYY	0.00∩	0.00	0.01∩	0.00U	0.02∩	0.00+	0.04	0.03+	0.04+	0.06I	0.02U	0.02	0.02
TOPOS	0.01∩	0.01	0.01∩	0.00∩	0.02∩	0.00U	0.00U	0.00I	0.02I	0.06I	0.01+	0.01	0.02
<i>A. alba</i>	—	0.02∩	0.06	0.02∩	0.02	0.07	0.09N	0.04	0.03	0.01	0.01	0.04	0.02
<i>A. pseudoplatanus</i>	0.01∩	—	0.01	0.01∩	0.05∩	0.02	0.03N	0.02	0.01N	0.00+	0.02I	0.02	0.01
<i>B. pendula</i>	0.01	0.00	—	0.00∩	0.00N	0.01	0.00	0.00I	0.00I	0.00N	0.00+	0.00	0.00
<i>F. sylvatica</i>	0.07∩	0.03∩	0.01	—	0.01∩	0.20	0.12N	∩	0.02∩	0.02I	0.03I	0.05	0.06
<i>F. excelsior</i>	0.01	0.05∩	0.00	0.01∩	—	0.04	0.03N	0.00	0.00	0.04∩	0.00	0.02	0.02
<i>P. abies</i>	0.19 ∩	0.11	0.15	0.33	0.15	—	0.08	0.09∩	0.15	0.09	0.10	0.14	0.07
<i>P. sylvestris</i>	0.02	0.01	0.00N	0.01∩	0.01	0.03	0.02	—	0.01I	0.01∩	0.02∩	0.01	0.01
<i>Q. robur</i>	0.00	0.00	0.00N	0.00∩	0.01∩	0.01	0.01N	0.00N	0.00	—	0.00N	0.00	0.00

Partitioning the biotic and abiotic predictor contribution

In our analysis of the respective contributions of biotic and abiotic factors in SDMs, we find that the joint contribution of both predictor sets is consistently small (except for *Pinus cembra*). This indicates that biotic predictors are largely independent of the abiotic predictors in their explanatory capacity. Abiotic predictors (topography and climate) may reflect constraints of the fundamental niche of the tree species, and hence, are expected to determine large-scale species ranges (Pearson and Dawson 2003). In contrast, small-scale distribution patterns are expected to be more strongly influenced by biotic processes such as competition or facilitation, as well as land-use, stochastic processes and local abiotic conditions (micro-climate, soil, nitrogen content). The largely unique influence of abiotic and biotic predictors in our study probably reflects that the small-scale processes are relatively independent of the effects of large-scale topo-climatic gradients. The main exception occurs with *Pinus cembra*, a species adapted to relatively extreme (cold) habitats. Abiotic predictors, with no independent contribution of the biotic predictors, constitute the main range determinants for this species. Furthermore, the large joint contribution of the two predictor sets for *P. cembra* indicates that influence of biotic processes likely mediates the influence of the abiotic environment. Notably, *P. cembra* mainly occurs where it is too cold for strong competitors such as *Picea abies* (cf. Table 7). As a consequence of our findings, we expect the addition of biotic predictors to improve the ability of species distribution models to predict small-scale distribution and abundance patterns, but not necessarily to produce a clear improvement in the prediction of species large-scale ranges.

Biotic predictor component and species traits

We find clear differences in the relative contribution of abiotic and biotic predictors when species are grouped according to traits. With the exception of the hypothesized effects of biotic predictors on models of species belonging to different shade tolerance groups and CSR-strategies, the data support our hypothesis regarding effects of biotic predictors on species that differ in their traits. The tree species whose modeled distribution are most strongly influenced by biotic predictors are adapted to undisturbed low-stress environments (competitive strategy), shade-tolerant as juveniles and adults, frequent dominants, and tend to have long distance seed dispersal. All these traits point to late-successional species with high competitive ability. A principle exception is the dispersal distance relationship where the effect from the transition from intra to interspecific interactions with distance from parent may be overriding. Thus, our results support the idea that models of species typified by occurrence in stressful or disturbed environments seem to profit less from biotic predictors, despite these species may be outcompeted during succession by species with a higher competitive ability, and thus, occur less often in abiotically suitable habitats due to negative biotic interactions.

