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Research

Tree cover at fine and coarse spatial grains interacts with shade tolerance to shape plant species distributions across the Alps

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The role of competition for light among plants has long been recognised at local scales, but its importance for plant species distributions at larger spatial scales has generally been ignored. Tree cover modifies the local abiotic conditions below the canopy, notably by reducing light availability, and thus, also the performance of species that are not adapted to low-light conditions. However, this local effect may propagate to coarser spatial grains, by affecting colonisation probabilities and local extinction risks of herbs and shrubs. To assess the effect of tree cover at both the plot- and landscape-grain sizes (approximately 10-m and 1-km), we fit generalised linear models (GLMs) for the plot-level distributions of 960 species of herbs and shrubs using 6935 vegetation plots across the European Alps. We ran four models with different combinations of variables (climate, soil and tree cover) at both spatial grains for each species. We used partial regressions to evaluate the independent effects of plot- and landscape-grain tree cover on plot-level plant communities. Finally, the effects on species-specific elevational range limits were assessed by simulating a removal experiment comparing the species distributions under high and low tree cover. Accounting for tree cover improved the model performance, with the probability of the presence of shade-tolerant species increasing with increasing tree cover, whereas shade-intolerant species showed the opposite pattern. The tree cover effect occurred consistently at both the plot and landscape spatial grains, albeit most strongly at the former. Importantly, tree cover at the two grain sizes had partially independent effects on plot-level plant communities. With high tree cover, shade-intolerant species exhibited narrower elevational ranges than with low tree cover whereas shade-tolerant species showed wider elevational ranges. These findings suggest that forecasts of climate-related range shifts for herb and shrub species may be modified by tree cover dynamics.

One important goal of ecology is to provide reliable forecasts of biotic responses to climate change (Pearson and Dawson 2003, Meier et al. 2010, Wisz et al. 2013). At the same time, obtaining a mechanistic understanding of the determinants of species distributions is still one of the greatest challenges (Thuiller et al. 2013). Climate has long been recognised as the main driver of species distributions (Pearson and Dawson 2003). However, many recent studies have shown that other factors, such as dispersal limitation, remnant population dynamics, transient eco-evolutionary dynamics, environmental disturbances, edaphic conditions, and biotic interactions, may modify species-specific responses to climatic drivers (Pounds et al. 1999, Root et al. 2003, Parmesan 2006, Lenoir et al. 2010, Normand et al. 2011, Bertrand et al. 2012). Among these, biotic interactions have been recently highlighted as a key factor that should be better incorporated into both species distribution models (SDMs) and biodiversity models (Boulangeat et al. 2012, Kissling et al. 2012, Linder et al. 2012, Wisz et al. 2013). Although previously thought to be of highest importance at fine spatial grains (see Eltonian noise hypothesis in Soberon and Nakamura 2009, Cooper and Belmaker 2010), recent studies have shown that biotic interactions can also significantly alter species distributions at coarse spatial grains and broad spatial extents (Bullock et al. 2000, Araújo and Luoto 2007, Gotelli et al. 2010, Meier et al. 2011).

In plants, both correlative (Pellissier et al. 2010, Meier et al. 2010, 2011, Kunstler et al. 2011, 2012, Meineri et al. 2012) and experimental studies (Klanderud 2005, Hector et al. 2012) have provided evidence for the importance of biotic interactions for species distributions. For example, shrub cover and abundance affect herb and dwarf shrub richness and abundance in tundra habitats (Pajunen et al. 2011), and the co-occurrence patterns of competing trees alter the distribution patterns of European beech (Meier et al. 2011). However, the importance of taller species (such as trees) in driving herb and shrub species distributions across large geographic regions has never been explicitly assessed (Linder et al. 2012) despite the well-known roles of light availability and shade tolerance in determining local plant community composition (Kobe et al. 1995, Valladares and Niinemets 2008). Furthermore, due to the sessile nature of plants, direct plant–plant interactions are commonly thought to mainly occur within short distances, and there are thus few studies of the impact of plant–plant interactions at coarser spatial grains (Linder et al. 2012, Wisz et al. 2013, but see Bullock et al. 2000).

Trees have been referred to as biotic modifiers (Linder et al. 2012) because of their abilities to modify microclimatic conditions (Pinto et al. 2010) and soil properties (Thomas and Packham 2007). In areas with high diurnal and seasonal climatic variation, dense tree cover dampens the microclimatic variability in the understory compared with open areas (von Arx et al. 2012). Additionally, trees add organic matter to the soil, often increasing nutrient availability (Augusto et al. 2002). However, the most important effect of trees is that they reduce light availability in the understory. As some species are adapted for photosynthesis under low-light conditions (Kobe et al. 1995, Valladares and Niinemets 2008), such species may benefit from a dense tree cover, whereas other (shade-intolerant) species are excluded. Hence, trees may have varying impacts on co-occurring herb and shrub species, ranging from competition to facilitation, depending on the shade tolerance of the interacting species. Despite their sessile nature, the effects of trees may propagate to coarser spatial grains (e.g. 1 km^2) via plant population dynamics, by affecting colonisation probabilities and local extinction risks of herbs and shrubs. For instance, an open gap in a forested landscape could be too small to support a viable population of a light-demanding species (Canham 1989) or too distant from source populations and/or too short-lived to be colonised. Similar processes may also occur for shade-tolerant species and small patches of dense tree cover in open landscapes (Jamoneau et al. 2011). These examples suggest the fine-grain occurrence of understory plants may be affected not only by tree cover at the same grain but also by landscape-grain tree cover through metapopulation-like dynamics.

Changes in the role and importance of biotic interactions along abiotic gradients have been discussed for decades, and we use this perspective as an additional way to study the effects of tree cover on herb and shrub distributions (Paine 1974, Kaufman 1995, Maestre et al. 2009). A frequent approach is to study their effects along the elevational ranges of the species (Normand et al. 2009, Kunstler et al. 2011, le Roux et al. 2012). The asymmetric-abiotic-stress-limitation hypothesis (AASLH) proposes that abiotic environmental and biotic interaction drivers constrain the upper and lower elevational limits, respectively (Paine 1974, Normand et al. 2009, Ettinger et al. 2011), assuming a stronger effect of competition in habitats not physiologically limited by abiotic conditions (i.e. the lower elevational limit). However, biotic interactions may ameliorate the limiting physiological conditions, thereby extending the upper elevational limits of certain species (Callaway et al. 2002). The stress gradient hypothesis (SGH) predicts varying biotic interactions as environmental stress decreases, with an increase in competition and a decrease in facilitation (Bertness and Callaway 1994, Maestre et al. 2009), supporting the role of biotic interactions in influencing both upper and lower elevational limits of species ranges (Defossez et al. 2011).

