Colonization and extinction dynamics match the distribution of European trees at continental scale

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Abstract

- **Aim:** Processes driving current tree species distribution are still largely debated, and uncertainties about processes at play remain. Attempts to relate environmental factors and population related metrics have shown mixed results, and the link between tree species range and their population dynamics are unclear. In this context, we would like to test the hypotheses that meta-population processes of colonization and extinction drive species distributions. - **Location:** Europe: Spain, France, Germany, Finland, and Sweden. - **Taxon:** Angiosperms and Gymnosperms. - **Methods:** For the 17 tree species analyzed we fitted species distribution model (SDM) relating environmental variables to presence absence data across Europe. Then using harmonized national forest inventories across Europe we tested whether colonization and extinction probabilities are related to occurrence probability estimated by the SDMs. Finally, we tested whether the equilibrium probability of presence derived from these models of colonization and extinction match the observed species distribution. - **Results:** We found that for most species that colonization probabilities increased with increasing occurrence probability, and conversely extinction probabilities decreased. We found that the equilibrium probability of presence derived from simple meta-population models was positively correlated but generally overestimated the SDM occurrence probability. - **Main conclusions:** Our study supports the view that meta-population dynamics are partly related to SDM occurrence probability. The over estimation of our simple meta-populations models probability of occurrence at equilibrium could be related to simplification of dispersal processes.

1 Introduction

The vast majority of species have restricted geographical range distributions (Holt & Keitt, 2000). Understanding the factors determining these ranges is fundamental to have insights on future species redistribution in the face of climate change. Species distribution is thought to be tightly connected to its ability to cope with local abiotic conditions and thus species' niche (Pulliam, 2000; Thuiller, Lavorel, & Araújo, 2005; Soberón, 2007). This view underpins most statistical species distribution models (SDM) that relate species presence with local environmental conditions. These models have been extensively used in recent years and provided very detailed descriptions of species environmental requirements based on occurrence data. They provide, however, very little indication on how species distribution arise from population dynamics. This is surprising because we start to have a rich theoretical understanding of how population dynamics controls species distribution and species range (Holt, Keitt, Lewis, Maurer, & Taper, 2005). The first and most classical view is that species ranges match the environmental conditions where birth rates exceed mortality rates (i.e. where the rate of population growth is above 1, Brown (1984)), but most existing studies did not support this assumption, see the review by Pironon et al. (2017). For instance, Thuiller et al. (2014) demonstrated that major demographic parameters of European tree species were not strongly correlated to the probability of occurrence derived from SDMs. Generally, only transplant experiments beyond species range have shown tendency of a decrease in population growth rate or some demographic rates (Hargreaves, Samis, & Eckert, 2013; Lee-Yaw et al., 2016). In addition, several studies did not find strong support for the abundance center hypothesis which propose that abundance should be higher in the center of the distribution (Murphy, VanDerWal, & Lovett-Doust, 2006; Sagarin, Gaines, & Gaylord, 2006).

A second class of theoretical explanations rely on the idea that demographic stochasticity increases close to species ranges and limits the persistence of the populations (Holt et al., 2005). Indeed, variability in demographic rates due to environmental variability, as well as stochastic demographic events, can have a considerable impact on population persistence (Boyce, Haridas, Lee, & Group, 2006; Ovaskainen & Meerson, 2010). Field tests of these mechanisms are extremely rare, and show weak support for this hypothesis. Csergő et al. (2017), using detailed demographic data for plant species (including trees), found no clear link between climate suitability, derived from a SDM, and several detailed population metrics including time to quasi-extinction, stochastic population growth rate or transient population dynamics.

The last class of mechanisms underlying species ranges is a regional equilibrium between colonization/extinction and dispersal (Holt et al., 2005; Holt & Keitt, 2000). This last category relates to the meta-population paradigm and proposes that species ranges arise from the gradient of three variables: the extinction rate, the colonization rate, and the habitat structure. An important simplification is that the dynamic of the local population is ignored when compared to regional dynamics (Drechsler & Wissel, 19997). Such models thus ignore the details of the population dynamics but rather focus on patch occupancy dynamics (extinction and colonization events). Few studies have focused on these processes for tree species (see Purves, Zavala, Ogle, Prieto, & Benayas, 2007; García-Valdes, Zavala, Araújo, & Purves, 2013; García-Valdés, Gotelli, Zavala, Purves, & Araújo, 2015; Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017). Results in North America (Tal-

luto et al., 2017) showed that metapopulation processes captured range shifts for most tree species. García-Valdes et al. (2013) inferred potential changes in species distribution in Spain, but we still lack studies that explore this mechanism at the European scale, covering a larger portion of species distribution.

Here we propose to analyze species extinction and colonization events at the local scale for the main tree species in Europe across their entire continental distribution using national forest inventories data for more than 80 000 plots. We decompose a colonization event as an outcome of a seed input and a successful recruitment. To describe environmental species distribution we use species occurrence probability estimated with ensemble SDM to the EU-Forest data set (Mauri, Strona, & San-Miguel-Ayanz, 2017), a large scale presence absence dataset over continental Europe.

We then analyze the relationship between the probability of occurrence derived from SDMs and the extinction/recruitment rates derived from NFI data to test the following hypothesis:

- Extinction rates increase when the SDM occurrence probability decrease.
- Recruitment rates decrease when the SDM occurrence probability decrease.
- The equilibrium probability of presence deduced using the estimated extinction/recruitment rates is coherent with the current SDM occurrence probability.

This allows us to evaluate the relative importance of extinction and recruitment in driving the range for different species. Finally, we discuss the implication of our results for the degree of equilibrium with current climate of these species.

2 Materials and Methods

For our analysis we first gathered data on tree population local extinction and colonization events from national forest inventories plots. Then, we computed the occurrence probability with SDM models fitted to the EU-Forest data. Subsequently, we modeled extinction and recruitment rates in function of SDM occurrence probability with two observations of occupancy data via a spatially inhomogeneous Markov chain. To represent the seed source needed for model calibration, we used estimation of species local frequency in 1 km grid which account for forest cover at a finer scale (JRC maps, see section 2.2). Finally, we derived the probability of presence at equilibrium based on the estimated extinction and recruitment rates.

2.1 NFI datasets

To calibrate our model, we required information on the presence/absence of each species at two different dates over a large geographical area to cover, as far as possible, the entire species distributions. We used a database of tree data from the National Forest Inventories (NFI) of Finland, France, Germany, Spain, Sweden, compiled as part of the FunDivEurope project (http://www.fundiveurope.eu, Baeten et al. (2013)).