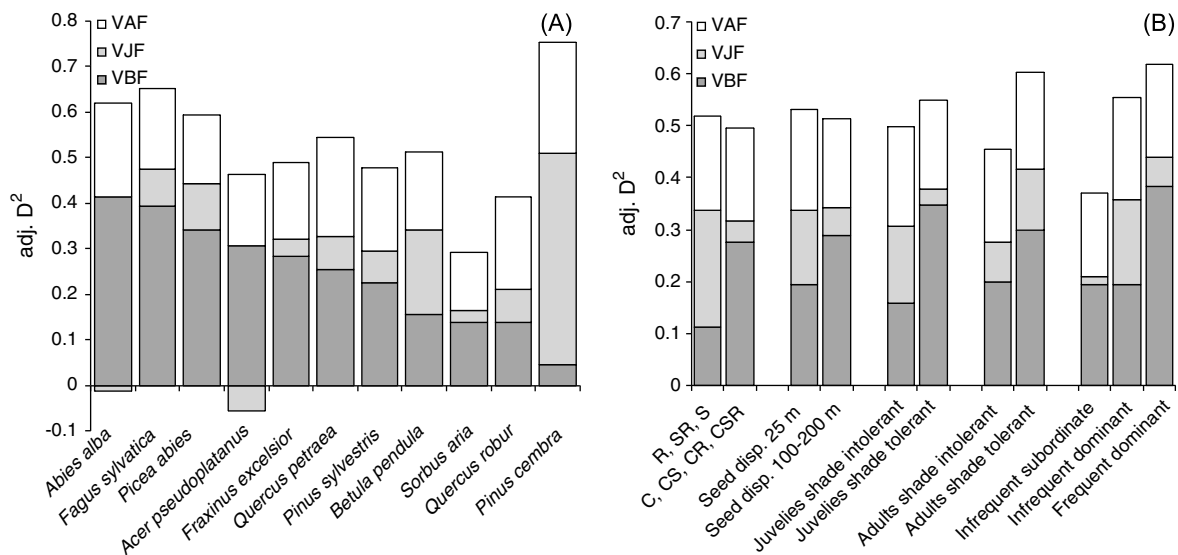


Figure 3. Graphical representation of variance partitioning results. (A) Partial deviance explained ($adj. D^2$) by the two sets of predictors for individual tree species. V_{BF} is the pure contribution of the biotic set of predictors, V_{AF} is the pure contribution of the abiotic set and V_{JF} is the joint fraction of both predictor sets. (B) Mean contributions of species adapted to undisturbed low-stress environments (C, CS, CRS) and stressful environments (R, S, RS); species with medium to long seed dispersal distances (average dispersal distance of 100–200 m) and short seed dispersal (average dispersal distance of 25 m); species with shade-tolerant juveniles and adults (values ≤ 5) and shade-intolerant juveniles and adults (values > 5); and dominant species that occur frequently at the landscape and subordinate and dominant species that occur infrequently.

Our results are in line with the assumption of Grime (1979), where species experience stronger biotic interactions in less disturbed, productive environments compared to more disturbed, stressed environments. For trees, biotic interactions are thus more likely important for competitive, shade-tolerant species, which primarily occur in late-successional, productive environments, where competition plays a strong structuring role, while they are less likely important for ruderal and stress-adapted, shade-intolerant species, which mainly occur in low-competition environments. In terms of species, we find that the strongest effects of biotic variables on tree species distributions were for the late-successional species *Picea abies* and *Fagus sylvatica* (Table 7). We caution that our correlative analyses detect only the shape of the mutual response, but not the direction of the effect. If one species imposes e.g. shade and thus reduces the abundance of another species, then the two species show a correlation. If two SDMs are fitted, where each species is once the dependent and once the predictor variable, we would find negative response directions for both. Accordingly, we interpret the large contribution of the biotic predictor set if strong competitors are used as dependent variables such that these competitive species impose stronger competitive control over others that we have added as predictors. This inversion of the influence was much lower if early-successional, and shade-intolerant species are considered. Experiments would be needed to detect causal relationships.