Here, we 1) incorporate tree cover into SDMs (cf. Linder et al. 2012) to measure its importance as a driver relative to climate and soil for fine-grain herb and shrub species distributions across a large region, the Alps, and 2) assess whether tree cover effects are affected by species-specific shade tolerances. Then, we 3) investigate whether tree cover effects occur only at fine spatial grains (plot grain: ~10 m) or if there are also detectable coarser grain (landscape grain: ~1 km) tree cover effects on fine-grain herb and shrub species distributions. Finally, we 4) evaluate whether tree cover affects herb and shrub elevational range limits, and if it does, whether the patterns are consistent with the AASLH or the SGH.

Material and methods

Study area

The study area covers the entire Alps (43°29′49″–48°53′00″N, 4°46′28″–17°04′00″E), as delineated by the Alpine Convention Boundary (Fig. 1; < www.alpconv.org >). Elevation ranges from sea level up to 4810 m a.s.l., and mean elevation is approximately 1037 m a.s.l. Mean annual temperature and precipitation range from –11.6 to 16.6°C and from 515 to 2883 mm yr^{-1}, respectively (WorldClim database; Hijmans et al. 2005). Soil conditions are diverse, with large areas of calcareous as well as siliceous bedrocks, and soil pH ranging from 3 to 8 (European Soil Portal; < http://eusoils.jrc.ec.europa.eu/ >). The main vegetation types are forest, agricultural land, scrubland, grassland, and scattered vegetation on rocks, with forests covering 40.4% of the study area (European Forest Data Center; < http://forest.jrc.ec.europa.eu >).

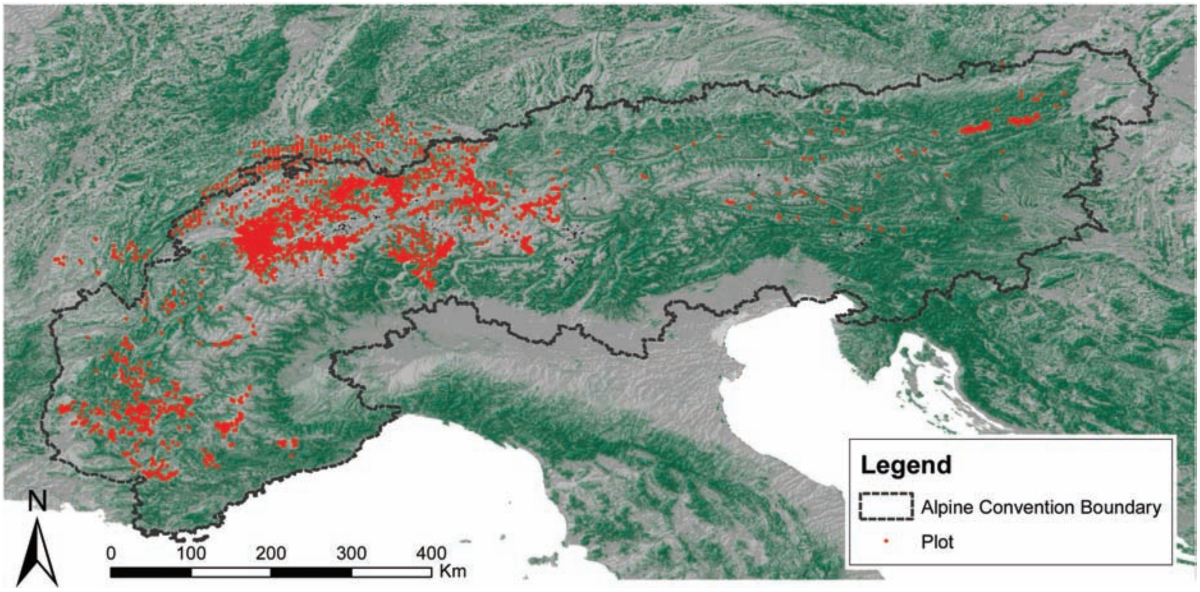

Figure 1. Spatial distribution of the 6935 studied vegetation plots across the Alps. The background colour indicates decreasing tree cover from green (100%) to light grey (0%) at the landscape grain (30″).

Data and study species

We compiled vegetation plot data from two different sources: 1) the Alps Vegetation Database (n = 35 735 plots from 1900 to 2009; Lenoir et al. 2012) and 2) a survey of the French National Alpine Botanical Conservatory at Gap (n = 1782 plots from 1980 to 2009; CBNA). This combined database covers a large elevational gradient from 0 up to 3412 m a.s.l., distributed across the entire Alps. We used Flora alpina (Aeschimann et al. 2004) as the taxonomic reference when integrating the databases. Note that each vegetation plot is an exhaustive list of all vascular plant species co-occurring within a given location at a given point in time and thus provides reliable information on both presence and absence data for a given species.

To avoid mismatches between plot locations and the raster-based predictor variables (see below), we selected those plots with a spatial reference of at least 500-m accuracy. To reduce pseudo-replication, we randomly selected one plot among those with identical spatial coordinates (i.e. plots from time-series and spatially nested plots). To estimate plot-grain tree cover, we selected plots having abundance-dominance indices and excluded plots having presence–absence data only. The final dataset comprised 6935 plots surveyed after 1980, with plot sizes ranging from 1 to 500 m^2 (see Supplementary material Appendix 1 for an assessment of the overall representativeness of the final dataset for all predictor variables relative to the original dataset). As our objective was to study the impact of tree cover on the distribution of lower-stature plant species, the smallest plots (1 m^2) were also relevant because they were the most common plot size for herbs and shrubs in open habitats. Consequently, we removed trees and tall shrub species – i.e. life forms coded 'p' and 'n–p' in Flora indicativa (Landolt et al. 2010) – as well as 634 herb and shrub species not listed in Flora indicativa. Finally, to limit noise in subsequent modelling analyses and to lessen the likelihood of overfitting due to the limited number of occurrences, we selected 960 herb and low-stature shrub species with more than 20 occurrences within the 6935 selected plots. The total number of occurrences per modelled species ranged from 20 to 3451, with an average of 264 occurrences.