Inventory protocols differed between NFIs (see Appendix section 1 for a detailed description of each survey protocol). Surveys were conducted within a circular plot with a fixed radius or in concentric subplots with different radius and minimum diameter at breast height (DBH) for all NFIs except Germany, where an angle-count method (basal area factor of 4 m^2ha^{-1}) was used. Because the DBH thresholds for trees to be recorded varied between the inventories, we only included trees with a DBH of 10 cm or greater. For each NFI, except France, two inventory surveys were conducted with a variable time interval (from 4 to 16 years, see Figure 1 b). The French inventory is based on single surveys where the growth of alive trees (based on a short core) and approximate date of death of dead trees are estimated and can be used to reconstruct the stand structure five years before the census, making it comparable with revisited plots data.

To avoid influences of management on the extinction and colonization events, we discarded plots where a management effect was reported between surveys. This led to a selection of 80 157 plots with 173 species. Within these species we selected the most abundant species (the cumulative basal area of species retained represented more than 95 % of the total basal area) and excluded exotic species and species for which maps of local presence were not available. This resulted in a selection of 20 species.

For each plot, a species was considered as present when at least one tree was observed. The succession of two surveys allowed then to deduce state transitions ($0 \rightarrow 1$ for local colonization, $1 \rightarrow 0$ for local extinction). Since several protocols are based on concentric circular plots with varying DBH thresholds, a newly observed tree might not be a recruited tree: its DBH during the first census was above 10 cm, but it was not recorded due to the higher DBH threshold for the subplot. We used a species specific growth model to estimate the probability that a new tree (present only in the second census) had a former DBH below 10 cm. The growth model was built as a generalized linear model using an aridity index, the sum growing degree days and tree DBH as explanatory variables. We thus considered a plot as colonized if the probability that the largest newly observed tree had a former DBH below 10 cm greater or equal to 0.5, otherwise the species was considered as present at both censuses ($1 \rightarrow 1$). This correction had a strong impact on the Spanish and German inventories, significantly reducing the number of colonization events. We decided to exclude from further analysis species with less than 10 events for extinction or colonization (*i.e. Quercus suber*, *Pinus pinea* and *Acer pseudoplatanus*), resulting in a final selection of 17 species.

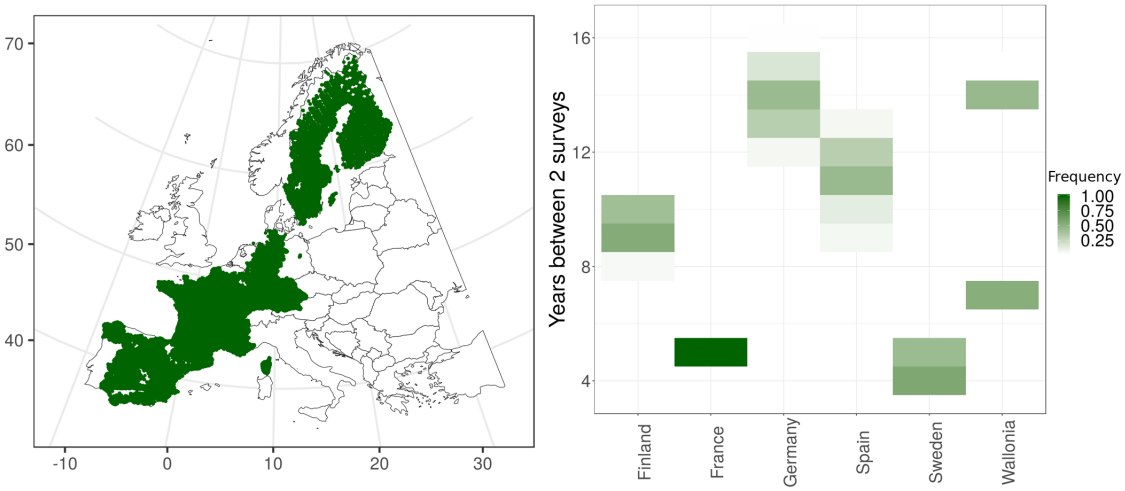

Figure 1: (a) :Locations (fuzzied at 500 m) of the NFI plots in Spain, France, Germany, Finland, and Sweden. (b) Distribution of number of years between subsequent surveys by country

2.2 Joint research center - species local frequency

The density of NFI plots is too low to accurately describe the local abundance of trees that can disperse seeds into the plot. Distances between NFI plots are about 1 km or above whereas most dispersal events occur in less than 100 m from the seed source (see for example Nathan, Safriel, and Imanuel (2001), Bullock et al. (2017)). To represent seed input into a plot, we thus used the species' local frequency (hereafter F_{JRC}) in the corresponding 1 km cell produced by the Joint Research Center (RPP - Relative Probability of Presence on JRC website https://forest.jrc.ec.europa.eu/en/european-atlas/atlas-data-and-metadata/), see San-Miguel-Ayanz, de Rigo, Caudullo, Houston Durrant, and Mauri (2016). Each map estimates the relative frequency of the species based on datasets of field observations as represented in the Forest Information System for Europe (FISE), which integrates National Forest inventories, BioSoil and Forest Focus datasets. The presence/absence data are assimilated at a spatial resolution of 1 km based on multiple smoothing kernels of varying dimension. Independent estimations of forest cover extracted from the Pan-European Forest Type Map 2006 (FTYP2006, http://forest.jrc.ec.europa.eu/forest-mapping/forest-type-map) are then used to rescale the species frequency by the cover of broadleaved forest, coniferous forest or other non-forest categories based on 25 m x 25 m pixels. We have chosen this variable because it summarizes a very large amount of data on a European scale and can be considered as an strong indicator of the proportion of adjacent plots in which the species is present within a 1 km patch.

2.3 SDM

We estimated species occurrence probability (P_{occ}) on each NFI plot with ensemble species distribution models fitted to the EU-Forest data set (Mauri et al., 2017) which provides species presence/absence on a 1 km grid. For each grid point we extracted mean annual temperature, precipitation of wettest quarter, temperature and precipitation seasonality from CHELSA climatologies (Karger et al., 2017), pH from SoilGrid (Hengl et al., 2017), and aridity index and actual evapotranspiration from CGIAR-CSI (Trabucco & Zomer, 2010). Then we fitted ensemble SDM models with BIOMOD2 (Thuiller, Lafourcade, Engler, & Araújo, 2009) using four different models (GAM, GLM, GBM, and Random Forest). Based on this ensemble model we estimated species occurrence probability on each NFI plot for all analyzed species. Details on the evaluation on the predictive power of the SDM are provided in the Appendix section 2 (see Figure 1 with performance scores of SDM for each species based on True Skill Statistic, TSS and Area Under the Curve of the Receiver Operating Characteristic, AUC).