Predictive power of different biotic predictor sets and single predictors

In our analysis, use of presence-absence (PA) as a response variable in the models results in less explained deviance than

do models using proportional data on basal areas (BA). This may indicate that our estimated realized niche of a species is better characterized with species performance data than with simple occurrence data, which is in line with the original definition of the realized niche based on net growth rate of populations (Pulliam 2000). Further, despite our original expectation that larger trees directly influence the occurrence of smaller trees since small trees are likely to suffer or die from competition by larger trees, species-specific relative abundances of large individuals (AB_L) explained significantly less deviance than did AB. If the species-specific component is removed and only overall shading of large individuals (LAI_L) was addressed, hardly any deviance is explained. This is surprising since leaf area and not biomass is assumed to be the underlying mechanism behind the self-thinning rule (Westoby 1984). Possibly, the method needs to be improved to accurately portray the influence by shading on target trees, i.e. leaves of trees from the same species are likely at least as important for shading effects as are the effects of shading from leaves of other species.

Degree days (5.56°C threshold) and moisture index from March to August were the best single predictors of the abiotic predictors set. These factors are important for species that grow primarily under cold (*Pinus cembra*) or dry (*Quercus-petraea* and *Q. robur*) conditions. In contrast, models of *Abies alba*, *Picea abies* and *Fagus sylvatica* show the highest impact by biotic variables (i.e. biomass of other species). As mentioned above, we interpret this as competitive strength of these three species compared to other species. The inclusion of the presence/absence or abundance of additional species as predictor variables need not reflect biotic interactions. It may also represent consequences of forest management, or simply the occurrence of co-varying distributions between pairs of species that do not necessarily interact. For

example, *P. abies* is dominant at high elevations and naturally occurs less frequent at low elevations. However, since it is commercially the most important tree species in the central Alps, it is sometimes planted at low elevations. Hence, biotic influences subsumed in this predictor may not only contain the natural interactions between tree species, but in some cases the effects of management. Finally, deviance in co-occurrence may also represent unmeasured or incompletely measured environmental deviance, notably micro-environmental heterogeneity that might not be captured by larger scale abiotic GIS layers. The direction of the trend between the biotic predictor and the response may indicate that species tend to occur in mixed stands or in stands with only one dominant tree species. Unimodal distributions, as seen in the responses of *F. sylvatica* and *Abies alba*, reflect a tendency of a species to occur often in mixed stands at intermediate densities.

Conclusion

Models are generally improved by representing other species as predictor variables in the models. Species that reflect interspecific facilitation, such as root symbionts, may be beneficial for better understanding the small-scale drivers of plant distribution. However, spatially explicit information of fungal or bacterial symbionts is difficult to obtain. Furthermore, to prevent overfitting, only few such predictor species can be included in a model. Hence, even where data are available, inclusion of these variables should be contingent on prior ecological knowledge to avoid fitting models with spurious interactions. Given the effects of biotic variables on the modeled distribution of trees, it seems unlikely that predictions for global warming at small spatial scales (resolution or grain) are credible if they are based solely on topo-climatic gradients. These predictions for global change could be improved by including community information and seed dispersal or migration effects (Engler and Guisan 2009). Further and more generally, biotic interactions may not only be dependent on species traits, but also on the position of sample locations along key climatic gradients (temperature, moisture). Competition, for instance, may be stronger towards the more favorable growing conditions (Bertness and Callaway 1994, Brown et al. 1996). These interactions may variably change in a changing climate.

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