We completed the database with descriptor and indicator values for most of the taxa from the Flora indicativa database (Landolt et al. 2010). Landolt et al. (2010) ranked most of the terrestrial plant taxa in the Alps according to their optimal occurrence along key environmental gradients using an ordinal scale ranging from 1 to 5. For the purpose of this study, we used one plant trait descriptor for life forms (LF) and six plant indicator values for air temperature (T), continentality (K), soil moisture (M), soil reaction [soil pH] (R), nutrient availability (N), and light (L). LF describes the Raunkiær life forms for plants and was used to select herbs, shrubs and trees. We classified species as shade tolerant (L = 1–2), semi-shade tolerant (L = 3), or shade-intolerant (L = 4–5) and, according to their optimal elevational belt, as colline (T = 4–5), montane (T = 3–3.5), subalpine (T = 1.5–2.5), or alpine and nival (T = 1).

Predictor variables

Because our objective was to investigate the effect of tree cover in SDMs on lower-stature plants at two different spatial grains (plot and landscape), we calculated two sets of predictor variables for climate, soil, and tree cover.

Plot grain

For five of the six indicator values (V: T, K, M, R, N) in a given plot, we computed the mean indicator value (V_{PMI}) by averaging the values of all species recorded in the respective plot. Note that the averaged values were not weighted by abundance (see Diekmann 2003 for a discussion of the use of weighted and unweighted averaged values). These climate and soil factors (T_{PMI}, K_{PMI}, M_{PMI}, R_{PMI}, and N_{PMI}) are well known to affect plant species distributions (Skov and Svenning 2004, Bertrand et al. 2012) and were used as predictor variables for the plot-grain SDMs (~10-m grain). To avoid circularity when fitting SDMs for a given focal species, we computed V_{PMI} after removing the indicator values of the focal species from all plant assemblages in which it occurred. Because the V_{PMI}s were calculated based on the species observed in each plot, these values represent the vegetation at the time when each plant assemblage was recorded. T_{PMI} characterises the mean temperature during the growth period, whereas K_{PMI} characterises the air humidity, daily and annual variation in temperature, and minimum temperature. M_{PMI} reflects the moisture in the soil during the growth period of the plants and was included in the climate models to provide information regarding water availability. R_{PMI} and N_{PMI} represent the pH and the amount of nitrogen in the soil, respectively.

To calculate tree cover at the plot grain (TC_{plot}), we used field information provided by the vegetation surveys. We calculated the cover percentage for all species taller than 2 m (recorded as vegetation layers 1, 2, 3, and 4 in the database) in each plot by transforming the original abundance-dominance indices to approximate percentage values and then summing the cover percentages for all the species in these four vegetation layers, as implemented in Turboveg (Hennekens and Schaminée 2001).

Landscape grain

To study the effect of coarse-grain tree cover on plot-level species occupancy, we prepared a similar set of predictor variables, but at the landscape grain (see Supplementary material Appendix 2 for similarities and differences between landscape- and plot-grain variables). Here, we used freely available data from various sources that are frequently used in SDMs, enabling their use in a broader set of studies where environmental information at finer spatial grains is not available. Using GRASS 6.4.2RC1 for Windows (GRASS Development Team 2011), we created a 30″ resolution grid in the geographic coordinate system and datum WGS84 (i.e. approximately 925 × 625 m or 0.58-km² cells) that encompassed the spatial extent of the final dataset. Then, we computed climate, soil, and tree cover variables at this spatial resolution.

We used monthly mean climatic data for current conditions (~1950–2000) from the WorldClim database (Hijmans et al. 2005) at 30″ resolution to calculate three climatic variables: growing degree days (GDD), absolute minimum temperature (AMT) and water balance (WBAL). The WorldClim data were estimated from long-term monitoring and subsequent spatial interpolation (Hijmans et al. 2005), offering a rough approximation of these metrics. To represent soil conditions, we downloaded two variables from the European Soil Portal – European Commission – (Jones et al. 2005, Panagos et al. 2012): the organic content in the topsoil (OCT) and soil reaction (pH). OCT was used as a surrogate for nutrient availability. Further details in the calculation of these variables are provided in Supplementary material Appendix 2.

The landscape-grain tree cover data were derived from the 'Forest Map 2000' provided by the European Forest Data Centre – European Commission (< http://efdac.jrc.ec.europa.eu/ >). This raster layer contains information on forest presence/absence at 25-m resolution and is in ETRS89 Lambert Azimuthal Equal Area projection. We re-projected the original data using the nearest neighbour method at the original resolution (~25 m). Subsequently, we resampled to 30″ resolution, computing the surface ratio (ranging from 0% for treeless areas up to 100% for completely forested areas) covered by forest in each grid cell. We refer hereafter to this variable as the landscape-grain tree cover (TC_{land}).

Tree cover and species distribution

To assess the importance of tree cover on species distributions relative to climate and soil, we fit species distribution models (SDMs) using four different combinations of predictors for all selected species in the final dataset: climate, soil and tree cover (CST); climate and soil (CS); climate and tree cover (CT); and climate alone (C). First, we ran models with predictor variables calculated at the plot grain. Then, we investigated whether the effect of tree cover was also observable at a coarser grain by fitting the same combinations of predictors with the independent variables calculated at the landscape grain. In a post-hoc analysis, we included TC_{land} in the CST models at the plot grain to evaluate their combined effect. All the predictor variables included in each model had low correlations (Supplementary material Appendix 2, Table A1), with the exceptions of K_{PMI} vs M_{PMI} (Spearman correlation, $r_s = -0.767$), GDD vs AMT ($r_s = 0.921$), GDD vs WBAL ($r_s = -0.898$), and AMT vs WBAL ($r_s = -0.779$). Most importantly, TC_{plot} and TC_{land}, which constitute the variables of greatest interest here, showed low correlations with soil and climate variables.

We used generalised linear models (GLMs) with a binomial family and a logistic link function in which all the predictor variables were included as linear and quadratic terms. However, to avoid interpreting the results solely based on a single algorithm, we performed supplementary analyses using Maxent (Phillips et al. 2006) and boosted regression trees (BRTs; Ridgeway 1999, Elith et al. 2008) (see Supplementary material Appendix 3 for more details on both methods). For each modelled species, the response variable is a binary variable (0/1) of presence (1) and absence (0) data. Given the high quality of the data, the absence data are reliable. For Maxent, which was designed to compare presences with a background sample, we used all selected plots (including those where the modelled species was present) as background. Our objective with this approach was to obtain comparable results between modelling approaches while minimising the effect of sampling bias (Phillips et al. 2009). The results from Maxent and BRTs were consistent with those obtained with GLMs (Supplementary material Appendix 3). Previous studies have also used data accumulated over long periods to infer and study biotic interactions (Araújo and Luoto 2007, Boulangeat et al. 2012, Hof et al. 2012, Kunstler et al. 2012), despite the complication that the strength and direction of the interactions could change over time (e.g. due to changes in environmental conditions). To assess whether interannual variation could affect the results, we performed a sensitivity analysis with logistic mixed models (LMMs) with survey year as a random effect. The results were highly consistent with those based on GLMs, indicating that such temporal effects did not bias the results and the reasoning (Supplementary material Appendix 4).