2.4 Patch occupancy transition model

The patch occupancy model is a spatially inhomogeneous Markov chain, the state vector being the patch occupancy of the N plots $X(t)$ at time t and the probability of transition between the two time successive patch occupancy patterns is:

$$P[\mathbf{X}(t+1)|\mathbf{X}(t)] = \prod_{i=1}^{N} \left[\begin{array}{llll} 1 - C_i(t) & if\ X_i(t) = 0 & and & X_i(t+1) = 0 \\ C_i(t) & if\ X_i(t) = 0 & and & X_i(t+1) = 1 \\ E_i(t) & if\ X_i(t) = 1 & and & X_i(t+1) = 0 \\ 1 - E_i(t) & if\ X_i(t) = 1 & and & X_i(t+1) = 1 \end{array} \right. \tag{1}$$

with N being the total number of plots observed, E_i the extinction probability in plot i, C_i the colonization probability in plot i.

The extinction probability (E) of a species in a plot only depends on the local grid conditions, i.e. the occurrence probability derived from the SDM (P_{occ}). The colonization probability (C) is divided into two contributions: recruitment probability (R) which depends P_{occ}, and seed availability (S). The recruitment probability R is the probability for at least one tree to reach 10 cm between two protocols, therefore integrates both growth and survival of the early stages of trees.

Colonization probability is simply expressed as the product of R and S, and each patch with a non-null seed availability can experience a colonization event. An explicit representation of seed availability via dispersal mechanisms was beyond the scope of this work because available data do not provide a detailed description of the seed source in the plots surroundings from where most dispersal events occur (Nathan et al., 2001). Because the JRC species local frequency data is based on the spatial integration of presence-absence observations, our seed source estimate can be influenced by data beyond the 1 km grid and long-distance seed dispersal events are not excluded.

Recruitment (R) and extinction (E) probabilities were related to the SDM occurrence probability P_{occ} with the following equations:

$$\begin{array}{l} logit(E_i) = \alpha + \beta * P_{occi} \\ logit(R_i) = \gamma + \delta * P_{occi} \\ C_i = R_i * S_i, with\ \ S_i = F_{JRCi} \end{array} \tag{2}$$

Differences in protocols between countries can influence the probability of observing the species and thus the probability of observing extinction and colonization events. To account for this protocol effect in our analysis we used fixed country specific intercept parameters (α and γ) as conventionally done. Given the low number of extinction and colonization events per species, it was not possible to include additional explanatory variables.

Because the time interval between two censuses may vary across plots (between 4 and 15 years), we standardized the parameters to a 5 years sampling interval as done in Talluto et al. (2017), the probability of an recruitment/extinction was computed as:

$$P(Event) = 1 - (1 - P(Event_{5years}))^{\frac{n}{5}} \tag{3}$$

with n being the number of years between the two censuses.

2.5 Calibration of the model

For each species, extinction and recruitment parameters were estimated separately using a Metropolis Hastings Monte Carlo sampling algorithm, with priors following a Cauchy distribution (Gelman,

Jakulin, Pittau, & Su, 2008; Ghosh, Li, & Mitra, 2018) using JAGS (Plummer, 2003). Convergence was checked by evaluating whether the Gelman-Rubin convergence statistic was below 1.1, as recommended by Brooks and Gelman (1998), using 4 chains.

2.6 Probability of presence at equilibrium

Given estimates of recruitment and extinction probabilities, one can derive a probability of presence at equilibrium (hereafter P_{eq}). The equilibrium can be defined in two ways. (1) We can assume that grid cells are open systems with a fixed seed source S, where the probability of presence in the grid cell is a function of extinction, recruitment and the value of seed source. In this case there is no feedback of the colonization and extinction on the seed source. (2) We can assume that grid cells are closed systems of interconnected suitable patches, with a feedback of the colonization and extinction processes on the seed source. In this case, an extinction probability exceeding the colonization probability would lead to a species absence.

Both types of equilibrium can be derived from the same equation:

$$\frac{dp}{dt} = C * (1 - p) - E * p = 0 \tag{4}$$

with p the proportion of suitable patches occupied.

The difference between the two types of equilibrium corresponds to different formulations of C. In the first formulation, S is constant over time and $C = R \times S$, while in the second formulation, S varies with P_{occ} and $C = p * R$. These two alternative formulations lead to the following equilibria:

- (1) when we consider a fixed seed source, and compute the equilibrium state for each plot: $P_{eq} = \frac{R \times S}{R \times S + E}$,
- (2) when we consider that the seed source is linked to the proportion of occupied patches within each 1 km grid cell, then the proportion of suitable occupied patches is $P_{eq} = (1 - \frac{E}{R})$.

For both formulations, we studied the relative impact of extinction and colonization (including seed availability and recruitment probability) on the equilibrium state by fixing one of the probabilities to its mean and letting the other vary based on our estimated slope of response to the SDM probability of occurrence. We also computed the probability at equilibrium, letting both extinction and colonization vary with P_{occ}. In the first model we can also set the fixed seed source to one (no dispersal limitation) or let the fixed seed source vary with P_{occ} based on their correlation.

3 Results

3.1 Recruitment/Extinction dependencies

For most species, recruitment probability increased with the SDM occurrence probability, and extinction probability decreased with the SDM occurrence probability, see Figure 2.

When considering recruitment probability, slopes were significantly positive (confidence interval not intercepting zero) except for *Quercus petraea*, *Abies alba* and *Picea abies* (see Table 1). For these species, the model fit was poor as indicated by their low value of ΔDIC (difference of deviance information criterion – DIC – between the model and a null model). No species showed a significant negative slope, i.e. a significant increase of recruitment probability when reaching the edge of the climatic niche.

For extinction, slopes were significantly negative (confidence interval not including zero), for all species except *Pinus nigra*, *Quercus pubescens*, *Pinus pinaster* and *Pinus halepensis* (see Table 2). These four species had the lowest value of ΔDIC. Only *Pinus pinaster* showed a posterior distribution of the slope that can be considered strictly positive.

