Chasing a moving target: projecting climate change-induced shifts in non-equilibrial tree species distributions

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Summary

1. The geographic distributions of plant species show marked correlations with the current climate, suggesting that they are likely to shift if climate changes. However, before projecting any such shifts, it is important to establish whether distributions are at equilibrium with the current climate. If they are not, distributional shifts could occur even without climate change, making it difficult to tease apart climate-induced shifts from shifts occurring naturally without climate change.

2. We forecast the geographical distributions of the 10 most common trees occurring in the Iberian Peninsula using a new method that relaxes the species–climate equilibrium assumption implicit in most species distributions models. For each species, we developed a spatially explicit patch occupancy model (SPOM) with climate-dependent extinction rates and with colonization rates that depend on both climate and local seed dispersal. Bayesian methods were used to estimate the colonization, extinction and seed dispersal functions against observed colonization and extinction events recorded in repeat surveys of 46 596 forest plots in the Spanish Forest Inventories (1986–96 and 1997–2007). We then simulated distributional changes between the years 2000–2100.

3. Without climate change, 9 of the 10 species substantially increased in regional frequency. These increases occurred primarily within current ranges, although some species also expanded across their range edges. With climate change, one temperate conifer species and two sub-Mediterranean species would reduce their frequency of occurrence across the studied region, whereas temperate broadleaved species were unaffected and Mediterranean species were either unaffected or increased their frequency of occurrence.

4. *Synthesis.* The analysis suggests that these species are substantially out of equilibrium, such that abundances and ranges would increase without climate change. Climate change may increase, decrease, stabilize or shift distributions, in a way that can only be understood by comparing predictions against baseline scenarios that account for these non-equilibrium range dynamics.

Key-words: Bayesian statistics, Iberian forests, local colonization and extinction rates, MCMC, metapopulation model, plant population and community dynamics, plant–climate interactions, seed dispersal, species distribution models, stochastic patch occupancy models

Introduction

At scales from global to local, plant species show marked correlations with climate and other aspects of the physical environment (see Stephenson 1990), implying that species distributions are likely to shift in response to climate change (Thomas *et al.* 2004; Thuiller *et al.* 2005; Araújo & Rahbek 2006). There is also evidence that distributions of many species are already responding to contemporary climate change (Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006) and palynological evidence indicates that distributions have

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shifted, often rapidly, in response to past climate changes (Carrión & Fernández 2009; Postigo Mijarra *et al.* 2009). More fundamentally, the demographic rates of trees are known to be correlated with climate (e.g. growth rates, Loehle 1998; recruitment, Ibáñez *et al.* 2007; and mortality rates, van Mantgem *et al.* 2009), suggesting that demographic rates will respond to climate change with knock-on effects for regional abundances and distributions.

Attempts to model the response of species distributions to climate change and other factors have mostly been carried out using 'bioclimate envelope modelling' (BEM; Pearson & Dawson 2003; Heikkinen *et al.* 2006; Araújo & Peterson 2012), which proceeds by 'regressing' the current distribution of a species against the climate its distribution is exposed to and then re-applying this 'regression' under an altered climate to produce a new distribution. BEM has a number of advantages, including that they can be applied rapidly to large numbers of species across regional scales given relatively sparse data. Specific implementations of BEM have been validated and shown to provide useful estimates of potential climate-induced distributional shifts (Araújo *et al.* 2005; Green *et al.* 2008; Dobrowski *et al.* 2010). However, it is also widely recognized that BEM does not account for a number of mechanisms that could affect species abilities to respond to climate change (Pearson & Dawson 2003; Hampe 2004; Araújo & Peterson 2012).

Chief among the assumptions of BEM are: (i) it assumes that species are currently at equilibrium with the current environment (Araújo & Pearson 2005; Varela, Rodriguez & Lobo 2009); (ii) it assumes that occurrence (or abundance) in a given location is independent of that in other locations, ignoring the spatial couplings and source-sink dynamics that are thought to be important for many species (Freckleton & Watkinson 2002; Segurado, Araújo & Kunin 2006); (iii) because BEM is based on static correlations, it cannot, by itself, predict the potential time-scale of response (but see Nogués-Bravo *et al.* 2008); (iv) it implicitly assumes lack of local adaptation (i.e. ecotypes within species: Chevin, Lande & Mace 2010); and (v) it assumes the distributions are not significantly affected by interspecific interactions (Leathwick & Austin 2001; Araújo & Luoto 2007). Because these features of BEM are so widely recognized, there is now a considerable amount of active research into methods that relax some of these assumptions (Iverson & Prasad 1998; Keith *et al.* 2008; Anderson *et al.* 2009; Brook *et al.* 2009; Benito Garzón *et al.* 2011; Fordham *et al.* 2012a). For reviews see Thuiller *et al.* (2008) and Kissling *et al.* (2012).

The concept of equilibrium has been predominant in the ecological literature for a long time (Rohde 2005). Ecosystems were considered to operate near equilibrium conditions, tending to rapidly equilibrate after disturbances (e.g. 'self-correcting mechanisms', Hutchinson 1948). While equilibrium views were predominant in earlier ecological theory (e.g. Pielou 1969; MacArthur 1972; Cody & Diamond 1975; Ehrlich, Ehrlich & Holdren 1977), non-equilibrium dynamics have been increasingly integrated (Chesson & Case 1986; Diamond & Case 1986; DeAngelis & Waterhouse 1987;

Krebs 2001). For a deeper revision on the concept and history of non-equilibrium see Rohde (2005).

In this study, we introduce a method based on a spatially explicit dynamic model (a SPOM: see below), which relaxes both the equilibrium (i above) and the spatial independence (ii above) assumptions, while naturally including the temporal scale (iii above). Rather than correlating the current species *distribution* with the current climate, our approach correlates short-term local *dynamics* (colonization and extinction rates) against the climate at the times and places at which those local dynamics occurred. In this kind of model, the species distribution (i) emerges 'bottom up' from the local dynamics, rather than being assigned 'top down' as a regression against climate, (ii) naturally shows time-lagged responses to climate change and other perturbations (e.g. land-use change or harvesting) and (iii) naturally exhibits internal spatial dependencies (e.g. intraspecific aggregation beyond that implied by the physical environment alone, and dispersal limitation where species are absent from suitable locations due to a lack of propagules).