To study the performance of models, we randomly selected 75% of the presence–absence data from the final dataset for each of the 960 modelled species to calibrate the models (training dataset) and withheld the remaining 25% to evaluate them (testing dataset). Although the testing datasets were not used to fit the models, they might not be spatially independent from the training datasets. This spatial dependency could bias model evaluation, overestimating the performance of the models; thus, caution should be taken in using the models to make projections, but it is less likely that this bias would affect the comparisons of the models. We used two threshold-independent measures, the nonparametric area under the curve of the receiver operating characteristics plot (AUC) and the parametric point-biserial correlation coefficient (COR), and one threshold-dependent measure, the true skill statistic (TSS). AUC has been widely used but is known to be sensitive to prevalence, whereas COR and TSS have been suggested to be unbiased by prevalence issues (Allouche et al. 2006, Liu et al. 2011). To calculate TSS and to obtain presence–absence predictions from the models, we used the species-model-specific threshold that minimised the difference between sensitivity (proportion of presences correctly predicted) and specificity (proportion of absences correctly predicted) in absolute terms for the training dataset. By using this threshold, our objective was not to assess the ability of the models to predict potential areas of suitability but rather to assess their ability to predict areas the species actually occupies.

Based on this set of 960 modelled species, we first evaluated the significance of incorporating tree cover into the SDMs, in addition to climate and soil. Because of the high number of samples, we used pairwise comparisons of model performance among the four candidate models (C, CS, CT, and CST) with species as the sampling unit (Blach-Overgaard et al. 2010). Boxplots were drawn with boxes showing the interquartile range of the difference in model performance between two candidate models of a given species for each of the six possible combinations of pairwise comparison (C:CS, C:CT, C:CST, CS:CT, CS:CST, and CT:CST) and for each of the three measures of model performances (AUC, COR, and TSS). The notches inside the boxes indicate the 95% confidence interval around the median of the difference between the two candidate models. If the notches of a box do not overlap the zero horizontal line, there is strong evidence (95% confidence) that the median difference in model performance between the two candidate models differs from zero. Additionally, the statistical significance of these differences was also tested using Student's *t*-test, with the sample units (species) assumed to be independent.

Finally, we assessed the relative importance of the variables for the herb and shrub distributions by using hierarchical partitioning. For each species, we ran all possible models with different combinations of the six predictors, modelled as linear terms. Then, the independent contribution of each variable was calculated and partitioned based on the entire set of models.

Tree cover and community composition

If light-mediated plant–plant interactions drive herb and shrub distributions, then the proportion of shade-tolerant species within the community should increase with tree cover; i.e. tree cover should negatively correlate with the mean indicator values of the plot for light (L_{PMI}). Due to the nested nature of TC_{plot} within TC_{land}, the two variables are correlated, and their effects on herb and shrub distributions could be confounded ($r_s = 0.387$). We disentangled their independent effects by regressing L_{PMI} against TC_{plot} and/or TC_{land}, using partial regressions to assess the effect of each tree cover variable while accounting for the other.

Tree cover and the elevational range limits

To estimate the effect of tree cover, TC_{plot}, on the elevational range limits of lower-stature plants, we compared two extreme scenarios (i.e. low vs high tree cover) using either real observations or simulations. For the real observations, we first selected two subsets of vegetation plots among all the plots in the dataset: one subset of plots with low TC_{plot} values ($\leq 50\%$; $n = 1869$) and another subset of plots with high TC_{plot} values ($> 50\%$; $n = 4158$). Because the plots were not evenly distributed across the elevational gradient, we performed stratified random sampling to obtain two subsets of plots that were uniformly and equally distributed between 0 and 2200 m a.s.l., selecting 50 plots at each 50-m elevation interval whenever possible ($n = 1238$ for each subset; mean $TC_{plot} = 15.7$ and 81.5% for the low and high subsets, respectively; Supplementary material Appendix 5). Then, for each species within each subset, we ranked its occurrences along the elevational gradient and selected the 1st and 99th percentiles as the lower and upper elevational limits. To reduce uncertainties due to the stratified random sampling, we replicated this computation 10 times and then computed the mean values. Finally, for each species, we calculated the elevational differences between the low and high tree-cover areas at both its lower and upper elevational limits.

For the simulations, we used the most complex model (CST) at the plot grain to predict the elevational limits for each species under the low and high tree-cover scenarios. All predictor variables were set to their original values except for TC_{plot}, which was set to 10 and 90% to simulate low and high tree-cover conditions, respectively. Then, we used the predicted occurrences of a given species (translated to presence–absence predictions by applying the species-model-specific thresholds) and applied the same approach as that applied with the empirical data to calculate the elevational differences between the low and high tree-cover scenarios at both the lower and upper elevational limits. We also compared these results among the different shade-tolerance groups of species using Student's *t*-test and assuming the sample units (species) to be independent.

All analyses were performed using R 2.14.0 (R Development Core Team) and the dismo, gbm, hier.part, and ncf packages (Hijmans et al. 2012, Oksanen et al. 2012, Ridgeway 2012, Walsh and Nally 2013).

Table 1. Median, minimum and maximum values for the area under the curve of the receiver operating characteristic plot (AUC), correlation coefficient (COR), and true skill statistic (TSS) for 960 herb and shrub species modelled with different sets of predictor variables (C: climate; S: soil; and T: tree cover). Evaluation was performed on the test datasets with 25% of the total plots.

