

# Evaluating the combined effects of climate and land-use change on tree species distributions

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## Summary

1. A large proportion of the world's biodiversity is reportedly threatened by habitat loss and climate change. However, there are few studies that investigate the interaction between these two threats using empirical data.

2. Here, we investigate interactions between climate change and land-use change in the future distribution of 23 dominant tree species in mainland Spain. We simulated changes up to year 2100 using a climate-dependent Stochastic Patch Occupancy Model, parameterized with colonization and extinction events recorded in 46 596 survey plots.

3. We estimated that the distribution of 17 out of 23 tree species are expanding and hence not at equilibrium with the climate. However, climate change will make the future occupancy of 15 species to be lower than expected if climate, and habitat, remained stable (baseline scenario).

4. Climate change, when combined with the loss of 20% of the habitat, was estimated to reduce species occupancies (relative to baseline projections) by an average of 23% if habitat loss was spatially clumped, and by 35% if it was scattered. If habitat loss occurred in areas already impacted by human activities, species occupancies would be reduced by 26%. Land-use changes leading to habitat gain (i.e. creation through reforestation) could slightly mitigate the effects of climate change, but a 20% increment in habitat would reduce climate change-driven losses in species occupancies by only ~3%.

5. *Synthesis and applications.* The distributions of the most common tree species in mainland Spain are expanding, but climate change threatens to reduce this expansion by ~18% for 15 of the 23 studied species. Moreover, if the habitat of these species is simultaneously lost, the occupancies of all of them will be reduced further, with variation depending on the spatial pattern of the lost habitats. However, we did not detect synergies between climate change and habitat loss. The combined effect (with 20% habitat loss) was 5–13% less than what it would be if the effects were additive. Importantly, reforestation could partially offset the negative effects of climate change, but complete mitigation would require an increase in forested land of ~80%, and the prioritization of territories that are less impacted by human activities.

**Key-words:** climate change mitigation, climatic disequilibrium, deforestation, habitat loss and fragmentation, Iberian Peninsula, Mediterranean, metapopulation dynamics, non-equilibrium dynamics, reforestation, stochastic patch occupancy model

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## Introduction

Human-induced climate change and habitat loss rank among the most important threats to biodiversity (Sala *et al.* 2000; Pereira *et al.* 2010). Several studies have assessed their potential impact on the long-term persistence of species (Bascompte & Solé 1996; Ovaskainen *et al.* 2002; Thomas *et al.* 2004; Thuiller *et al.* 2005; Araújo *et al.* 2008; Garcia *et al.* 2012), but their effects have been seldom studied in combination (but see Travis 2003; Pearson, Dawson & Liu 2004; Jetz, Wilcove & Dobson 2007; Pompe *et al.* 2008; Hof *et al.* 2011a; Ponce-Reyes *et al.* 2013). When studied, the combined impacts of climate and habitat loss have been assessed using either theoretical simulations or correlative macroecological approaches. Theoretical work suggests these two threats can act in synergy, having a greater effect on species distributions than expected based on simple addition of both impacts (i.e. additive effect; e.g. Travis 2003). Here, we provide a dynamic data-driven process-based assessment of the combined effects of climate and habitat loss on the distribution of the most common tree species in mainland Spain.

Ongoing climate change effects on species distributions have already been documented (Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006), and many studies forecast greater impacts in the future (Thomas *et al.* 2004; Thuiller *et al.* 2005; Araújo *et al.* 2008; Garcia *et al.* 2012). Past climate changes in the Iberian Peninsula have modified the species composition of tree communities (Carrión & Fernández 2009; Postigo Mijarra *et al.* 2009), and there is evidence of current contraction and expansion of tree species distributions across this region (García *et al.* 1999; Mejías, Arroyo & Ojeda 2002; Castro *et al.* 2004; Arrieta & Suárez 2006; Jump, Hunt & Peñuelas 2006; Peñuelas *et al.* 2008; Uribe *et al.* 2013). In addition, climate change forecasts project substantial decreases in the potential distribution of tree species in the Iberian Peninsula (Benito Garzón, Sánchez de Dios & Sainz Ollero 2008; but see García-Valdés *et al.* 2013). Throughout Europe, some tree species are also expected to lose climatically favourable areas (Thuiller *et al.* 2005; Engler *et al.* 2011), whereas others are expected to gain new areas (Kramer *et al.* 2010; Araújo *et al.* 2011).