Some species, such as *Populus tremula*, *Acer campestre* and *Alnus glutinosa*, exhibited a very broad posterior for the slope parameters. This is probably related to the small range of probabilities of occurrence for these species.

Model performances according to the True Skill Statistics (TSS, see (Allouche, Tsoar, & Kadmon, 2006)) varied from good ($TSS > 0.5$), average ($0.3 < TSS < 0.5$), to poor ($TSS < 0.3$) depending on the species and process (Tables 1 and 2). Recruitment models showed good performance for all species but *Quercus pubescens*. Extinction models showed average performance for 10 (59 %) species but poor performance for *Pinus halepensis, Pinus pinaster, Quercus ilex, Populus tremula* and *Quercus pubescens* and good scores for *Quercus petraea* and *Quercus pyrenaica*. Model scores were not related to the number of observations. Given the scarcity of colonization or extinction events, we also tested the robustness of our results by resampling data to decrease the number of zero and found that the results were robust to the prevalence of the extinction or colonization events (see Appendix section 4).

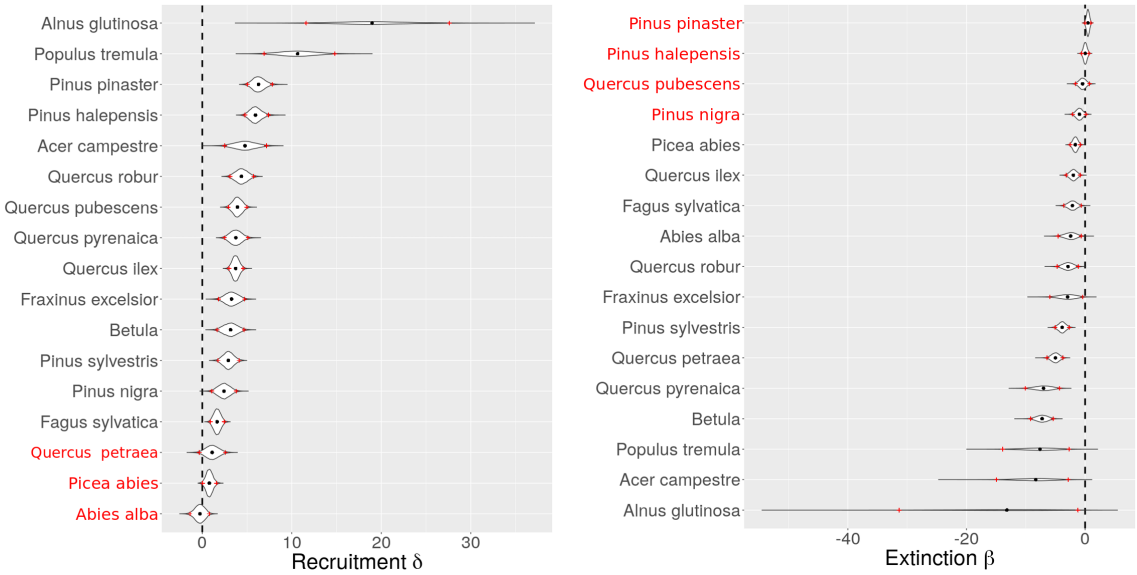

Figure 2: Posterior distribution of the slope of response of recruitment (left, δ) and extinction (right, β) to P_{occ}. Black points are posterior medians, red crosses indicate the 95th percentile intervals. Species in red have their interval crossing 0.

Species	Nb of events	Median β	95% Interval β	TSS	Δ DIC
Pinus sylvestris	149	2.9	1.8/4.1	0.60	-25.5
Picea abies	231	0.8	0.0/1.6	0.73	-2.7
Fagus sylvatica	160	1.7	0.9/2.4	0.62	-17.0
Quercus robur	103	4.4	3.1/5.7	0.65	-46.6
Quercus petraea	48	1.1	-0.3/2.6	0.66	1.3
Pinus pinaster	66	6.3	5.0/7.8	0.82	-118.9
Quercus ilex	351	3.7	3.0/4.6	0.64	-122.7
Pinus nigra	48	2.4	1.1/3.8	0.74	-11.4
Abies alba	53	-0.3	-1.4/0.8	0.63	1.3
Pinus halepensis	50	5.9	4.8/7.4	0.90	-136.2
Quercus pubescens	87	3.9	2.9/5.0	0.76	-61.4
Betula	265	3.2	1.7/4.7	0.58	-20.5
Fraxinus excelsior	121	3.3	1.8/4.7	0.53	-17.4
Quercus pyrenaica	85	3.7	2.5/5.1	0.85	-40.0
Alnus glutinosa	47	19.0	11.6/27.6	0.64	-25.8
Populus tremula	73	10.7	6.9/14.8	0.61	-32.7
Acer campestre	97	4.8	2.5/7.2	0.69	-15.7

Table 1: Estimates of β, the slope of recruitment response to P_{occ} per species and their 95% confidence interval (see Materials and Methods for details on the model). ΔDIC is the difference of deviance information criterion – DIC – between the model and a null model. TSS is the True Skill Statistics. Nb of events is the number of colonization events. TSS are calculated using the median of parameter posterior distributions.

Species	Nb of events	Median α	95 % Interval α	TSS	Δ DIC
Pinus sylvestris	151	-3.9	-5.1/-2.7	0.27	-43.6
Picea abies	98	-1.7	-2.5/-0.8	0.31	-13.2
Fagus sylvatica	44	-2.1	-3.6/-0.8	0.31	-7.5
Quercus robur	70	-2.9	-4.5/-1.3	0.38	-11.4
Quercus petraea	101	-5.0	-6.4/-3.7	0.44	-67.8
Pinus pinaster	227	0.5	0/1.0	0.18	-1.7
Quercus ilex	50	-2.0	-3.2/-0.8	0.24	-9.7
Pinus nigra	67	-1.0	-2.1/0.1	0.15	-1.0
Abies alba	18	-2.5	-4.6/-0.6	0.35	-6.4
Pinus halepensis	117	0.0	-0.6/0.7	0.10	2.0
Quercus pubescens	40	-0.4	-1.6/0.8	0.19	1.1
Betula	188	-7.3	-9.3/-5.4	0.25	-66.0
Fraxinus excelsior	40	-2.9	-5.8/-0.4	0.30	-4.5
Quercus pyrenaica	36	-7.0	-10.2/-4.4	0.43	-36.6
Alnus glutinosa	21	-13.0	-32.1/-1.1	0.49	-6.8
Populus tremula	75	-7.7	-13.7/-2.6	0.28	-12.0
Acer campestre	30	-8.4	-15.3/-3.0	0.33	-12.5

Table 2: Estimates of α, the slope of response of extinction to P_{occ} per species and their 95% confidence interval (see Materials and Methods for details on the model). ΔDIC is the difference of deviance information criterion – DIC – between the model and a null model. TSS is the True Skill Statistics. Nb of events is the number of extinction events. TSS are calculated using the median of parameter posterior distributions.