	Models	AUC [0.5 to 1]		COR [–1 to 1]		TSS [–1 to 1]	
		median	min–max	median	min–max	median	min–max
Plot	CST	0.945	0.581–0.999	0.400	−0.012–0.869	0.680	−0.011–0.965
	CS	0.941	0.558–0.999	0.382	−0.005–0.859	0.673	−0.007–0.968
	CT	0.928	0.607–0.999	0.331	−0.007–0.862	0.674	−0.004–0.977
	C	0.918	0.577–0.999	0.297	0.008–0.836	0.675	0.032–0.993
Landscape	CST	0.866	0.500–0.999	0.225	−0.014–0.784	0.507	−0.007–0.981
	CS	0.863	0.498–0.998	0.223	−0.014–0.780	0.488	−0.018–0.982
	CT	0.849	0.518–0.995	0.204	−0.018–0.776	0.535	−0.088–0.969
	C	0.844	0.386–0.995	0.193	−0.026–0.768	0.536	−0.234–0.968

Results

Fine- and coarse-grain tree cover effects for plot-level species distribution

Species distribution models with predictor variables calculated at the plot grain for the 960 herb and shrub species generally had higher performance than models with predictors at the landscape grain (Table 1). For both of these, the climate-only models (C) performed well, but including soil or tree cover (CS and CT models) improved the overall performance, except for TSS (Table 1 and Fig. 2). Furthermore, including tree cover in addition to climate and soil (CST models) resulted in an additional improvement in performance over the CS models (Table 1 and Fig. 2; paired $t_{(959)} = 5.273$ and $p < 0.001$ and paired $t_{(959)} = 4.359$ and $p < 0.001$ for AUC at the plot and landscape grain, respectively). Importantly, using TC_{land} with TC_{plot} as predictors with the climatic (C) and soil (S) variables improved the performance according to COR (paired $t_{(959)} = 2.947$; $p < 0.005$).

Focusing on the CST models, which showed the best model performances at both the plot and landscape grains, we found different patterns in the relative importance of

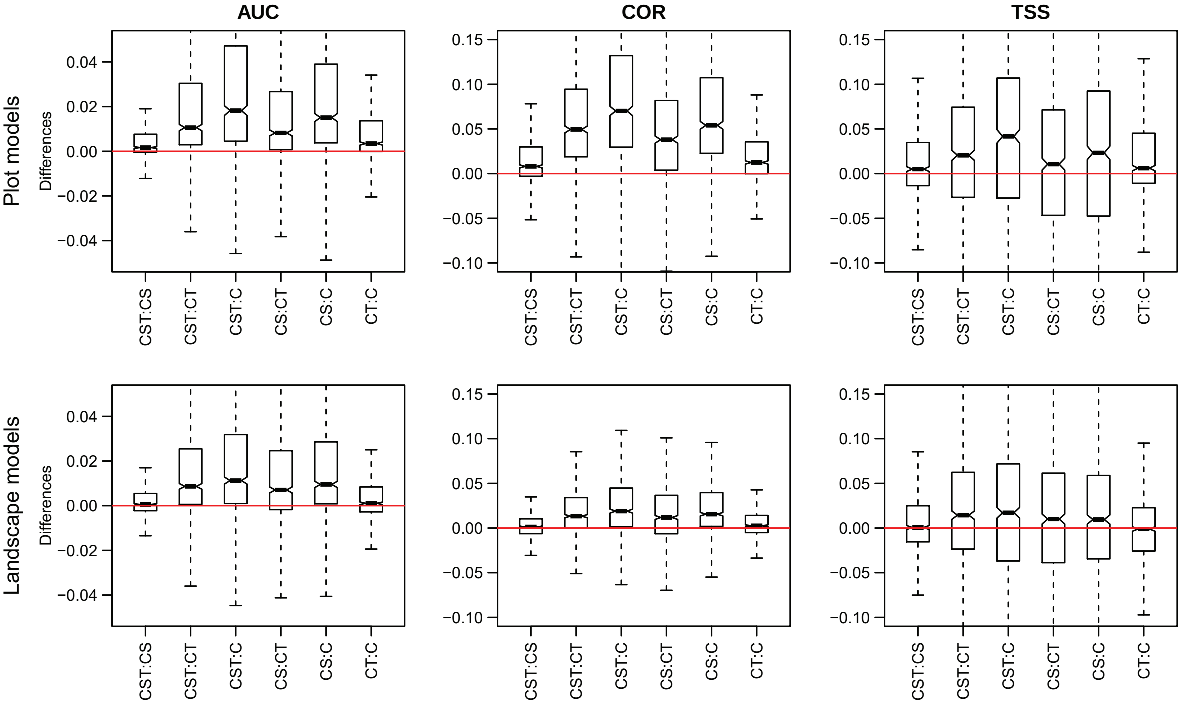

Figure 2. Pairwise comparisons of model performances for 960 herb and shrub species modelled with different sets of predictor variables (C: climate; S: soil; and T: tree cover) among four candidate models (C, CS, CT, and CST) and based on three different measures: area under the curve of the receiver operating characteristic plot (AUC), correlation coefficient (COR), and true skill statistic (TSS). Boxplots show the difference in model performance between two candidate models of a given species for each of the six possible combinations of pairwise comparison (C:CS, C:CT, C:CST, CS:CT, CS:CST, and CT:CST) and for each of the three measures of model performances (AUC, COR, and TSS). Notches inside the boxes indicate the 95% confidence interval around the median of the difference between the two candidate models. The horizontal line represents no difference between the candidate models, and the two candidate models differ in performance when there is no overlap between the notches of a given box and this line. Note the change in scale for AUC.

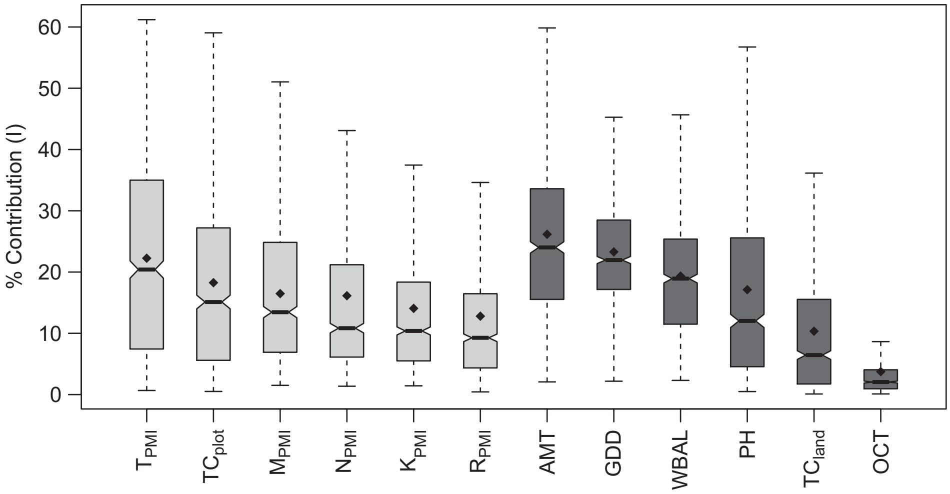

Figure 3. Relative variable importance (I) for 960 herb and shrub species as independent variance explained by each variable (as linear predictors) in a hierarchical partitioning with all the predictor variables as linear terms. Boxplots show the per cent contributions across all species. Diamonds represent mean values. Variables are ordered by decreasing relative importance. Variables are coloured by scale, with the plot-grain variables in light grey: air temperature (T_{PMI}), continentality (K_{PMI}), soil moisture (M_{PMI}), nutrients (N_{PMI}), soil reaction (R_{PMI}) and tree cover at the plot-grain (TC_{plot}); and the landscape-grain variables in dark grey: growing degree days (GDD), absolute minimum temperature (AMT), water balance (WBAL), organic content of the top soil (OCT), soil reaction (pH) and tree cover at the landscape grain (TC_{land}).