Forecasts of species distributional shifts under climate change are commonly achieved using correlative species distribution models (SDMs; Pearson & Dawson 2003; Heikkinen *et al.* 2006; Araújo & Peterson 2012) that explore the relationship between known species distributions and aspects of the environment (also known as ecological niche models, bioclimatic envelope models and habitat suitability models). These models rely on correlations estimated in a single moment in time. Therefore, correlative SDMs do not explicitly consider fundamental dynamic mechanisms that may affect species distributions (but see Nogués-Bravo *et al.* 2008). Although the calibration of correlative SDMs can be implemented without

species being in full distributional equilibrium with the climate (complete range filling), it is assumed for operational reasons that species occupy their climatic limits (full niche filling; Araújo & Pearson 2005; Svenning & Sandel 2013), which may not always be true (Baselga & Araújo 2010; Hof *et al.* 2012; Munguía *et al.* 2012).

Habitat loss due to logging, mining, deforestation, agriculture, urban expansion and other reasons is another major threat to biodiversity (Sala *et al.* 2000; Pereira *et al.* 2010). Habitat loss also leads to the fragmentation of landscapes (e.g. Lande 1987), which disconnects populations, decreases gene flow and reduces source-sink population dynamics (e.g. Bascompte & Solé 1996; Freckleton & Watkinson 2002; Alagador *et al.* 2012). Consequently, the critical threshold in habitat loss that signals the local extinction of a species depends on its spatial arrangement (Bascompte & Solé 1996; Bascompte & Rodríguez 2001; but see Montoya *et al.* 2010). Spatially correlated continuous habitat loss tends to produce less-fragmented landscapes and has a weaker impact on species populations than, for example, spatially scattered habitat loss (Bascompte & Solé 1996; Travis 2003). Nevertheless, there is a strong collinearity among habitat loss and fragmentation (see Rueda *et al.* 2013), and their effects are often difficult to differentiate (Fahrig 2003; Hof *et al.* 2011a; but see Didham, Kapos & Ewers 2012).

Climate change and habitat loss are believed to interact in synergy (Travis 2003). For example, habitat fragmentation can affect species dispersal rates, preventing individuals or propagules from escaping climate change (Collingham & Huntley 2000). At the same time, climate change can reduce the persistence of isolated populations in fragmented landscapes (Warren *et al.* 2001). Conversely, this raises the possibility of using habitat creation to partially offset the impacts of climate change. However, the combined effects of climate change and habitat loss (or creation) on particular species distributions remain poorly explored.

In this study, we used a climate-dependent Stochastic Patch Occupancy Model (SPOM), developed by García-Valdés *et al.* (2013), to study the combined effects of climate and habitat change. This model is calibrated with the colonization and extinction rates of tree species in permanent survey plots, and it can simulate the timing of climate and habitat change effects on species distributions. Moreover, this model can be parameterized for species that are not in climatic equilibrium, as is the case for many trees at both Iberian (García-Valdés *et al.* 2013) and European scales (Svenning & Skov 2004). This is possible because the SPOM correlates local short-term processes (colonizations and extinctions), instead of static variables (the presence/absence distributions), with climatic and spatial variables.

Using the SPOM, we simulated changes in tree species distributions from the year 2000 to the year 2100 under a baseline scenario (stable climate and habitat), a climate change scenario, and eight spatial patterns of habitat loss

and creation. We aimed to determine (i) the relative contribution of climate change and habitat loss in changing tree species distributions in mainland Spain during the 21st century; (ii) whether the combined effect of climate change and habitat loss is additive, multiplicative or semi-redundant (i.e. both threats affect the same populations, and hence, the combined effect is smaller than the sum of the two impacts); and (iii) the extent to which increased habitat (e.g. through reforestation) can offset the negative impacts of climate change.

## Materials and methods

### FOREST DATA

Data were collected from the second (1986–1996; Villaescusa & Diaz 1998) and third (1997–2007; Villanueva 2004) Spanish Forest Inventories (SFIs). Survey plots were uniformly distributed in  $1 \times 1$  km grid across all forested areas in Spain. Plots had four size-dependent concentric subplots of variable radii, and the minimum diameter at breast height for trees to be recorded in the smallest subplot was 7.5 cm. The inventories included 46 596 permanent plots in peninsular Spain, with approximately 10 years between surveys, and 30 478 plots that were surveyed only in the last inventory. Only permanent plots were used for parameterization of the model, and all plots from the last inventory were used as the starting point for the simulations. We extracted data from all the species with at least ten presences in each inventory, five recorded changes from absent to present between inventories and five recorded changes from present to absent. *Pinus radiata* and *Populus nigra* distributions largely reflect human management, while the distribution of *Ulmus minor* is strongly affected by mortality due to Dutch elm disease. These three species were excluded from the analysis because their distributions were not determined by the factors considered in the SPOM. Finally, 23 species were included, four of which were identified at the genera level only (see Table S1 in Supporting Information). See García-Valdés *et al.* (2013, 2015) for more detail on data characteristics.