This bottom-up approach to modelling species distributions allows us to simultaneously address two related and widely discussed topics in the species distributions modelling literature. First, under rapid climate change, distributions may show time-lagged responses and thus fail to keep up with the pace of climate change (Davis 1989; Malcolm *et al.* 2002; Nathan *et al.* 2002; Svenning & Skov 2007). Such lagged responses could occur even if species were currently at equilibrium with the current climate. To address this issue, a number of studies have constrained BEM projections, for example, to represent dispersal limitation (Araújo *et al.* 2004; Thomas *et al.* 2004; Thuiller *et al.* 2005; McKenney *et al.* 2007). Secondly, distributions may currently be out of equilibrium with the current climate (Fig. 1). If so, the distributions might change in the future even without climate change (or any external forcing), and estimates of environmental suitability for different species from the current distribution will possibly underestimate the true limits of tolerance to climate parameters (Fig. 1).

Ecologists are beginning to address the problem of non-equilibrium of species distributions with current climate, chiefly using indirect methods. For example, Svenning & Skov (2004) examined anomalies against bioclimate envelope models fitted to the current distributions of European trees, concluding that many species are absent from many suitable locations (see also Munguía *et al.* 2012); and Arajo & Pearson (2005) found that taxa with better dispersal showed a tighter relationship of community dissimilarity vs. climate dissimilarity, implying that taxa with poorer dispersal had not yet equilibrated against climate (see also Hof *et al.* 2012). In contrast, as explained in a recent SDM paper (Pagel & Schurr 2012), it is possible to define a model within which geographical distributions emerge from local dynamics (as they do in reality) and then parameterize this model against data, without assuming equilibrium. This bottom-up approach, which is similar in spirit to that employed here, combines data on both local dynamics and geographi-
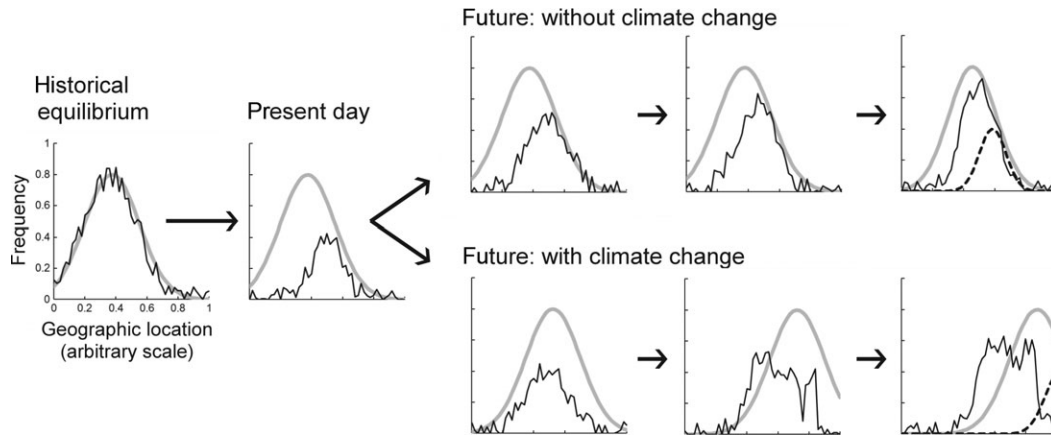
Fig. 1. An illustration of the dynamics of a species, which is currently non-equilibrial against climate, with and without climate change. In each panel, the equilibrium distribution is shown in grey vs. the actual distribution in black. Even if the distribution was once approximately at equilibrium with the climate (far left), a perturbation could have resulted in the current distribution being substantially out of equilibrium (second from left). If so, in a future without climate change, the distribution will tend to gradually rebound toward the equilibrium (top right three panels). With climate change, the distribution will show a complex pattern of change, constantly approaching an equilibrium that is itself always changing, and so is never reached (bottom right three panels). With or without climate change, the bioclimate envelope approach of re-applying the present-day climate vs. frequency correlation into the future (right two panels, black dashed lines), does not project the future distribution. Rather, projection requires a dynamic model that simulates how the distribution might change through time.

cal distributions but has yet to be applied for any actual species.

The bottom-up approach allows estimating the degree of non-equilibrium exhibited by the distributions of species as follows. Scaling up from the local dynamics observed in the forest plots, the model can project how the geographical distributions would change under a scenario of no change in any external forcing (such as the environment, forest area, or disturbance regimes). If the distribution is currently at equilibrium, then there should be no systematic tendency to change under such business-as-usual scenario (although it may drift slightly in a stochastic model like ours). In contrast, if the distribution undergoes directional change, in terms of total abundance and/or the distribution across geographic space, then this indicates (subject to important caveats, see Discussion) that the distribution is currently out of equilibrium. Having carried out the business-as-usual simulations to estimate the degree of current non-equilibrium, we can then carry out additional simulations in which the climate is changing according to one or other scenario. This allows us to view the potential effects of climate change against the stable climate baseline.

Materials and methods

STUDY REGION AND DATA

Continental Spain holds a great variability of environmental conditions, including a strong north–south aridity gradient and a weaker west–east one. In addition, the presence of several mountain chains (ranging from sea level to 3500 m a.s.l.) not only greatly increases the environmental heterogeneity, but provides numerous, near orthogonal, temperature and aridity gradients.

We extracted presence and absence data of the 10 most common tree species in mainland Spain from the Spanish Forest Inventory (SFI, Villaescusa & Diaz 1998; Villanueva 2005). The selected species were: *Pinus sylvestris, Pinus pinea, Pinus halepensis, Pinus nigra, Pinus pinaster, Quercus robur, Quercus petraea, Quercus pyrenaica, Quercus faginea* and *Quercus ilex*. In this inventory, each survey plot consisted of four concentric subplots: with radius 5 m (to measure trees with 7.5–12.5 cm of diameter at breast high (-DBH-), with radius 10 m (to measure trees with 12.5–22.5 cm of DBH), with radius 15 m (to measure trees with 22.5–42.5 cm of DBH) and with radius 25 m (to measure trees with more than 42.5 cm of DBH). Plots were uniformly distributed in a 1 × 1 km grid across all forested areas (occupied by woody vegetation). To achieve simplicity, any record of a tree of one specific species in any of the subplots was considered to define the presence of the species in the plot. We considered a variety of alternative definitions (e.g. excluding small trees, or using data from only the smallest radius) but we considered that all such alternatives implied difficulties in defining colonizations or extinctions that exceeded those that occur when using the simple definition applied here. Additional analyses suggested that the plots were large enough to be representative of the actual presence or absence of species, and the gain and loss of species, within the immediate surroundings of a plot (see Appendix S1 in Supporting Information).

For each species, we noted presence or absence in each of the 46 596 plots that were visited in two subsequent surveys (between 1986 and 2007) with an average interval of 10 years (permanent plots). This allowed us to identify local colonization events (0 → 1 transitions) and local extinction events (1 → 0 transitions) with which to parameterize and validate our model (see below). Additionally, another 30 478 plots were visited only in the last survey (non-permanent plots). We used occurrences in both permanent and non-permanent plots (77 074) as the starting point for simulations from year 2000 to year 2100.