each predictor variable (Fig. 3). At the plot grain, T_{PMI} was by far the most important predictor variable, followed by TC_{plot} and M_{PMI}. Hence, TC_{plot} was more important than some climatic (K_{PMI} and M_{PMI}) and soil variables (N_{PMI} and R_{PMI}). At the landscape grain, AMT was the most important predictor variable, followed by GDD

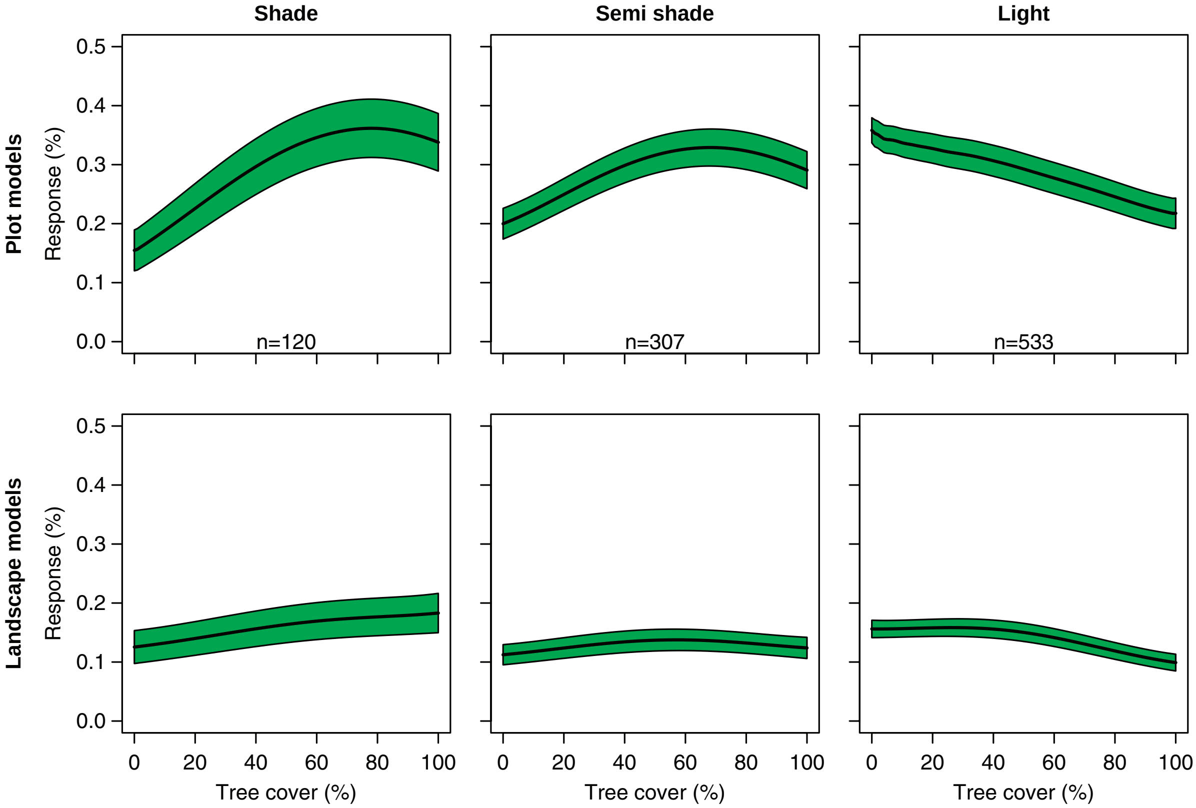

Figure 4. Mean response curves of all 960 species to the tree cover gradient using CST models at both plot and landscape grain. The black line represents the mean response curve, and the green area shows the 99% confidence intervals. To compute these response curves, all other predictor variables were set to their mean values. The total number of herb and shrub species in each shade tolerance group (L1–L2 for shade; L3 for semi-shade; and L4–L5 for light) is at the bottom of the graph.

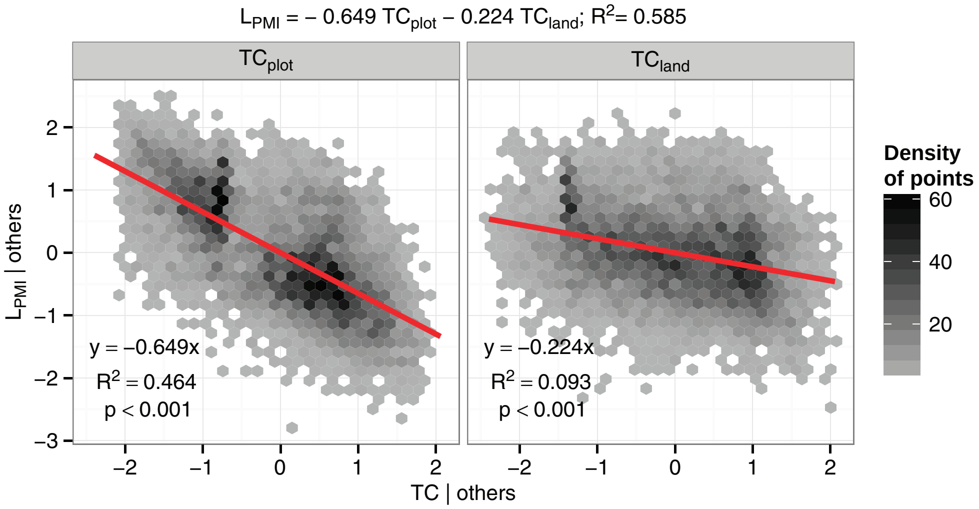

Figure 5. Pure effect of plot-grain tree cover (TC_{plot}) on the plot mean indicator value for light (L_{PMI}) after accounting for the effect of landscape-grain tree cover (TC_{land}) on L_{PMI} and pure effect of TC_{land} on L_{PMI} after accounting for the effect of TC_{plot} on L_{PMI}. All regression analyses were performed with standardised values. Hexagons represent point densities in a grey scale.

and WBAL. Tree cover at the landscape grain (TC_{land}) was less important than at the plot grain but still more relevant than OCT (Fig. 3). The response curves of different species along the tree-cover gradient, as estimated by the CST models, differed among the colline, montane and subalpine groups of herb and shrub species (Fig. 4). As expected, the shade-tolerant species showed an increasing probability of occurrence with higher values of tree cover, whereas shade-intolerant species showed a decreasing trend with higher tree cover, with the semi-shade-tolerant species having an almost flat response curve.