### CLIMATE DATA

We used a climatically stable scenario (i.e. climatic variables were kept constant), and a changing climate scenario, with 10-year time steps from the year 2000 to the year 2100. The climate change scenario was the outcome of an ensemble of seven general circulation models (see Fordham *et al.* 2012, 2013) of a high CO<sub>2</sub> concentration stabilizing reference scenario (WRE750; Wigley, Richels & Edmonds 1996). We used the GCM ensemble projection for the year 2000 to calibrate the model, avoiding biases associated with the use of different climatic models for calibration and simulation. Climatic variables included total annual precipitation [mm] and mean annual minimum temperature [°C] (see García-Valdés *et al.* 2013 for details on the climatic model and the variable selection).

### STOCHASTIC PATCH OCCUPANCY MODELLING

We parameterized the SPOM with observed changes on tree species occupancy in the permanent plots (García-Valdés *et al.* 2013). All forested plots (i.e. with woody vegetation) were

considered available habitat for all tree species. The probability of a species colonizing a plot depended on the probability of seeds being dispersed to the plot and the probability of these seeds establishing and growing sufficiently to be recorded in the following inventory. Dispersal was parameterized with a logistic kernel function, which used the distances to the neighbouring plots (up to 50 km) that were occupied by the species in the first inventory. Dispersal could be either random with respect to habitat (for wind-dispersed species), or directed with respect to habitat (for animal-dispersed species). The probability of seed establishment and growth was defined using a unimodal bell-shaped logistic function of the climatic conditions in each plot. The probability of local extinction depended exclusively on the climatic conditions found within each plot, as represented by a unimodally shaped logistic function.

Model parameters for each species were estimated under a Bayesian framework. Each model and accompanying parameters likelihood was calculated as the probability of observing a specific transition (colonization or extinction) from one inventory to the next. We used the Metropolis–Hastings MCMC algorithm to generate parameter estimates with 50 000 iterations after burning. Details on model characteristics can be found in Appendix S1 and in García-Valdés *et al.* (2013). The parameter posterior distributions can be found in Appendix S2.

### HABITAT CHANGE

Different simulated spatial patterns of habitat loss were used to decipher the effects of fragmentation from those of habitat loss alone. Spatially aggregated habitat loss produces less fragmentation of the remaining habitat than disaggregated loss of habitat. We explored, therefore, three different levels of spatial aggregation: from completely disaggregated habitat loss, simulated by removing habitat patches at random; followed by partially aggregated habitat loss, simulated by removing spatially continuous habitat patches around multiple (100) randomly selected sites; to completely aggregated habitat loss, simulated by removing spatially continuous habitat patches around one single site, also selected at random. On a more applied level, we explored the effect of removing habitat primarily in areas that are highly impacted by human activities (high Human Influence Index, HII; Sanderson *et al.* 2002).

We used a similar approach to simulate habitat creation. We reproduced habitat growth in a totally disaggregated fashion (random new habitat patches), in a partially aggregated fashion (continuous new habitat patches around 100 sites) and in a completely aggregated fashion (continuous new habitat patches around one single site), and we created habitat in areas that are currently less impacted by human activities (low HII). We simulated habitat change (loss and creation) along the 21st century up to 20%, 40%, 60% and 80% of the initial available habitat.

### MODEL DESIGN AND ANALYSIS

If the distribution of a species is not at climatic equilibrium, the SPOM would predict that the species would change its distribution (expand or contract) even if climate and habitat remained stable. For this reason, we compared the effects of climate and habitat change on each species future (year 2100) distribution, against the future distribution of the same species if climate and habitat had remained stable (baseline scenario; see also Anderson