As an estimate of potential climate change for this region, we selected a high CO_2 concentration stabilizing reference scenario (WRE750; Wigley, Richels & Edmonds 1996), and we used an ensemble of seven General Circulation Models (hereafter GCM ensemble), produced using MAGICC/SCENGEN 5.3, http://www.cgd.ucar.edu/cas/wigley/magicc, (see Fordham *et al.* 2012b). The seven GCMs that were included were: CGCM3.1 (T47), MIROC3.2

(medres), PCM, UKMO-HadCM3, ECHO-G, IPSL-CM4 and MRI-CGCM2.3.2 (http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php). There is of course considerable uncertainty in future climate, not least because of uncertainty in emission scenarios (Stott & Kettleborough 2002; Hawkins & Sutton 2009). However, models are in agreement that Spain is likely to become hotter and drier over the next 200 years (IPCC 2007). Thus, we consider the nature of our reported results for the effects of climate change, and our qualitative conclusions derived from them, to be robust, but the temporal rate of the effects needs to be viewed with caution.

Climate varies over short distances in Spain because it is so mountainous. Therefore, the GCM ensemble predictions were downscaled to 1×1 km, using the 'change factor' method, where the low-resolution climate signal (anomaly) from the GCMs is added directly to a high-resolution baseline observed climatology (Hulme, Raper & Wigley 1995). Bi-linear interpolation of the GCM data ($2.5 \times 2.5°$ longitude/latitude) to a resolution of $0.5 \times 0.5°$ longitude/latitude was used to reduce discontinuities in the perturbed climate at the GCM grid box boundaries (Fordham, Wigley & Brook 2011). An advantage of this method is that, by using only GCM change data, it avoids possible errors due to biases in the GCMs' baseline (present-day) climate.

Parameter estimation required that we also had data, for each survey plot, on the average climate during the interval between surveys (1986–2007). For consistency with the climate change projections, we used the projection for year 2000 from the same WRE750 GCM ensemble as a proxy of the climate in this interval, as well as for the business-as-usual stable climate scenario (baseline).

Climate in this study was defined based on two key climatic variables, one related to water availability (Total Annual Precipitation) and the other related to temperature. Initially, we considered two temperature variables: Mean Annual Maximum Temperature (T_{max}) and Mean Annual Minimum Temperature (T_{min}). The two variables are strongly correlated but they are linked to two different processes affecting tree species persistence (Montoya *et al.* 2009): T_{max} relates to drought, while T_{min} to freezing. Because we already included a variable that relates to drought (precipitation), we opted to select T_{min} for our study.

THE MODEL

We parameterized an environment-dependent SPOM (Etienne, ter Braak & Vos 2004; Ovaskainen & Hanski 2004) using observed changes in occupancy of survey plots between the two consecutive national forest surveys that cover a great variety of climatic and spatial conditions. The state of the SPOM at time t is defined by a series of 1/0 values for $X_{j,q}(t)$, representing the presence ($X_{j,q}(t) = 1$) or absence ($X_{j,q}(t) = 0$) of species j within patch q at time t. This state changes through time via local colonizations (where a local patch goes from absence to presence) and extinctions (where a local patch goes from presence to absence). These events are random such that, between any one time t and the next time $t + 1$, any patch q not occupied at time t can become colonized, but with a probability that depends on the local environment at q at time t, as well as the seed rain into patch q at time t (while the seed rain itself depends on the number and proximity of occupied patches). Similarly, any local patch q that is occupied at time t can suffer a local extinction, with a probability that depends on the local environment at q at time t. Thus, the dynamics of the SPOM are completely specified by the set of probabilities, for each patch q at each time t, of the probabilities of the changes in state:

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

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

The model can reach a state of pseudo-equilibrium (also called a quasi-stationary state) if the species does not go extinct and local colonizations and extinctions still occur, but at the same average rate over the whole distribution (and in any subset of that distribution). Once pseudo-equilibrium is reached, the overall frequency and the frequency within any subset of the geographical distribution do not undergo any directional change through time (Etienne, ter Braak & Vos 2004; Ovaskainen & Hanski 2004), although it can still drift slightly due to the stochasticity of the model. Thus, by assuming that pseudo-equilibrium has been reached, Purves *et al.* (2007) were able to parameterize a SPOM against data from a single forest survey, to examine the potential importance of local and directed dispersal in determining the distributions of three *Quercus* species in central Spain. But this means that Purves *et al.* (2007) were still assuming equilibrium. In contrast, here we parameterize the SPOM against observations of local colonizations and extinctions (see Parameter estimation and model selection below).

CLIMATE-DEPENDENT COLONIZATIONS AND EXTINCTIONS

We made the local extinction and colonization rates, $E_{j,q}(t)$ and $C_{j,q}(t)$, a function of the local climate associated with q and t. Local extinction was made dependent on temperature and rainfall in three alternative ways: models denoted E0 had no environmental dependency on extinction; models denoted E1 had a monotonic effect of temperature and precipitation on extinction; models denoted E2 had a unimodal effect of temperature and precipitation on extinction. We used the same approach for colonizations with models being denoted as C0, C1 and C2. Using all possible combinations for extinctions and colonizations, we had nine possible models for each species, from E0C0 to E2C2.

The mechanisms controlling colonization differ from those affecting extinctions. In addition to climatic factors, colonization also depends on seed rain [$S_{j,q}(t)$]. Seed rain into a focal patch was calculated as a function of the spatial proximity of the other occupied patches, up to 50 km from the focal patch. For each species, we had to decide whether to make the seed dispersal process (i) *random* with respect to habitat, such that seeds leaving a donor patch are scattered randomly, including to unsuitable habitat such as farmland or (ii) *directed* with respect to habitat, such that seeds land only within suitable habitat (forest). In keeping with natural historical expectations, and with the findings of Purves *et al.* (2007) and Montoya *et al.* (2008), we used random dispersal for tree species that are known to be primarily wind dispersed and directed dispersal for tree species that are known to be primarily animal dispersed. To simulate the seed rain into each patch, it was necessary to define the seed output for the occupied plots and also the dispersal kernel, which describes how the seed input from a donor patch to a recipient patch declines as a function of the distance between the two patches. Rather than attempt to set these dispersal parameters from prior knowledge, we estimated

them using a negative exponential function, the distance and number of occupied plots, and the surrounding forest patch configurations.