Fine- and coarse-grain tree cover effects on plot-level community composition

Both TC_{plot} and TC_{land} had negative effects on L_{PMI} (Fig. 5) and together explained a large percentage (58.5%) of the lower-stature plant species composition in terms of their shade tolerance. Partial regressions showed that TC_{plot} and TC_{land} had significant independent effects (Fig. 5), with a stronger unique effect of TC_{plot} (46.4% explained variance) than TC_{land} (9.3%).

Tree cover modifications of elevational range limits

Testing the effect of changes in tree cover at the plot grain on the elevational range limits of lower-stature plants, we found contrasting patterns depending on species shade tolerance (Fig. 6). Based on the empirical data, the elevational range of shade-intolerant species was narrower under high tree cover conditions due to negative differences at the upper limits for the colline and montane species groups and due to both negative and positive differences at the upper and lower limits, respectively, for the subalpine species group. In contrast, the elevational range of shade-tolerant species was greater under high tree cover due to negative differences at the lower limits for the colline species group and due to both negative and positive differences at the lower and upper limits, respectively, for the montane and subalpine species groups. Semi-shade tolerant species showed weaker patterns with no clear trend. The outputs from the simulations were largely consistent with the results based on observations, although with a tendency to predict weaker tree-cover effects than were empirically observed (Fig. 6).

Discussion

This study provides the first broad-scale quantitative assessment of the role of tree cover in the distributions of multiple herb and shrub species and their elevational range limits at two contrasting spatial grains (coarse vs fine). Notably, we found that tree cover was correlated with distribution and community patterns not only at the vegetation plot level but also at a much coarser grain, near 1-km. These results are thus in line with recent findings regarding the effects of biotic interactions at large spatial scales (Gotelli et al. 2010, Wisz et al. 2013), exemplifying how local interactions could be observable at coarser grains (but see Cooper and Belmaker 2010). Additionally, the results suggest that tree cover could lead to important modifications in the elevational range limits of plant species based on their shade tolerances, suggesting an important role of biotic interactions such as competition and facilitation.

Plant–plant interactions are important at coarse spatial grains

Tree cover improved the overall performance of the models for herb and shrub species distributions (Fig. 2). The pairwise comparisons between the candidate models suggest a secondary but important role of tree cover relative to climate

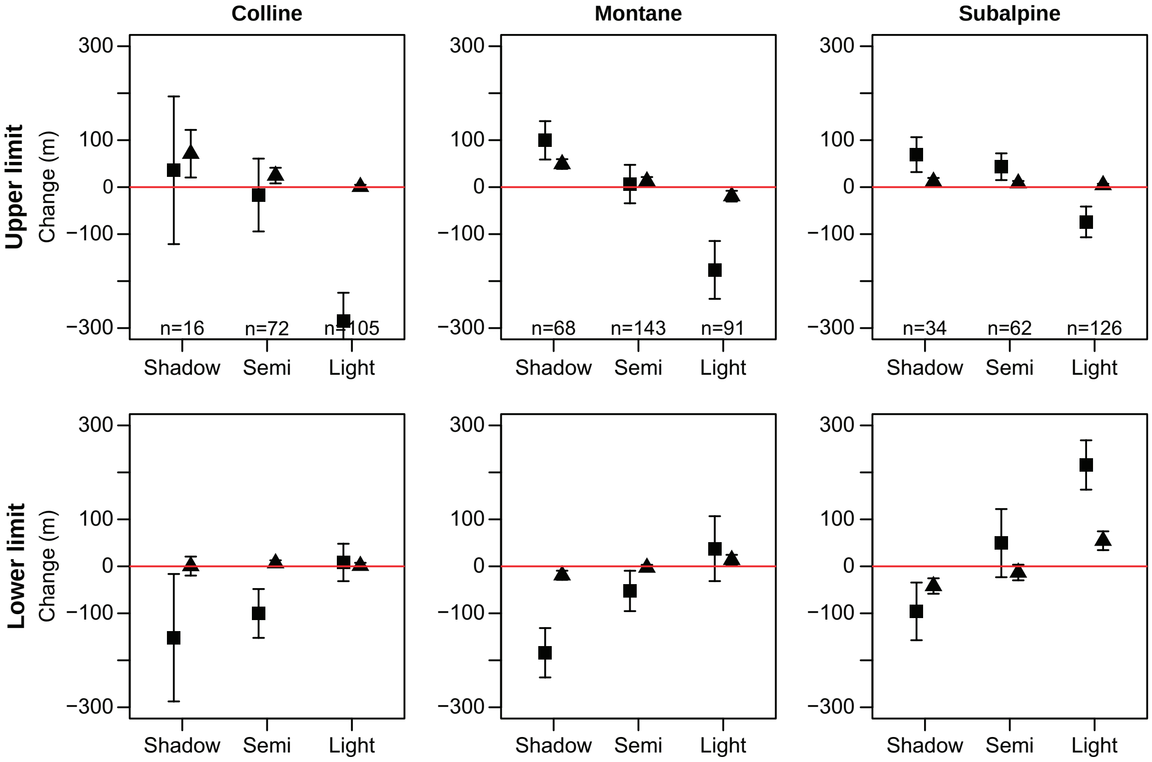

Figure 6. Differences in the elevational range limits of different species between low and high tree cover conditions for 717 herb and shrub species: 193 from the colline belt, 302 from the montane belt and 222 from the subalpine belt. Squares indicate observed differences based on empirical data between high (> 50%) and low tree cover (≤ 50%), subtracting the latter from the former. Triangles show the same differences based on simulated data obtained from the predictions of the CST models at the plot grain. The simulation was run with the predictor variables for each plot at their calibration values, except for tree cover, which was set at 90% and 10% to simulate high and low tree cover, respectively. Bars indicate the 99% confidence intervals for the mean values calculated with one-sample Student's *t*-tests. Horizontal lines indicate no difference in the elevational distribution of the species between the high and low tree cover conditions.

and soil variables. The analysis of variable contributions (Fig. 3) for the most complex models (CST) showed that tree cover is more important than soil for models at the plot grain. At this grain, tree cover played a stronger role than at the coarse landscape grain (Fig. 3), likely reflecting the direct effect of the nearest neighbouring trees (Fig. 4) on herb and shrub distributions.