Since the ranges of P_{occ} differ across species, and the link function is not linear, the slope is not sufficient to evaluate the magnitude of recruitment and extinction variability. We thus also computed the relative contribution of P_{occ} extinction and recruitment (Figure 3) as the difference between the probability of extinction (colonization) at the low *vs.* high end of its respective range (respectively 5 and 95 % percentiles of P_{occ}).

For most species, the relative contribution was higher for recruitment than for extinction, (most species are above the diagonal in the Figure 3, particularly for *Quercus ilex*, *Quercus pubescens* and *Pinus halepensis*). Only *Quercus petraea* and *Abies alba* were below the diagonal with a higher relative contribution of P_{occ} on the extinction rate than on the recruitment rate.

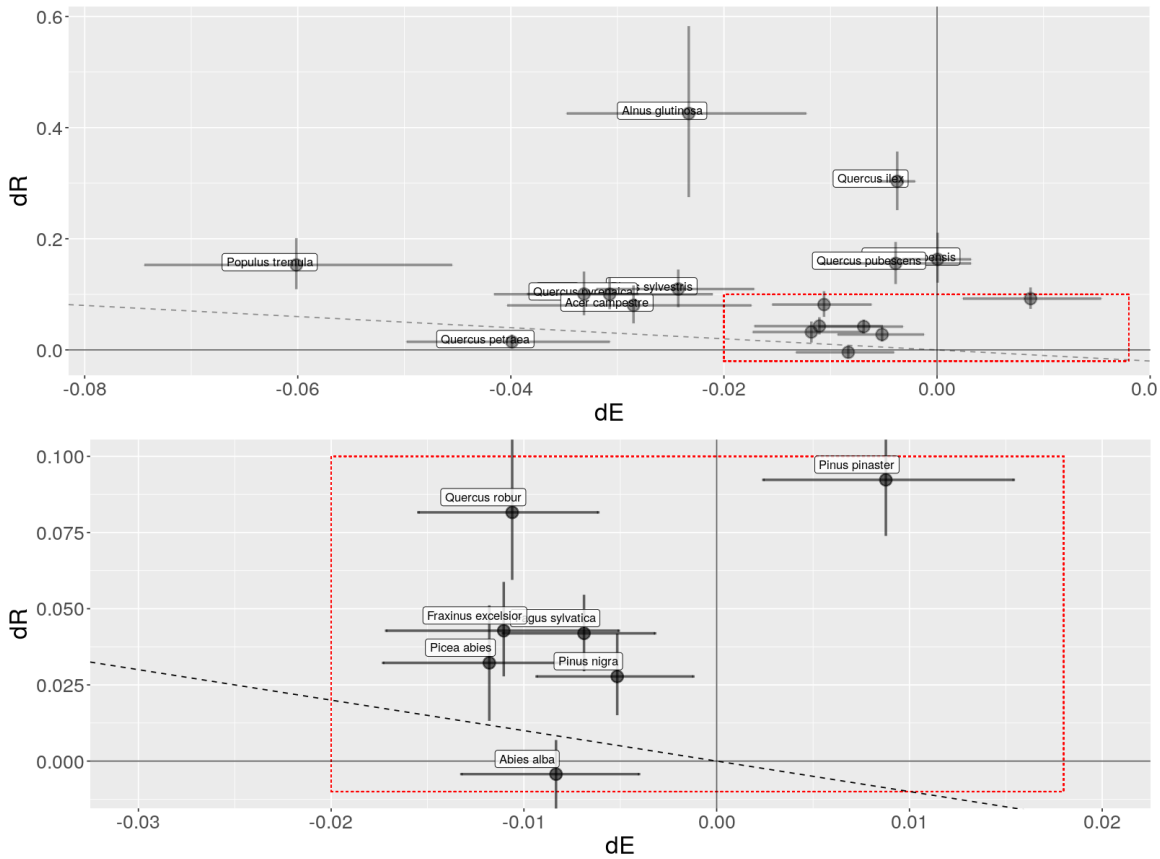

Figure 3: Relative contribution of the probability of occurrence to recruitment/extinction probabilities (dR and dE, respectively). For each species, dE and dR are calculated as the differences at high P_{occ} (95th centile) and low P_{occ} (5th centile). Bottom Figure is a zoom of the top Figure, illustrated with red lines. Negative dE means a higher extinction rate at low occurrence probability; positive dR means a lower colonization at low occurrence probability. On both plots dashed line represents $dR = -dE$.

3.2 Equilibrium

The probabilities of both colonization and extinction depend on the SDMs' probability of occurrence P_{occ}. As a consequence the probability of presence at equilibrium P_{eq} is directly a function of P_{occ}. However, the shape of the function and the match between P_{eq} and P_{occ} depend on the estimates of the slopes and intercepts of the colonization and extinction models (see Appendix section 5). We observed a positive relationship between P_{eq} and P_{occ} for the four different methods of computing the probability of equilibrium with a fixed seed source (see Figure 4).

The relationship was always positive when we accounted for the variation of both recruitment and extinction probability, but there is no clear evidence that either recruitment or extinction probability had a stronger contribution to P_{eq}. When the seed source was fixed to one, P_{eq} showed less variation and overall overestimated P_{occ} (see Figure 4). P_{eq} is above 0.5 when colonization probability exceeds extinction probability, which was almost always the case when dispersal limitation was not included (S set to one). Notable exceptions were *Pinus sylvestris* and *Pinus pinaster* for which extinction at low P_{occ} was substantially higher than the recruitment probability.

The impact of seed variations was variable between species. Including variations in S had a strong impact on P_{eq} range, which can be more than twice the P_{eq} range without S (for *Quercus ilex, Fagus sylvatica*, *Abies alba*, and *Picea abies*). When the seed source (S) was set to the observed JRC value in each cell, P_{eq} was very close to P_{occ} but generally still slightly overestimated P_{occ} (black lines in figure 4). For four species the mean of P_{eq} was lower than P_{occ} for at least some value of P_{occ} (*Pinus nigra, Pinus pinaster, Pinus sylvestris*, and *Quercus robur*).