PARAMETER ESTIMATION AND MODEL SELECTION

Before the model can be used to make projections, it needs to be parameterized from (AKA fit to) data. We used simple Bayesian methods to estimate the parameters of all nine possible models for each of the 10 species. We used flat (uninformative) priors on all parameters, meaning that the results of the analysis depended only on the likelihood. In this case, the likelihood was simply the probability of observing, for a particular species, the local colonization or extinction events recorded in the inventory, given a particular model, and accompanying set of parameters. Once the likelihood is defined, it is a simple matter of using sampling methods, such as the Metropolis – Hastings MCMC algorithm that we used, to generate parameter estimates, including credible intervals, for each combination of model type and species (for further details see Appendix S2).

After each of the 90 models had been parameterized, we used Akaike's information criterion (AIC, Akaike 1974) to compare them. AIC provides information about the quality of a model in comparison with others, discounted according to the number of free parameters. By comparing the AIC of models that included the effect of climate on local dynamics (E1, E2, C1, C2) with others that did not (E0 and C0), we assessed the importance of climate on the local dynamics.

To provide a visual estimate of model accuracy, beyond that provided by simple comparison of the AIC values, we first calculated the projected colonization and extinction probability, with respect to the time between the first and second survey, for each plot and for each species. We then: (i) divided the plots into classes according to these probabilities (i.e. for plots beginning in state 0, colonization probability 0–1%, 1–2% and so forth; and for plots beginning with state 1, the same for extinction probabilities); (ii) calculated, for each of these classes, the fraction of plots observed to undergo local colonization between both surveys, and the same fraction for local extinctions. Finally, we plotted the projected colonization and extinction probabilities against the observed colonization and extinction fractions. For this methodology, we used 75% of the data for parameter estimation and 25% for the comparison, and we excluded all probability classes with a sample size smaller than five plots.
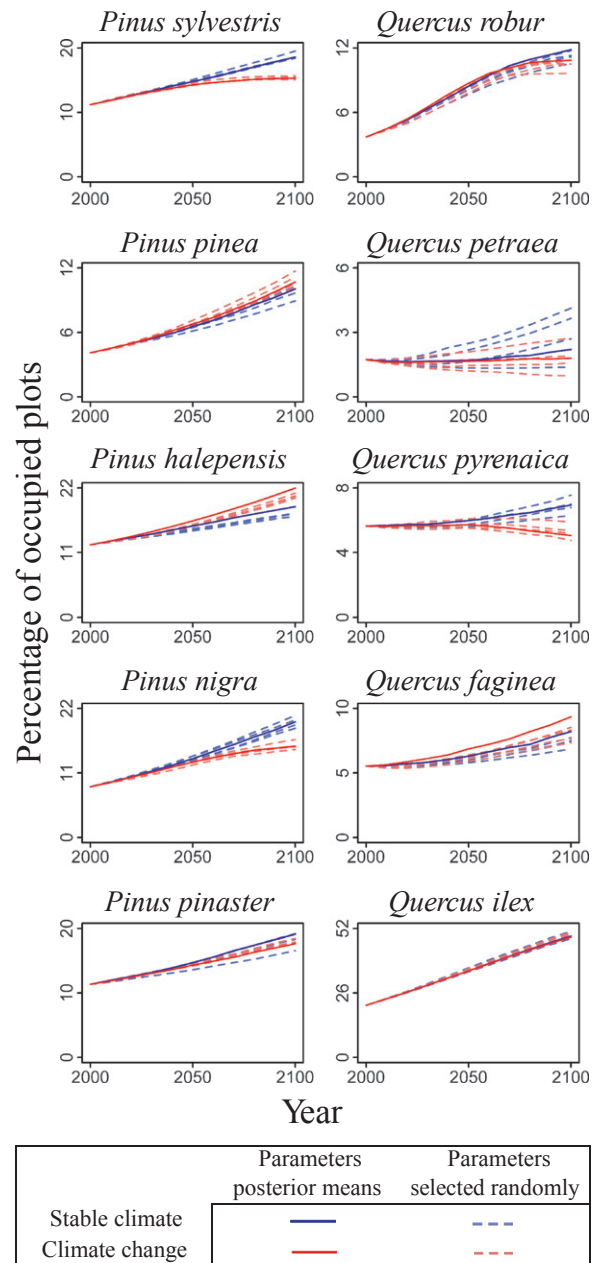
PROJECTIONS

Using the calibrated SPOM, we simulated changes in species occurrences within each of 77 074 forest plots (i.e. all plots visited at the time of the last survey: see *Study region and data*, above) for the period 2000–2100 for two different scenarios: one with climate held constant (stable climate or climate-change-free baseline) and the other with climate changing according to the spatially explicit projection from the GCM ensemble. Each model time step lasted 10 years, so predictions from the GCM ensemble were averaged into 10-year periods, from 2001 to 10, 2011 to 20, up to 2100.

For each species and scenario, we carried out five simulations. One using the posterior means (Bayesian means) for the parameter values and the four others using parameters drawn randomly from the posterior distribution generated by the MCMC algorithm (see Appendix S2). We carried out multiple simulations for each species and scenario both because SPOMs are stochastic, and so can return different outputs under the same conditions and parameter values, and because the SPOM parameters themselves are uncertain. The spread of projections that we present (Fig. 2) includes both sources of uncertainty.

From these projections, we calculated regional frequencies (fraction of survey plots occupied by each species) for each time step (every 10 years from year 2000 to year 2100). We also generated maps of local frequency (number of occupied plots in each 10×10 km grid-cell) in year 2000 and year 2100 under both climate scenarios.

LIMITATIONS

The model and parameter estimation procedures used here present a number of important advantages over previous approaches, but also

Fig. 2. Simulated frequency (percentage of occupied plots) between the years 2000–2100 of the ten most common tree species in Iberian Spain, with or without climate change. The multiple lines represent uncertainty in model projections (one run using the posterior mean parameters, plus four runs using parameters drawn randomly from the joint posterior).

presents some limitations that need to be considered to properly interpret its predictions (see details in the Discussion). The most important of the disadvantages are: the SPOM is specified at a scale of 1×1 km, whereas the true scale of colonization/extinction events could be different from this; the model is parameterized with data from one temporal interval only and so might be missing important events that occur more rarely (e.g. episodic disturbances); the model assumes that a 10-year period is long enough for an unoccupied plot to become occupied and a source of seeds; the model does not include biotic interactions (e.g. competition) as well as some potentially important environmental variables; and the model is parameterized with data from the SFI, which uses relatively small plots and a variable radius subplot system. Moreover, the parameter estimation assumes that the estimated temperature and precipitation for each plot is correct, whereas in reality, there will be mismatches, leading to an 'errors in x' problem that could lead to an underestimation of the effects of climate change (see McInerny & Purves 2011). Each of these issues represents avenues for future development.