*et al.* 2009; García-Valdés *et al.* 2013). For each species, we used the Bayesian mean for each parameter, which represents the most likely value given the parameter posterior distribution (see Appendices S1 & S2). For the current analysis, we decided to use this single estimation (Bayesian mean) for each parameter and to focus on differences between scenarios among all species. An alternative would be to use more than one estimation per parameter, with, for example, an error propagation function that shows the parameter's uncertainty in the predictions (see García-Valdés *et al.* 2013 for an example). Next, we ran each scenario 10 times to reduce biases associated with the random selection of the starting patch, or patches, and to report the variability produced by the inherent stochasticity of the model. We explored the relative differences between each alternative scenario and the baseline in the year 2100 for each species and model run. We created barplots showing mean and confidence intervals (from the 10 runs) of these differences, for each species and scenario. We also created box-plots aggregating the results from different species (mean value of each species), first using all species together and then dividing the species depending on their response to climate change. Our modelling approach, as any simplification of a complex reality, carries a number of limitations. We have detailed some of these limitations in Appendix S3, along with possible solutions and improvements for the future.

## Results

### BASELINE, CLIMATE CHANGE AND HABITAT LOSS

With a stable climate and habitat (baseline scenario), the occupancy of 17 out of 23 species expanded through the 21st century a median of 60% in comparison with current levels (Fig. S1). The occupancy of the remaining six species declined by 51%.

With climate change, the future occupancies of 15 of 23 species were reduced by 18% in median (Figs 1 and 2), in comparison with the baseline. Meanwhile, climate change increased the occupancy of 8 out of 23 species by 10% in median, again compared with the baseline. Loss of 20% of the habitat during the 21st century under a stable climate also decreased the occupancy of 22–23 out of 23 species (Fig. 1), with median occupancy reductions between 18% and 25%, depending on how habitat loss was spatially structured (Fig. 2). The combination of climate change and the loss of 20% of the habitat resulted in decreased occupancy, compared with the baseline, for 21–23 of out 23 species (Fig. 1), and median reductions in occupancy of 26–35% (Fig. 2).

Averaged across all species, continuous loss of habitat around multiple sites produced the greatest negative effect, with median reductions in occupancy of 25% in a stable climate and 35% in a changing climate. Random habitat loss had the second-greatest negative effect on species occupancies, with median reductions of between 21% and 30%. Habitat loss biased towards the most human-affected regions reduced median occupancy between 21% and 26%. Finally, completely continuous habitat loss around a single site produced the lowest impact and reduced median occupancy between 16% and 23%. The

results for this last pattern exhibit strong variation between runs, with generally larger confidence intervals than the other patterns (Fig. 1), reflecting the importance of the geographical location of the randomly selected starting patch. Each pattern of habitat loss reduced the number of colonizations and increased the number of extinctions to different degrees. Colonizations suffered a relative reduction of between 8% and 16% under stable climate compared to baseline projections and between 25% and 32% under climate change (Fig. S2). Extinctions increased between 33% and 65% under a stable climate and between 12% and 56% under climate change. Such extinctions can be classified as direct extinctions (occurring in eliminated patches) or indirect extinctions (occurring in the remaining non-eliminated patches). The frequency of both types of extinctions varied depending on the spatial pattern of loss, but the indirect extinctions were more common, representing between 59% and 71% of all extinctions under stable climate and between 57% and 69% under climate change (Fig. S3).

When occurring independently, both climate change and habitat loss reduced the occupancy of 15 of the 23 species (Fig. 1). Meanwhile, for 7–8 species, climate change increased their occupancies whereas habitat loss decreased them. For this last group of species and with the exception of *Pinus halepensis*, the negative effect of habitat loss was greater than the positive effect of climate change. Our results also indicated that the spatial pattern of habitat loss modified the strength of the combined effect. With 20% completely continuous habitat loss, the joint effect was 5% smaller in mean than the additive effect, and if habitat loss was biased towards human-impacted areas, the joint effect was 13% smaller than the additive effect (Fig. S4). If 40% of the initial available habitat was lost, the combined effect was 11–15% smaller than the additive effect.