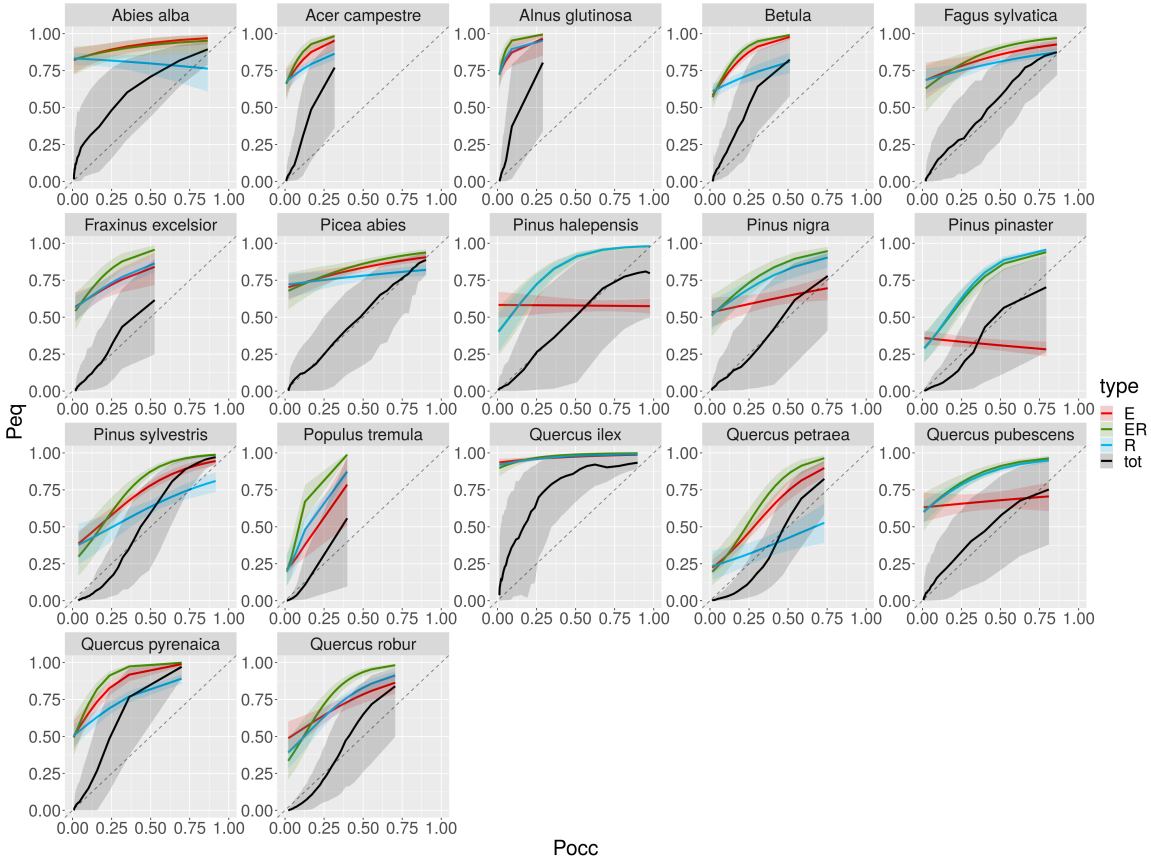

Figure 4: Equilibrium probability of presence (P_{eq}) against SDM occurrence probability (P_{occ}), calculated with seed source set to one and varying extinction (E in red), varying recruitment (R in blue), both (ER in green). S was computed with the seed source based on its correlation with P_{occ}.Black line (tot) is the equilibrium when considering all variations (E, R and S).

The second formulation of the equilibrium for a closed system leads also to a positive relationship between P_{eq} and P_{occ} for the three different ways of computing the equilibrium (E, R, and ER) (see Figure 5). In contrast with the fixed source method, we observed that at low values of P_{occ}, P_{eq} was below P_{occ}. In addition, P_{eq} could reach zero, meaning an absence of the species and quicly rise to higher values with a steeper slope than in the fixed seed source method.