Results

MODEL SELECTION AND VALIDATION

Models including climate-dependent extinction and colonization rates provided the lowest AIC values for all species (Table S1), indicating that temperature and precipitation were consistently supported as explanatory variables. For most species, unimodal relationships between climate and the local dynamics (models type E2 and C2) had lower AICs (7/10 and 6/10 species, respectively) compared to simpler, monotonic relationships (models type E1 and C1). The combination of E2 and C2 (E2C2 model) was the best model for 5 of 10 species (followed by E1C1 and E2C1, which were best for two species each and by E1C2, which was best for one species). Also, a unimodal relationship with climate is more biologically realistic than a monotonic one, since monotonic relationships can lead to unrealistic rates in extreme environments (e.g. colonizations either become more likely in warmer environments, no matter how warm; or more likely in colder environments, no matter how cold). Thus, for consistency among species, we opted in our simulations to use model E2C2 for all 10 species. However, to test how this model selection might affect our results, we repeated the simulation process using for each species the lowest AIC model, even when they were not the E2C2, obtaining very similar results (Fig. S1).

The parameter estimates associated with model E2C2 indicated substantial species differences in the response of colonizations and extinctions to both temperature and precipitation (Fig. S2), as well as significant species differences in the dispersal parameter (see Appendix S2 and Table S2). We also parameterized a simpler logistic model that included only precipitation or temperature as predictors, finding that, overall, both variables were roughly equal in importance, but with their relative importance differing among species (Table S3). Such differences in the climate dependence of the local dynamics imply that the species are likely to have contrasting distances to equilibrium in their distributions and will respond differently to climate change.

Visual comparison of projections vs. observations suggested that, in general, colonizations were reproduced more accurately than were extinctions (Fig. S3). Lower probabilities of colonization and extinction appeared to be better projected than higher probabilities, likely due to the greater amount of available data for lower probability classes, with the accuracy of projections varying among the species.

SIMULATIONS: NON-EQUILIBRIUM

Simulations maintaining current climate (stable climate scenario) projected that average frequency (occupied fraction of all surveyed plots) would keep increasing for the whole 21st century in 9 of the 10 species (Fig. 2 blue lines). Among these nine species, eight showed a continuous increase of occupancy up to 2100, with little sign of reaching an asymptote. Using formal error propagation allowed us to estimate the uncertainty on the projections (the dashed lines in Fig. 2). For most species (8/10), the spread of projected frequencies for the year 2100 was well above the frequency for the year 2000, implying that the results are robust to parameter uncertainty. The exceptions were *Quercus petraea*, which shows almost no trend in any case (Fig. 2, spread of blue lines), and *Quercus pyrenaica*, for which the spread of projected frequencies at 2100 appears to be only marginally significantly above zero. Thus, according to the simulations, the dominant tree species in mainland Spain are currently far from equilibrium with current climate conditions and are likely to remain so for at least the next 100 years.

Inspection of the projected geographic distributions in 2100 for the stable climate scenario (Figs 3 and S4) showed that the projected increases in average frequency occurred primarily through an increase in the fraction of occupied plots within the overall range currently occupied by each species (local scale increment). Although most species also showed some range expansion (regional scale increment: Figs 3 and S4), this expansion is substantial for two species alone (*Quercus faginea* and *Pinus pinea*).

SIMULATIONS: RESPONSE TO CLIMATE CHANGE

Projections including the effects of climate change also showed increased frequency for most (8/10) species (Fig. 2, red lines), the exceptions being *Quercus petraea* and *Quercus pyrenaica*. However, as shown by the stable climate projections (Fig. 2, blue lines), such increases are also expected without climate change. Viewing these projections against the stable climate baseline (Fig. 2, red vs. blue and Fig. 3, middle vs. right side maps), reveals that the species can be divided into three groups according to the projected effect of climate change on their regional frequency of occupancy (Fig. 2) and geographic distribution (Figs 3 and S4). We term the first group species with low vulnerability because they show a similar projection with or without climate change (Fig. 2 red vs. blue). This group includes *Quercus robur*, *Quercus petraea*, *Pinus pinaster*, *Quercus faginea* and *Quercus ilex*. For one of the species in this group (*Quercus petraea*), the lack of climate change effects can be attributed to parameter
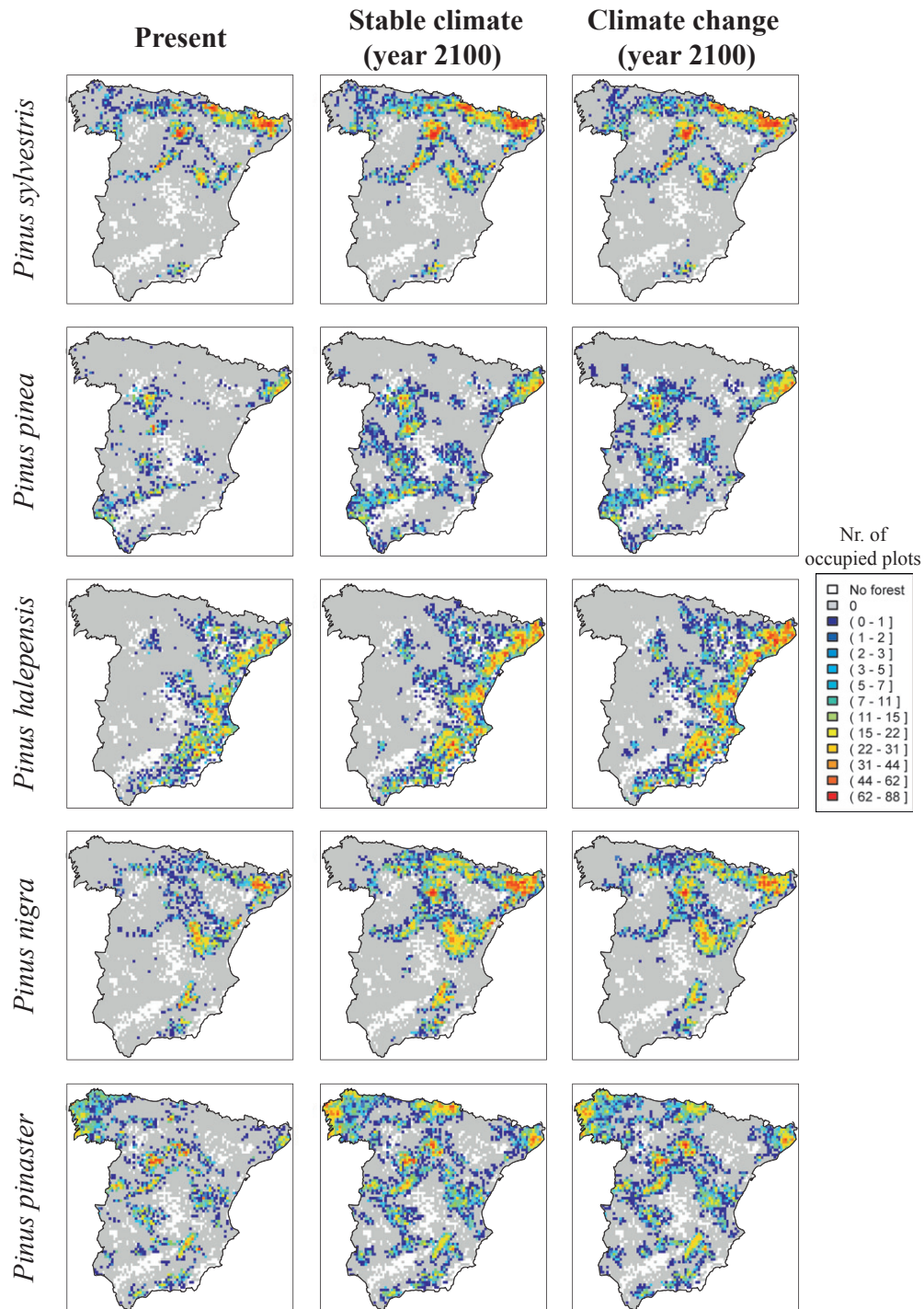
Fig. 3. Geographical distributions, current observed vs. projected with and without climate change. Without or without climate change, most species show a small amount of range expansion by 2100 (middle vs. left, and right vs. left). However, a comparison with Fig. 2 shows that the projected substantial increases in regional frequency by 2100 mainly result not from range expansion, but from increases in frequency within the range (e.g. compared *Quercus robur* in this figure, vs. Fig. 2). Colours show number of occupied plots in 10 × 10 km grid-cells (the inventory data, and model, is one a finer resolution of 1 × 1 km, too fine to show here). For an impression of how the model works, an interactive version can be found on the web page below, in which the values of the parameters can be changed by the visitor (http://research.microsoft.com/en-us/people/dpurves/sample.aspx).