When the predictor variables were measured at the landscape grain, climate remained the main driver, but soil became more important than tree cover (Fig. 3). The changes in variable importance across spatial grains could reflect the differences between the two sets of predictors (i.e. their time frame, origin, and the particular variable represented). Regardless of this grain-dependent change, tree cover still improved model performance at the coarser grain (Fig. 2). Additionally, including TC_{land} with TC_{plot} in the CST models provided small but significant improvements in model performance. Interestingly, response curves along the tree cover gradient at the landscape grain were similar to those at the plot grain, although more flattened (Fig. 4), suggesting that shade-tolerant species might be favoured not only by dense tree cover in their direct vicinity but also by being in a forested landscape, and vice versa for shade-intolerant species. These tree cover effects extended up to 1 km for most species and even further in some cases (see Supplementary material Appendix 6 for a supplementary analysis).

The community-level analysis confirmed the structuring role of tree cover in terms of shade tolerance. Indeed, the significant negative effects of tree cover at both plot and landscape grain on the community-based index of light conditions were consistent with the results of the SDMs (Fig. 5). Furthermore, partial regression analyses showed 1) that tree cover in the direct vicinity is more important than tree cover in the surrounding areas and 2) that their effects act independently of each other, with only a small proportion of shared variation (3.2%). These patterns (Fig. 4–6) suggest that tree cover could affect plot-level species occurrences not only via direct local processes (Gravel et al. 2010, Wisz et al. 2013) but also via landscape-scale effects, e.g. metapopulation dynamics (Eriksson 1996, Ehrlén et al. 2006). In accordance with Bullock et al. (2000), who showed that competition between related plant species could have effects at coarse spatial grains, the results contradict the generalised idea that biotic interactions primarily matter at local and fine spatial grains (Pearson and Dawson 2003). Our findings highlight the importance of considering biotic interactions (e.g. plant–plant, plant–pollinator or plant–grazer interactions) in large-scale studies of plant distributions and diversity patterns (Greve et al. 2012), including predictive models projecting future climate and land use changes (Araújo and Luoto 2007, Thuiller et al. 2013).

Plant–plant interactions relate to shade tolerance

Species response curves along the tree cover gradient (Fig. 4) clearly differed in shade tolerance. Notably, shade-tolerant species were positively correlated with tree cover. This pattern suggests that these species benefit from the altered abiotic conditions that a dense tree cover offers, resulting in a wider elevation range than under low tree cover, in otherwise unsuitable conditions (Fig. 4 and 6). However, shade-intolerant species were negatively correlated with dense tree cover at both elevational range limits and thus had a narrower elevation range than at low tree cover despite the regionally suitable climatic conditions (Fig. 4 and 6).

For shade-intolerant species, tree cover showed an asymmetric pattern regarding elevational limits. For subalpine shade-intolerant species, an increase in tree cover increased the lower elevational range limits, whereas it did not modify the upper limits (Fig. 6). Such a trend would be consistent with the asymmetric-abiotic-stress-limitation hypothesis (AASLH), suggesting that tree cover could act as the limiting factor, through light competition, that sets the lower elevational range limits of shade-intolerant plant species distributions (Normand et al. 2009). For colline and montane shade-intolerant species, an increase in tree cover decreased the upper elevational range limits (Fig. 6). Such a trend suggests the negative effects of biotic interactions through competition towards the upper elevational range limits of plant species distributions, which is inconsistent with both the stress gradient hypothesis (SGH) and AASLH, since SGH propose positive effects through facilitation (Callaway et al. 2002) and AASLH purely abiotic constraints at the upper elevational range limit (Defossez et al. 2011, Kikvidze et al. 2011, Pottier et al. 2013).

For shade-tolerant species in the montane and subalpine vegetation belts, an increase in tree cover increased the upper and decreased the lower elevational range limits (Fig. 6), most likely reflecting facilitation processes. Although these results would support the importance of biotic interactions in determining both limits of species ranges (Callaway et al. 2002), they are a deviation from the SGH, which predicts an increase in competition and a decrease in facilitation as abiotic stress decreases (Maestre et al. 2009). Such a pattern (deviating from the SGH) towards the lower elevational range limit most likely reflects the fact that most lowland areas are human-altered open habitats (Supplementary material Appendix 7).

Implications of the use of biotic interactions in species distribution models

The addition of tree cover generally improved the model predictions of herb and shrub species distributions compared with models including only climate and soil variables, especially for the threshold-independent measures (Table 1). These results are thus in line with the increasingly recognised importance of including biotic factors as important drivers in SDMs (Gilman et al. 2010, McMahon et al. 2011, Kissling et al. 2012, Linder et al. 2012, Boulangeat et al. 2012, Wisz et al. 2013). However, several factors have prevented their extensive inclusion in SDMs so far. On the one hand, knowledge of interacting species and the nature of the interaction are required but not always available. To manage this problem, exploratory analyses on co-occurrences have been performed (Pellissier et al. 2010, Kunstler et al. 2011, 2012), or interactions have been inferred between congeners or species with similar environmental requirements (Meineri et al. 2012). However, these approaches should be carefully implemented because they can lead to misinterpretations if some important variables or species were not included in the analyses, if the supposed interactions do not apply, or if the interacting species do not have overlapping distributional ranges (Ovaskainen et al. 2010, Meineri et al. 2012). On the other hand, biotic interactions can involve multiple species, which would reduce the impact of any abiotic variable included in these models (Kissling et al. 2012). As an alternative, we used a synthetic index that summarises the information regarding biotic interactions through one or few variables, representing the effect itself (as a modulator in the sense of Linder et al. 2012) instead of the numerous species that generate it (Boulangeat et al. 2012).

Our results also have implications for the use of SDMs to predict plant responses under climate change scenarios and biodiversity conservation. Such responses are increasingly recognised as not being as straightforward (Dullinger et al. 2012) as initially thought (Lenoir and Svenning 2014), for example simple poleward and upward range shifts (Parmesan 2006, Wilson et al. 2007, Lenoir et al. 2008). Indeed, the results of the present study suggest that biotic factors can be important additional drivers that influence species-specific range shifts. The long life cycles of trees, however, implies long time periods to generate such vegetation dynamics (Lenoir et al. 2008, Svenning and Sandel 2013), and therefore, dynamic models accounting for transient population dynamics should ideally be used to predict the future of plant distribution and diversity (Araújo and Luoto 2007, Meier et al. 2011, 2012, Dullinger et al. 2012, Hof et al. 2012, Thuiller et al. 2013).

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Supplementary material (Appendix ECOG-00954 at <www.ecography.org/readers/appendix>). Appendix 1–7.