Effects of climate, species interactions, and dispersal on decadal colonization and extinction rates of Iberian tree species

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ABSTRACT

We studied the relative importance of climate, abundance of potentially competing species, and dispersal in explaining local colonization and extinction rates of tree species throughout mainland Spain. We used a Bayesian framework to parameterize a patch occupancy model to 23 species censused in 46,596 permanent plots in a 1×1 km grid across most Spanish forests. For most species, dispersal was the single best predictor of colonization, whereas climate and dispersal were equally important as predictors of extinction. Precipitation was positively correlated with the colonization rate of 12 out of 13 deciduous broad-leaved species, and negatively correlated with the extinction rate of nine of them. In contrast, precipitation equally decreased colonization and extinction of five out of eight of needle-leaved species (*Juniperus* and *Pinus* spp.). There was, however, marked variation among species in the magnitude of these effects, with some species exhibiting contrasting patterns for the colonization and the extinction process. Abundance of competing tree species (= summed plot basal area) was consistently correlated with decreased colonization of all needle-leaved species, and it increased the extinction rate of 6 out of 8 of these species. It had, nonetheless, weak facilitative effect on some broad-leaved species by promoting colonization (3 of 13 species) and decreasing extinction (7 of 13 species). With local colonization and extinction data, non-equilibrial and dynamic species distribution modelling can be improved by incorporating measures of biotic interactions and dispersal effects, along with traditional climate variables.

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1. Introduction

Species distribution models (SDMs) have been widely used in conservation planning and management, in forecasting the effects of invasive species and climate change, and in assessing the risk of disease transmission (Araújo and Peterson, 2012). SDMs, especially under scenarios of climate change, have traditionally been fit with climatic variables only (Pearson and Dawson, 2003), yet it is well known that non-climatic factors affect the distribution of species, especially at local scales (Davis et al., 1998; Hampe, 2004; Ibáñez et al., 2006; Iverson and Prasad, 1998; Pearson and Dawson, 2003). In particular, dispersal dynamics (Engler et al., 2009) and species interactions may be important but are not well-studied (Araújo and Luoto, 2007; Godsoe and Harmon, 2012; Kissling et al., 2012; Pulliam, 2000; Wisz et al., 2013), perhaps because it is challenging to incorporate these factors into realistic SDMs (Araújo and Rozenfeld, 2014).

One of the challenges is that, until recently, many analyses in biogeography and macroecology have been based on correlations between the static presence of individual species and potential predictor variables (Gotelli et al., 2009). Moreover, SDMs fit with static records of species occurrences implicitly assume that species distributions are in climatic equilibrium (Pearson and Dawson, 2003; Svenning and Sandel, 2013). Although such equilibria may exist for

some species at particular spatial scales (Araújo and Pearson, 2005), many distributions are dynamic (Montoya et al., 2007; Peterson et al., 1999; Skov and Svenning, 2004; Woodward et al., 1990), such as those of poorly dispersing taxa that might rarely achieve equilibrium with climate (Araújo and Pearson, 2005; see also Hof et al., 2012), or those of taxa that were strongly affected by human activities in the past (e.g. tree species in mainland Spain, García-Valdés et al., 2013, 2015). Species distributions ultimately result from dynamic local colonizations and extinctions, and ideally, the individual contribution of dispersal, species interactions and climatic variables to colonization and extinction should be quantified. However, the temporally replicated data needed for such analyses are rare.

Here, we investigated the relative importance of variables measuring effects of climate, species interactions, and dispersal as predictors of local colonization and extinction of tree species in mainland Spain (Fig. 1). To do so, we used a climate-dependent patch occupancy model (developed by García-Valdés et al., 2013) to study plot-level colonization and extinction rates of tree species from two consecutive nation-wide forest inventories in Spain. Specifically, we quantified the relative importance, and direction of influence, of each of these three drivers, and tested for consistent differences between broad-leaved and needle-leaved species, and between wind- and animal-dispersed species.

These analyses can provide the foundation for a dynamic metacommunity model that could be used to simulate forest tree species distributions under different climate and habitat change scenarios. The spatial scale of this study encompasses a large regional extent (1000 km), but a relatively small spatial grain (25 m radius plots through a 1×1 km grid). Dynamic census data collected at such scales allowed us to study how the processes of colonization and extinction, which ultimately lead to species distributions at regional scales, depend on local drivers.