uncertainty leading to a large spread of projections in both scenarios. But the other species in this group show marked dynamics, with limited uncertainty, under both scenarios, and yet little effect of climate change, implying that the conclusion that these species may not be severely affected by climate change is robust to parameter uncertainty.
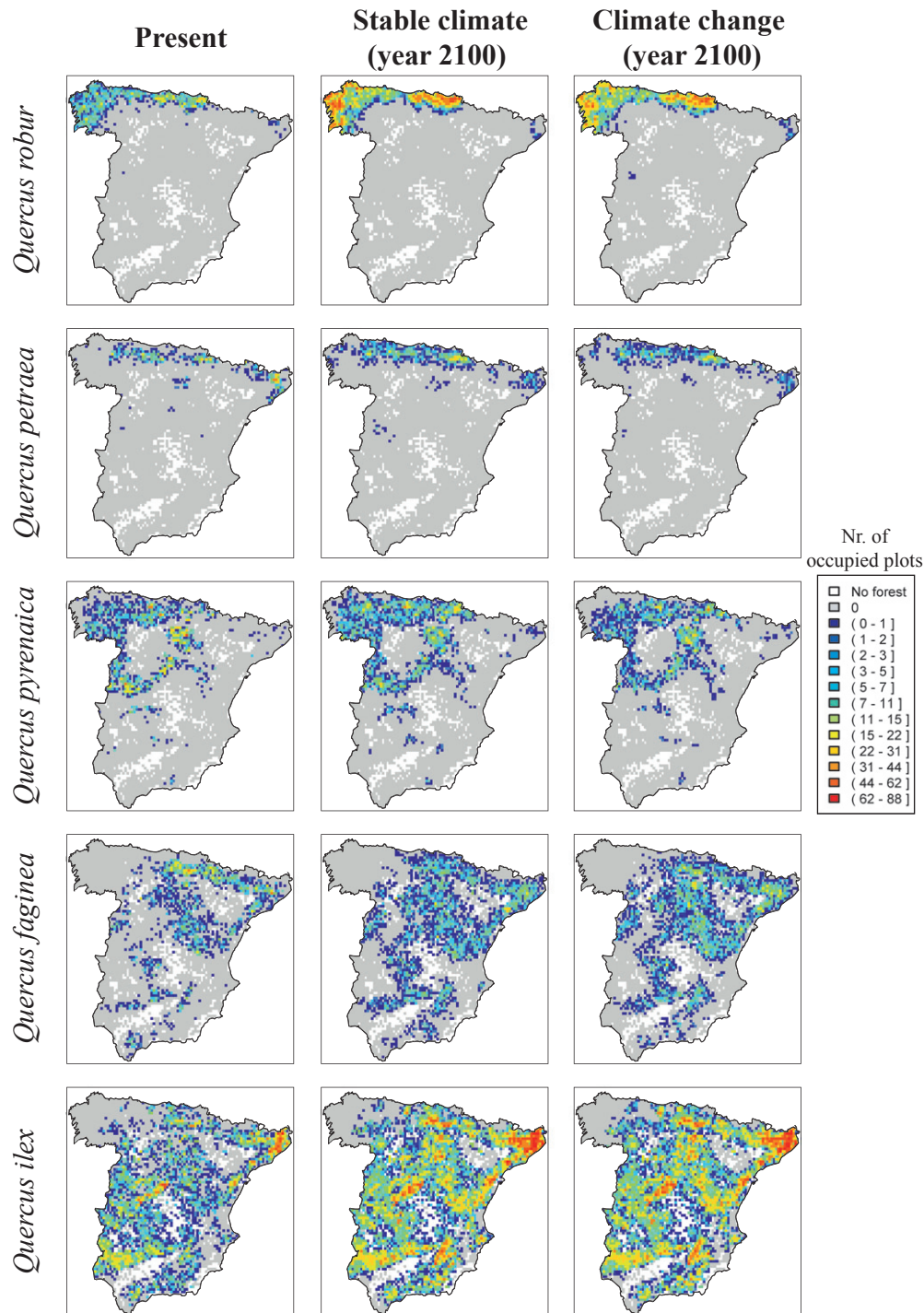
Present

Stable climate (year 2100)

Climate change (year 2100)

Quercus robur

Quercus petraea

Quercus pyrenaica

Quercus faginea

Quercus ilex

Nr. of occupied plots

- No forest
- 0
- (0 - 1]
- (1 - 2]
- (2 - 3]
- (3 - 5]
- (5 - 7]
- (7 - 11]
- (11 - 15]
- (15 - 22]
- (22 - 31]
- (31 - 44]
- (44 - 62]
- (62 - 88]

Fig. 3. (continued)

The second group are the species with high vulnerability to climate change and comprise *Pinus sylvestris, Pinus nigra* and *Quercus pyrenaica*. Without climate change, these species are projected to increase in occupancy and expand their ranges, whereas with climate change, the simulations project that increases would be less pronounced (*Pinus sylvestris, Pinus nigra*), or even reversed (*Quercus pyrenaica*). The third group include what we call favoured species: *Pinus pinea* and *Pinus halepensis*, which are projected to increase

without climate change but are expected to increase even more with climate change. According to the model, the projected 2000-to-2100 increase for *Pinus halepensis* would be almost 50% greater with climate change than without. For all three groups of species, the effects of climate change were primarily on frequency within the range, with the projected species ranges being very similar in the two scenarios (Fig. 3, compare middle and right panels; and seen more clearly in Fig. S4).