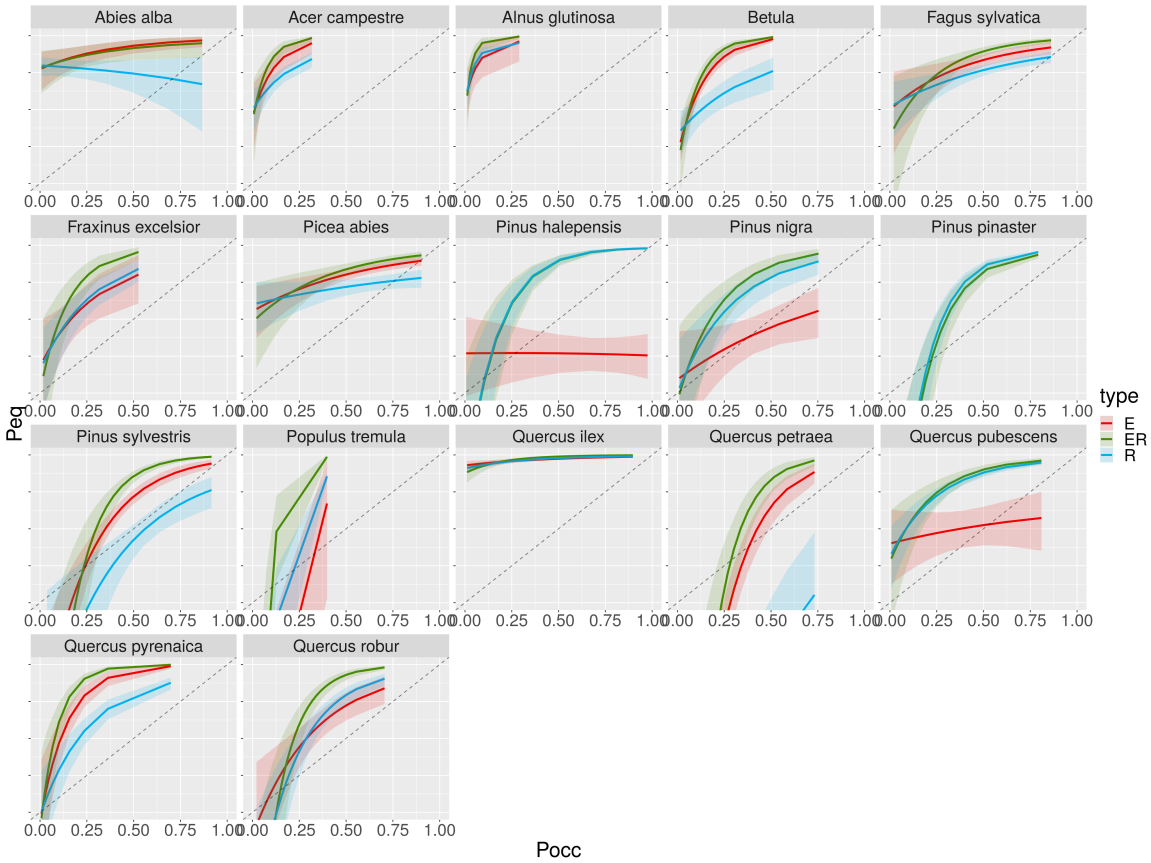

Figure 5: Equilibrium probability of presence (P_{eq}) against SDM occurrence probability (P_{occ}), calculated with closed formulation and varying extinction (E), varying recruitment (R), both (ER).

4 Discussion

Overall, our results showed that when SDM derived probability of presence decreases, the recruitment probability decreases and the extinction probability increases. We also found that the equilibrium probabilities of presence, derived from recruitment and colonization probabilities are positively correlated with the observed occurrence probability.

4.1 Variation of extinction and recruitment probability within species range

Our results reveal that species occurrence probability as defined by the SDM based on environmental variables is positively related with colonization events and negatively related with extinction events. Only few species showed non significant links between SDM and extinction or recruitment (*Quercus pubescens,Pinus pinaster, Abies alba* and *Pinus halepensis*). Only *Pinus pinaster* showed an opposite response for extinction. The lack of relationships or opposite relationships for species belonging to the genus *Pinus* might be related to their intensive management and recent introduction in several regions (particularly in the case of *Pinus pinaster*). Current presence/absence data might be biased for highly managed species.

Overall, the relationship between species occurrence probability was stronger with recruitment than with extinction. Thuiller et al. (2014) proposed that assuming shade tolerant species are better competitors, we could expect them to show a closer relationship between SDMs and the recruitment or extinction probability as this link would be less blurred by competition. Our results did not show such difference between shade and shade intolerant species. This is in agreement with the results of Thuiller et al. (2014) based on a analysis of tree basal area growth.

For the other species our results are compatible with Holt et al. (2005), and SDMs appear to be a valuable descriptor of the patch occupancy dynamics. Other studies on forest ecosystems have already shown that tree population extinction-colonization probabilities respond to the climate niche of species. This was generally done with models of patch occupancy (Talluto et al., 2017; Purves et al., 2007; García-Valdes et al., 2013) using polynomial functions of climatic variables (such as temperature and aridity). A key difference between our model and previous patch occupancy models in forests is that we did not use directly climatic variables but instead used the SDM occurrence probability as a descriptor of species environmental niches. Given the low number of colonization or extinction events in our data, using an SDM to summarize the species climatic niche might be more powerful than fitting complex multivariate responses to climatic variables. A similar approach has also been developed for birds in Britain by Araújo, Williams, and Fuller (2002), and highligted a negative relationship between local extinction probability and the probability of occurence.

The links between SDM and extinction/recruitment rates seems stronger than links to demographic rates (growth rate and carrying capacity by Thuiller et al. (2014), population growth rate, time to quasi-extinction, transient population dynamics by Csergő et al. (2017). This might indicate that links between population processes and species distribution are easier to capture with integrative meta-population metrics than with detailed population level metrics, which could be related to an issue of observation scale: colonization/extinction is a direct dynamical approach to

presence/absence. On the other hand, upscaling population dynamics to presence/absence is not evident, due to non-linearity or temporal variability.

4.2 Equilibrium *vs.* non-equilibrium of species distribution

If the distribution of a species is currently in equilibrium, we would expect a close relationship between the SDM and the probability of presence computed at equilibrium. Observing a positive correlation, however, does not rule out that there may be a lag between the equilibrium and the current distribution due to climate change. Simulations (not presented here) show that as soon as the lag is not too large there should still be a positive correlation between the two probabilities. Results from our model tend to show that current species distribution is not far from a potential equilibrium. However the match between the extinction-colonization derived probability of presence and the SDM occurrence probability is not perfect. When we accounted for variation of both recruitment and extinction probability we found a positive relationship between the predicted probability of presence at equilibrium and the SDM occurrence probability for both the fixed seed source and the closed models. We can see a good overall agreement between P_{eq} and P_{occ}. However, for most species, we observe a higher P_{eq} than P_{occ}, which would result in a higher prevalence in the area where the species is already present. We observed underestimation of P_{occ} only with the closed population models. The lower performances of extinction model when compared to recruitment may induce a weaker effect of extincion on P_{eq} than if the discriminating power of the extinction model was higher. Higher extinction slopes would lead to higher variations in the P_{eq} range, especially in the open population formulation.

The idea that each species is in current equilibrium with the environment has been criticized by Svenning and Skov (2004), based on the idea that most European tree species do not fully fill their potential ranges. This situation could be the result of a post-glacial migration lag as illustrated in Svenning, Normand, and Kageyama (2008). The lag would strongly affect *Abies alba*, the *Pinus* genus and the *Quercus* genus. This argument has however been partly contradicted by previous SDM results (Araújo & Pearson, 2005) and large dispersal rates found based on pollen records (Giesecke, Brewer, Finsinger, Leydet, & Bradshaw, 2017). Interestingly, we found a weak response of colonization and extinction to SDM occurrence probability for *Abies alba*, a species with a recorded slow expansion rate (Giesecke et al., 2017). For most species, the congruent signs of both recruitment and extinction rates dependencies (positive for recruitment and negative for extinction) support the hypothese of a partial equilibrium of current species distribution. In Eastern North America, results from a SPOM model (Talluto et al., 2017) identified species out of equilibrium with climate at range margins. Their model formulation is closer to our closed formulation (a species is present at equilibrium when colonization probability exceeds extinction probability). A SPOM developed by García-Valdes et al. (2013) in Spain also concluded on a non-equilibrium : simulations based on their model with constant climatic conditions lead to an increased fraction of occupied plots, but most species did not show range expansion.