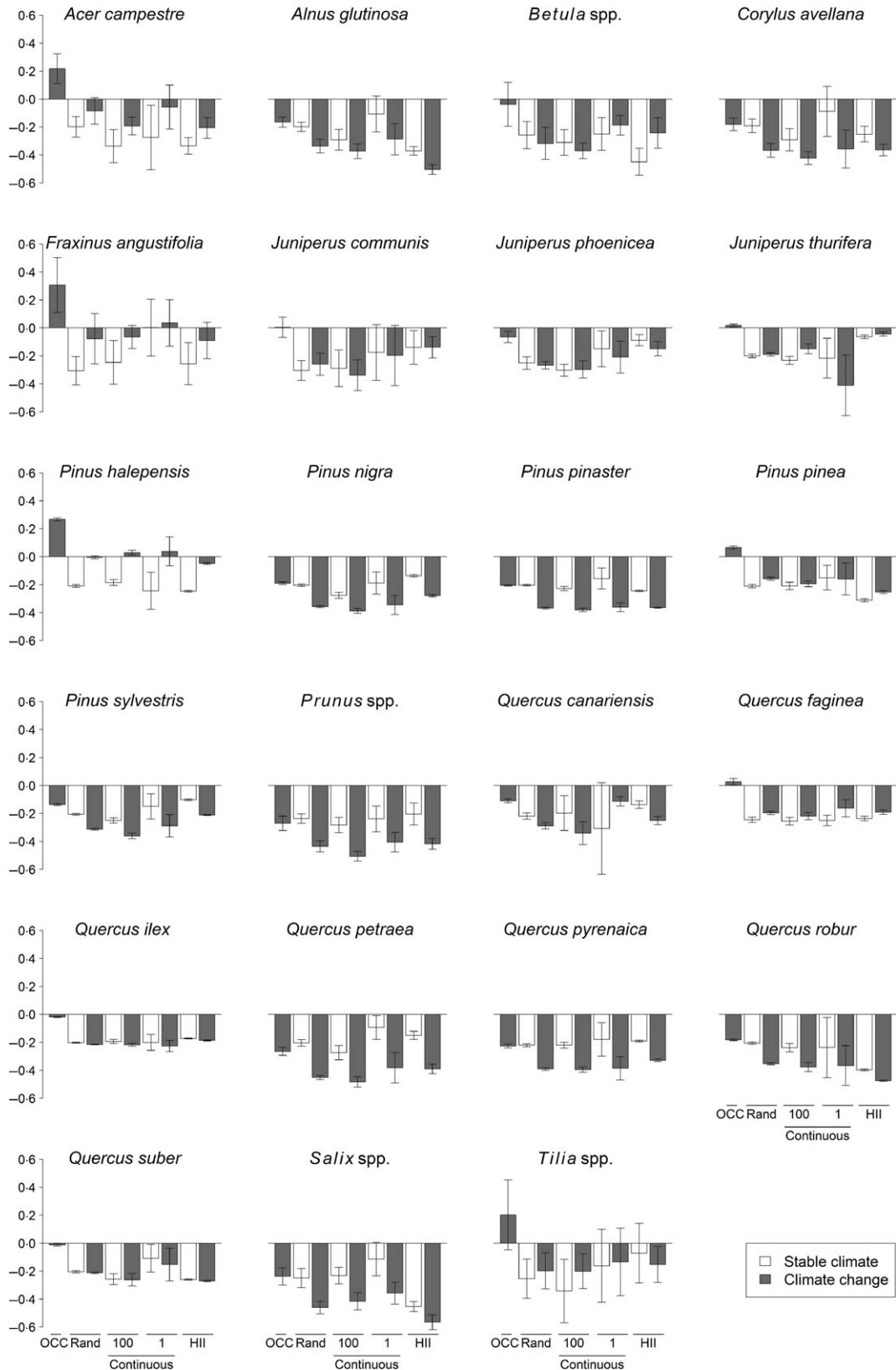
### CLIMATE CHANGE AND HABITAT CREATION

Habitat creation under a stable climate increased species occupancies in comparison with the baseline (Figs 2 and 3), although these changes were not similar in importance to those triggered by habitat loss (Figs 1 and 2). Twenty percentage habitat creation achieved approximately 4–5% median increase in occupancy depending on the spatial pattern of creation, while 40% increase in habitat had more differentiated effects depending on the spatial pattern of the created habitat (Fig. S5), with the completely continuous pattern resulting in the greatest occupancy increase (14%). Habitat creation had no considerable effect on the number of extinctions and changed species occupancy mainly by increasing colonizations (Fig. S2), although the number of these colonizations occurring in new habitat was significantly smaller than the number of colonizations occurring in old habitat patches (which represented 93–95% of all colonizations; Fig. S3).