Discussion

We use tree species occupancy changes in forest plots throughout continental Spain to model species distributions from year 2000 to year 2100. Most modelled species distributions are currently out of climatic equilibrium, and we predict that species could increment their regional frequency of occurrence until the end of the century without climate change. Climate change would modify regional frequency: in almost all cases frequencies would increase. Our approach has a number of advantages, as well as disadvantages that we discuss below.

NON-EQUILIBRIUM

Our results are consistent with the view that modelled tree species are far from equilibrium with current climate, such that they would potentially increase in frequency of occurrence if the climate was held constant for the next 100 years. Non-equilibrium in species distributions might have arisen for at least two reasons. First, the vegetation in the Mediterranean region has a long history of large-scale anthropogenic impacts. Large areas once occupied by forest were transformed to croplands and the remaining forest patches have since been managed for different purposes (Blondel & Aronson 1999). In recent decades, however, rural depopulation has dramatically affected land use in different European regions; in particular, montane and Mediterranean areas have undergone agricultural abandonment and several land-use change models project the continuation of this pattern of abandonment throughout the 21st century (Rounsevell *et al.* 2006). Sheep grazing and agricultural abandonment have already caused substantial increases in oak forest cover (Debussche, Lepart & Dervieux 1999; Rousset & Lepart 1999, 2000), and coppicing has mostly ceased in Mediterranean *Quercus* woodlands, affecting forest structure and composition (Debussche, Debussche & Lepart 2001). All these changes in land use and forest management are leading to substantial forest expansion in some regions (Antrop 1993; Blondel & Aronson 1999; Araújo *et al.* 2008). The SFI reports an increment of 5.94% in forested area in Spain over the last decade alone (Villaescusa & Diaz 1998; Villanueva 2005). Successional trajectories and rate of recolonization are contingent upon local environmental conditions, species interactions and dispersal vectors. Similarly, silvicultural practices can accelerate or slow down secondary succession by favouring one species over others and thus promoting changes in species dominance once management intensity decreases (Urbieta, Zavala & Marañón 2008). Nonetheless, recovery can be surprisingly rapid. For example, 10 years after abandonment, 45% of total woody species richness has been found to be present in dry Mediterranean areas (Bonet & Pausas 2004) and 20% in mesic Mediterranean areas (Escarre *et al.* 1983).

Secondly, there is also a possibility that some species are out of equilibrium with the current climate partly because there has been insufficient time for them to reach equilibrium since the last ice age (Svenning, Normand & Kageyama

2008). Palynological records have indeed shown that the tree species composition of the Iberian Peninsula has changed continually during the last several thousands of years due to a combination of natural changes (especially rebound from the species minima during the Last Glacial Maximum; Carrión *et al.* 2001b), disturbances such as fire (Carrión *et al.* 2003a) and contingency to initial conditions (Carrión *et al.* 2001a). For example, *Quercus* species have been gradually spreading from their Iberian refugia to their current distributions in the region (Brewer *et al.* 2002; Petit *et al.* 2002; Carrión *et al.* 2003b) and may still not have reached their potential (equilibrial) distributions. In a similar vein, Svenning & Skov (2004) estimated that many European tree species occupy less than 50% of their estimated potential ranges and suggested that this is mostly due to continuing post-glacial expansion and dispersal constraints (see also Araújo & Pearson 2005; Montoya *et al.* 2007; Baselga & Araújo 2010).

Whatever the mechanisms driving non-equilibrium among tree species distributions, one of the consequences of this pattern is that species are predicted to undergo increases in their frequency of occurrence during the next 100 years, regardless of whether the climate changes or not. Moreover, if the climate and anthropogenic factors such as forest management and herbivore densities continue to change, then the equilibria toward which the species are heading will themselves continue to change. If so, each of these species could remain in a transient state, continually chasing but never reaching an ever-changing equilibrium (Fig. 1).

CLIMATE CHANGE

According to our projections, the three species more vulnerable to climate change are *Pinus sylvestris, Pinus nigra* and *Quercus pyrenaica*. The montane conifer *Pinus sylvestris* is sensitive to drought during seed establishment (Castro *et al.* 2004), growth (Gómez-Aparicio *et al.* 2011) and mortality (Martínez-Vilalta & Piñol 2002; Rebetez & Dobbertin 2004). It is classified as highly vulnerable because under climate change its rate of expansion in the north-west and rate of increasing abundance in areas currently occupied in the north-east will both decrease. *Pinus nigra* is a sub-mediterranean conifer whose growth is highly influenced by drought (Martín-Benito *et al.* 2008; Gómez-Aparicio *et al.* 2011) and under climate change its expansion within its north-eastern Iberian range will slow down, as well as its range expansion in the central part of the Peninsula. The sub-mediterranean deciduous (marcescent) *Quercus pyrenaica* is the slowest growing oak under high mean annual temperature in the study (Gómez-Aparicio *et al.* 2011). Climate change will switch its trajectory from increasing to decreasing, especially noticeable in the north-western part of Spain.

The effect of climate change can be largely attributed to interspecific differences in drought tolerance. The broad-leaved *Quercus robur,* however, presents a low vulnerability accordingly to our results. Yet it is a typical cool temperate species, and its Iberian range is considered to be constrained

by water availability (Benito Garzón, Sánchez de Dios & Sainz Ollero 2008). Moreover, *Quercus robur* is less tolerant to drought than *Pinus sylvestris* or *Pinus nigra* (Niinemets & Valladares 2006). A possible explanation may have to do with its current distribution and habitat physiography. Specifically, *Pinus sylvestris*, *Pinus nigra* and *Quercus pyrenaica* currently occupy the Central, Iberian and Penibetic mountain systems which are mountainous systems within the Central plateau. Thus, for these populations, their ability to survive climate change by moving upwards in this region is limited and their expansion will be lower than the one projected in the stable climatic baseline. Meanwhile, *Quercus robur* inhabits low elevation portions of the mountains in northern Iberia – relatively cooler and more humid than the rest of the Peninsula – which means that it still have enough altitude to gain to escape increasing aridity (Benito Garzón, Sánchez de Dios & Sainz Ollero 2008). Interspecific differences in drought tolerance and dispersal are thus key factors determining future species ranges under climate change in this region, but future trajectories and species-specific vulnerability will also be contingent upon current habitat structure (Montoya *et al.* 2010).