2. Material and methods

2.1. Tree census data and abiotic variables

We recorded decadal colonization of unoccupied plots and extinction of occupied plots between the second (1986–1996; Villaescusa and Díaz, 1998) and third (1997–2007; Villanueva, 2004) Spanish Forest Inventories. In both inventories, the same 46,596 permanent plots located in a 1×1 km grid across most forests in mainland Spain were surveyed. Each plot was formed by four concentric sub-plots of different radii ranging from 5 to 25 m. The minimum size for trees censused in the smallest sub-plot was 7.5 cm of diameter at breast height. In each survey, the identities and sizes of trees were recorded. A total of 72 tree species was recorded across mainland Spain, with tree species richness per plot ranging from 1 to 9 (average = 1.51 tree species/plot). We used 23 tree species, including four taxa that could be identified only to genus (Table A.1). We excluded species with fewer than 10 incidences in each census and with fewer than 5 colonizations or extinctions. We also excluded *Pinus radiata* and *Populus nigra*, because their distributions largely reflect planting, and *Ulmus minor*, because its distribution largely reflects mortality from Dutch elm disease. See García-Valdés et al. (2013) for more detail on data characteristics.

Climate predictors were obtained from a regional climate model, which itself was based on data from 5426 weather stations, and downscaled through ordinary co-kriging to match the forest inventory 1×1 km grid (Gonzalo, 2008). To select only two relevant climatic variables, we explored co-linearity using Principal Component Analyses (package 'stats'; R Core Team, 2014), of 14 climate variables that are recognized as physiologically important for trees

(analyses not shown). We selected first the variable *maximum temperature of the hottest month* (*TMMH*) because it had the strongest correlation (0.337) with the first PCA axis (which explained 53.2% of the variance). The second axis explained 25.5% of the variance, and the two variables most strongly correlated with it were *winter precipitation* (*Pw*; −0.408) and the *minimum temperature of the coldest month* (*TMMC*; −0.426). Of these, we selected *Pw* because that way we had an energy- and a water-related variable, instead of two energy-related ones (see Hawkins et al., 2003).

To quantify interspecific interactions, the presence, density, or basal area of the other 72 species in the database could theoretically be used as predictor variables, but this would add 72 potential predictor variables to the model. To keep the analysis simpler and to facilitate model calibration, we used the summed basal area of all individuals from other tree species in the plot (BA, in mm^2) as a simple aggregate index of the potential strength of interactions with other species. Such interactions might reflect direct competition for shared resources such as space, light, water, and soil nutrients, as well as indirect effects that are mediated through other species of pollinators, herbivores, seed predators, and dispersers. Statistical associations between BA and each studied species might reflect competitive effects (if greater BA in a plot produces a decrease in colonizations and/or an increase in extinctions), or a facilitative effect (if greater BA produces an increase in colonizations and/or a decrease in extinctions). This latter effect could be particularly important in the drought-prone southern regions of Spain (Pugnaire et al., 1996).

For each census plot and species, we represented the effects of dispersal as a metric calculated with a logistic-shaped dispersal kernel function (see Eqs. (3–6)). We fit this function with the distance from the survey plot to all other plots occupied by the same species, within a 50 km radius, to simulate random dispersal. To simulate directed dispersal, we weighed this function by the distance to all the suitable (= forested) plots.

We explored correlation between the variables of all studied drivers (package 'stats'; R Core Team, 2014), but found no strong association among them (Appendix A). Finally, to test whether the results were influenced by recent silvicultural activities, we repeated the analysis excluding 17891 plots that, in the last inventory, showed signs of human intervention such as logging, tilling, or other major land-use changes. We found no important changes in the results when these managed plots were excluded (analyses not shown).

2.2. Model structure

The model is described by the following set of functions, in which the probability of species j being present [$X_{j,q}(t+1) = 1$] or absent [$X_{j,q}(t+1) = 0$] within plot q at time $t+1$ is:

$$P\left[X_{j,q}(t+1)|X_{j,q}(t)\right] = \begin{cases} C_{j,q}(t) & \text{if} \quad X_{j,q}(t) = 0 \quad \text{and} \quad X_{j,q}(t+1) = 1 \\ 1 - C_{j,q}(t) & \text{if} \quad X_{j,q}(t) = 0 \quad \text{and} \quad X_{j,q}(t+1) = 0 \\ E_{j,q}(t) & \text{if} \quad X_{j,q}(t) = 1 \quad \text{and} \quad X_{j,q}(t+1) = 0 \\ 1 - E_{j,q}(t) & \text{if} \quad X_{j,q}(t) = 1 \quad \text{and} \quad X_{j,q}(t+1) = 1 \end{cases} \quad (1)$$

where $C_{j,q}(t)$ is the probability of local colonization and $E_{j,q}(t)$ is the probability of local extinction, for species j in plot q between t and $t+1$.

2.2.1. Colonization rate

The probability of colonization of plot q by a species j (Eq. (2)) was determined by the dispersal into the plot (Eqs. (3–6)), and by the probability of seedling establishment and growth to the point of detection in the next inventory (Eqs. (7–9)).

$$C_{j,q}(t) = S_{j,q}^{\lambda} \alpha_{j,q} \quad (2)$$