4.3 Future redistribution

For low occurrence probability, the match between the equilibrium probability of presence and the SDM occurrence probability, is important to understand future changes in species distribution as this corresponds to the edge of the niche. For instance, we could expect a reduction of the species range when P_{eq} is notably lower than P_{occ} in low P_{occ} areas, as observed for *Pinus pinaster, Pinus sylvestris*, and *Quercus petraea*. These results for *Pinus sylvestris* are coherent with simulations by Cheaib et al. (2012) and the sensitivity of the species to warming (Reich & Oleksyn, 2008) which may reduce its southern range.

It is likely that a higher P_{eq} than P_{occ} would result in range increases, as predicted for *Alnus glutinosa*, *Fraxinus excelsior* or *Quercus ilex* which is in agreement with previous results by Ruiz-Benito et al. (2017) in which climate change was expected to favour angiosperm traits/strategies. Given the model formulation, we cannot conclude on the direction of species range expansion since the model does not differentiate between hot and cold edges

Several range dynamic models have already used SDMs to build dynamic meta-population models, including range dynamics models and population viability analysis. SDM outputs are used either directly to define which grid cells are colonizable (see Engler and Guisan (2009)), or influence demographic information (Nenzén, Swab, Keith, & Araújo, 2012) via for example patch carrying capacity. Our approach differs as we do not explicitly model dispersion, and do not put any a priori on links between SDMs and dynamic processes. In this study, results support the hypothese that SDMs are a coherent descriptor of meta-population dynamics, and the potential usefulness of SDMs for distribution projection models which go beyond a criticized correlative predictive approach (Journé, Barnagaud, Bernard, Crochet, & Morin, 2019).

4.4 Different model types to compute the equilibrium, and dispersal

The two models used to compute equilibrium are two extreme cases of dispersal ability. In the open system formulation, dispersal is fixed arbitrarily to the current neighborhood conditions and does not change with time, while in the closed source model, dispersal is limited to the 1 km pixel. Reality probably lies in between these two cases, and dispersal kernel formulation as well as seed production are keys to go beyond these two simplified models (Nathan & Muller-Landau, 2000). Long-distance seed dispersal can be crucial for long-term expansion rates of species ranges (Clark, 1998; Higgins & Richardson, 1999), and should be addressed when considering applying a dynamic meta-population model on a longer time scale. The first formulation, based on current seed availability estimation, is more optimistic, as illustrated by the tendency of $P_{eq}$to overestimate P_{occ}. In the second formulation, equilibrium depend only on current environmental conditions (as summarized by the SDM), and the absence of dispersal between plots leads to strong variability. As illustrated by theoretical work, dispersal distance, through kernel formulation and its parameters have direct impact on potential population size (Law, Murrell, & Dieckmann, 2003) and its environmental responses (Snyder & Chesson, 2004). In addition, species range filling is closely linked to dispersal ability (Schurr et al., 2007).

4.5 Limitations of patch occupancy models

Several factors might have contributed to limit our ability to estimate the links between SDM and meta-population dynamics. First, the NFI data do not provide a perfect knowledge of the absence/presence at the plot scale. With protocols that are based on concentric circular plots, we might miss the presence of trees larger than 10 cm DBH. We partially corrected this issue by accounting for the probability that the tree was below 10 cm at the first census with a growth model, we verified that residuals of the growth model were not biased along climatic axes, and we used model uncertainties to estimate this probability. But this approach is not perfect and the dataset probably might still contain colonization events that are not true colonizations but observation errors. Conversely, we might have wrongfully excluded some colonization events for trees with extreme growth.

Secondly, detailed recruitment data does not exist at the European scale, therefore recruitment is here limited to the ingrowth of adults crossing the 10 cm DBH threshold as an effective recruitment. The use of saplings data could improve dynamic projections.

Even though we excluded plots with record of management intervention between the two censuses, management may still have had an impact. For example, the atypical responses of *Pinus pinaster* and *Pinus nigra* can be linked to the fact that these species are highly managed, and have been introduced in several regions. More broadly, the characterization of species climatic niche by an SDM suffer from being parametrized on a current distribution, and therefore account for a realized niche rather than a fundamental niche (Pulliam, 2000, e.g.). SDMs may then fail to capture some climatic dependencies.

Different studies on patch occupancy models calibrated with NFI data have tried to formally include dispersal in the model (Purves et al., 2007; García-Valdés et al., 2015). García-Valdes et al. (2013) tried to infer the parameters of the dispersal kernel based on the Spanish forest inventory data. We considered that actual knowledge on the potential seed source surrounding a plot is insufficient to draw mechanistic conclusions on seed dispersal. Field studies show that mean distance of seed dispersal are short for most tree species (Nathan et al., 2001; Bullock et al., 2017; Cain, Milligan, & Strand, 2000), therefore direct dispersal between plots should be restricted to extremely rare events (distance > 1 km) and the tail of the kernel distribution. It is thus very unlikely that these models were really estimating a dispersal kernel (as indicated by the very large mean dispersal distance inferred) but rather captured a degree of spatial auto-correlation in the species distribution and the recruitment process. Here, we use an estimate of local frequency which takes into account observed presence/absence and smoothing kernels as well as fine scale forest cover maps (building on the approach of Talluto et al. (2017)). We believe that if we want to include dispersal kernels in the model it is better to use external information on the shape and parameters of the dispersal kernel (see Schurr et al. (2007) or Schurr et al. (2012) for example).

Finally, our approach does not include biotic interactions and disturbances that might influence population extinction and recruitment probabilities (Case, Holt, McPeek, & Keitt, 2005; Svenning et al., 2014; Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018). Trophic interactions in a broader sense may have a potentially large impact on recruitment estimation. For instance ungulate browsing may induce spatially varying limitations on recruitment for *Abies alba* (Kupfer-

schmid, 2018), and ungulate preferences could lead to limitation of certain species (see e.g. stronger preference for *Pinus sylvestris* over *Pinus nigra* might reinforce *Pinus sylvestris* drought sensitivity, Herrero, Zamora, Castro, and Hódar (2012)). Given the small number of colonization and extinction events, a reliable estimate of tree species interactions with our data seems unrealistic.

5 Conclusions

We tested how extinction/colonization rates were related to the variation of the occurrence probability derived from SDM. For most tree species, we found an increase of recruitment probability and a decrease of extinction probability with the SDM occurrence probability. Both relationships are in agreement with the hypothesis of range limits linked to extinction/colonization rate variations along an environmental gradient (Holt & Keitt, 2000). Models of species distribution build on the metapopulation framework offer the promise to provide additional insights into the processes controlling species distribution and future changes in response to climate change.

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