Using a BEM fitted on similar data, Benito Garzón, Sánchez de Dios & Sainz Ollero (2008) projected that in 2080, under an A2 climate change scenario, all species modelled herein (some considered at the subspecies level) would decrease in potential area of distribution between 73% and 100% in the Iberian Peninsula while gaining only between 0.3% and 26%. In contrast, the projections presented here (Fig. 2) imply that even under climate change, 8 of 10 species will gain more than they would lose during the next 100 years. However, there are also some reassuring similarities between the two studies. Benito Garzón, Sánchez de Dios & Sainz Ollero (2008) project that the greatest declines would be among tree species that we classify as with low vulnerability (*Pinus sylvestris*, *Pinus nigra* ssp. *salzmannii*, *Quercus pyrenaica*, *Quercus petraea* and *Quercus faginea*), while limited declines would be expected for *Quercus robur*, which we classified as low vulnerability. Likewise, they project the smallest declines for species classified as low vulnerability or favoured by climate change in our analysis (*Pinus pinaster*, *Quercus ilex spp. ilex*, *Pinus pinea* and *Pinus halepensis*). *Quercus ilex* is a specific case in which a one to one comparison between the two studies is not possible, because we modelled it as a species, while Benito Garzón, Sánchez de Dios & Sainz Ollero (2008) modelled it as two subspecies. For example, our models projected the species to exhibit low vulnerability to climate change, while they found one of subspecies to be susceptible to small declines and the other to be susceptible to strong declines. All in all, the rank of species sensitivity to climate change between the two studies is comparable, with our study focussing on near-term, non-equilibrial dynamics, and Benito Garzón, Sánchez de Dios & Sainz Ollero (2008) focussing on changes in the potential (i.e. equilibrium) distributions.

MODEL DEVELOPMENT

The analysis presented here was a first attempt to scale observed climate dependence of local patch dynamics to plausible projections of the regional dynamics of these species in the future. It was natural to define the SPOM at the same spatial scale as the data (one plot per 1 × 1 km cell). Although the dynamic pattern of colonization is likely to occur on finer spatial scales, our projections are expected to be robust with respect to the spatial scaling issue. The reason is that, so long as the calculated seed rain is correlated with the true seed rain, and this correlation holds approximately constant within the species range, we would expect the simulations to capture the dynamics recorded in the data (e.g. see Fig. S2). Nonetheless, we highlight finer-scale modelling as one important aspect of model development in the future, especially through the integration of complementary data from local vegetation surveys.

There is also a potentially important temporal scaling issue, following from the fact that the data correspond to events over a single time period alone (1986–2007). The model employed here predicts distributions, as they emerge from local dynamics parameterized against data taken over a short interval. Any survey of such limited temporal extent stands the risk of missing important events that did not happen in that period, but which could be critical in setting the long-term dynamics of the species. Moreover, it is next to certain that the dynamics of these species in the future will be affected by events not recorded in the inventory data, including pest outbreaks, changes in forest management and fires. Moreover, the combination of drier and warmer climate and more flammable vegetation may result in novel disturbance regimes (Venevsky *et al.* 2002), leading to autosuccesional dynamics and contingent dynamics (Zavala, Espelta & Retana 2000; Carrión *et al.* 2001a). The decadal updates of Forest Inventory databases that are being implemented in many European countries will allow to reduce uncertainty and to periodically revise this model structures and parameters, and hence projections.

It is also important to note that, like many other SDM implementations, our analysis did not include the effects of biotic interactions among species (but see Kissling *et al.* 2012); in the same plot, we can find more than one species, and as it is used for simulations, the model allows more than one species, but it does not measure the effect of the interactions between them. Our modelling approach also neglects many potentially important environmental variables (e.g. fine-scale soil variation) as well as fine-scale dynamics occurring within plots (e.g. changes in the size or age distributions of individuals). This model also assumes that, in one plot, 10 years is enough time for colonization, for growth and becoming a source of seeds which might be unrealistic for some species, but preferable for us than making any preliminary assumptions of the time lag between colonization and tree maturity. Finally, the subplot variable radius survey methodology used in the SFI might also be overestimating colonizations by including, as recruits, trees already present

in the first survey but that were below the size threshold considered in their specific subplot. This bias, however, in unlikely to have a significant impact and was the best possible alternative (see Appendix S1). Thus, model projections presented herein, like any modelling that relies on simplifications to characterize complex realities, need to be interpreted with caution.

Conclusions

Several studies have sought to provide more complex SDM, accounting for demographic processes like dispersal, birth and death rates (Keith *et al.* 2008; Anderson *et al.* 2009; Brook *et al.* 2009; Fordham *et al.* 2012a), considering intraspecific variability (Benito Garzón *et al.* 2011), including vegetation and landscape configuration (Triviño *et al.* 2011) or using soil characteristics and other environmental variables besides the purely climatic ones (Iverson & Prasad 1998). Nevertheless, the model we present herein incorporates a number of characteristics that are advantageous when projecting climate change effects on species distributions. Specifically, it does not require the assumption that distributions are at equilibrium with climate, and all variables, including dispersal, are inferred from plot-level data, rather than from *a priori* assumptions or by matching predicted distributions to observed distributions. SPOMs have another advantage: they can be fitted with coarse-level data on local colonizations and extinctions, unlike individual-based models of forest dynamics that usually require detailed data on the growth, mortality and recruitment of individual trees. For all these reasons, we believe that the consideration of non-equilibrium dynamics in the modelling of species distributions is essential to explain mechanisms underlying forest dynamics and to properly assess climate change effects.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Spatial scale and the definition of presence/absence.

Appendix S2. Detailed model description and parameterization.

Table S1. Log-likelihood, AIC, ΔAIC and BIC values for all combinations of model and species.

Table S2. Parameters estimates for the E2C2 model.

Figure S1. Regional changes in species frequency from year 2000 to 2100 using the lowest AIC model (rather than the E2C2 model) for each species.

Figure S3. E2C2 model validation for every species.

Figure S4. Differences in local occupancy in 2100 between the climate change and stable climate scenarios.