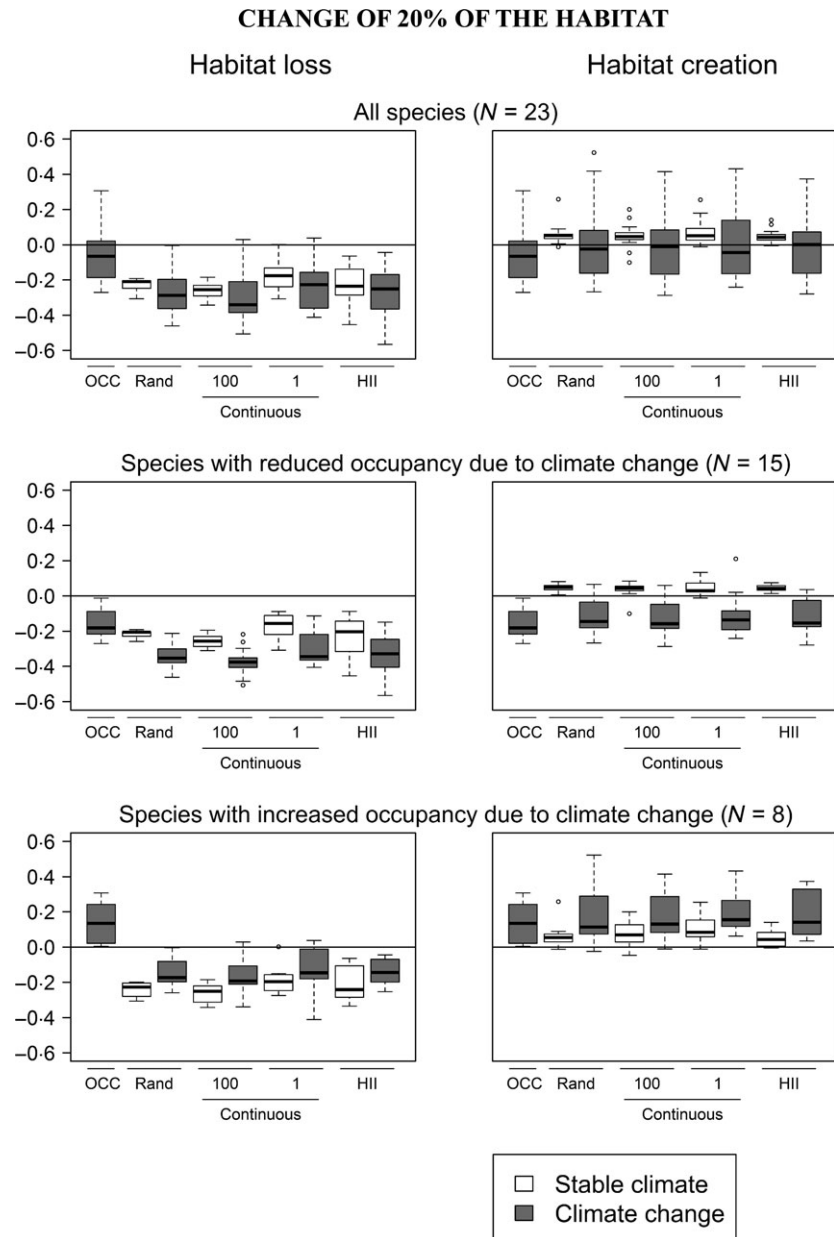
Future species losses in occupancy due to climate change were not easily mitigated by habitat creation



### LOSS OF 20% OF THE HABITAT



**Fig. 1.** Bar-plots of the mean  $\pm$  confident interval (out of 10 simulations) relative difference in species occupancies in the year 2100 between each climate and habitat loss (20%) scenario and the baseline scenario. OCC stands for only climate change, and the four spatial patterns of habitat loss are random, partially continuous around multiple (100) sites, completely continuous around one (1) single site and biased towards areas currently impacted by human activities (HII).



**Fig. 2.** Box-plots of the relative difference in numbers of occupied patches in the year 2100 between each climate and habitat change scenario (up to 20% of current habitat) and the baseline scenario. Species were divided into those subject to decreased ( $N = 15$ ) and increased ( $N = 8$ ) occupancy with climate change. OCC means only climate change, and the four spatial patterns of habitat loss are random, partially continuous around multiple (100) sites, completely continuous around one (1) single site and biased towards areas currently impacted (habitat loss) or non-impacted (habitat creation) by human activities (HII).

(Fig. 2). With the creation of 20% of new habitat, the losses in occupancies produced by climate change were reduced by approximately 3%. If 40% of new habitat was created following a continuous spatial pattern, the negative effect of climate change was reduced by 10% (Fig. S5). An 80% increase in new habitat was required to completely reverse, in median, the negative effects of climate change on threatened species (Fig. S6), and this occurred only if habitat was restored in areas with low human impact.

## Discussion

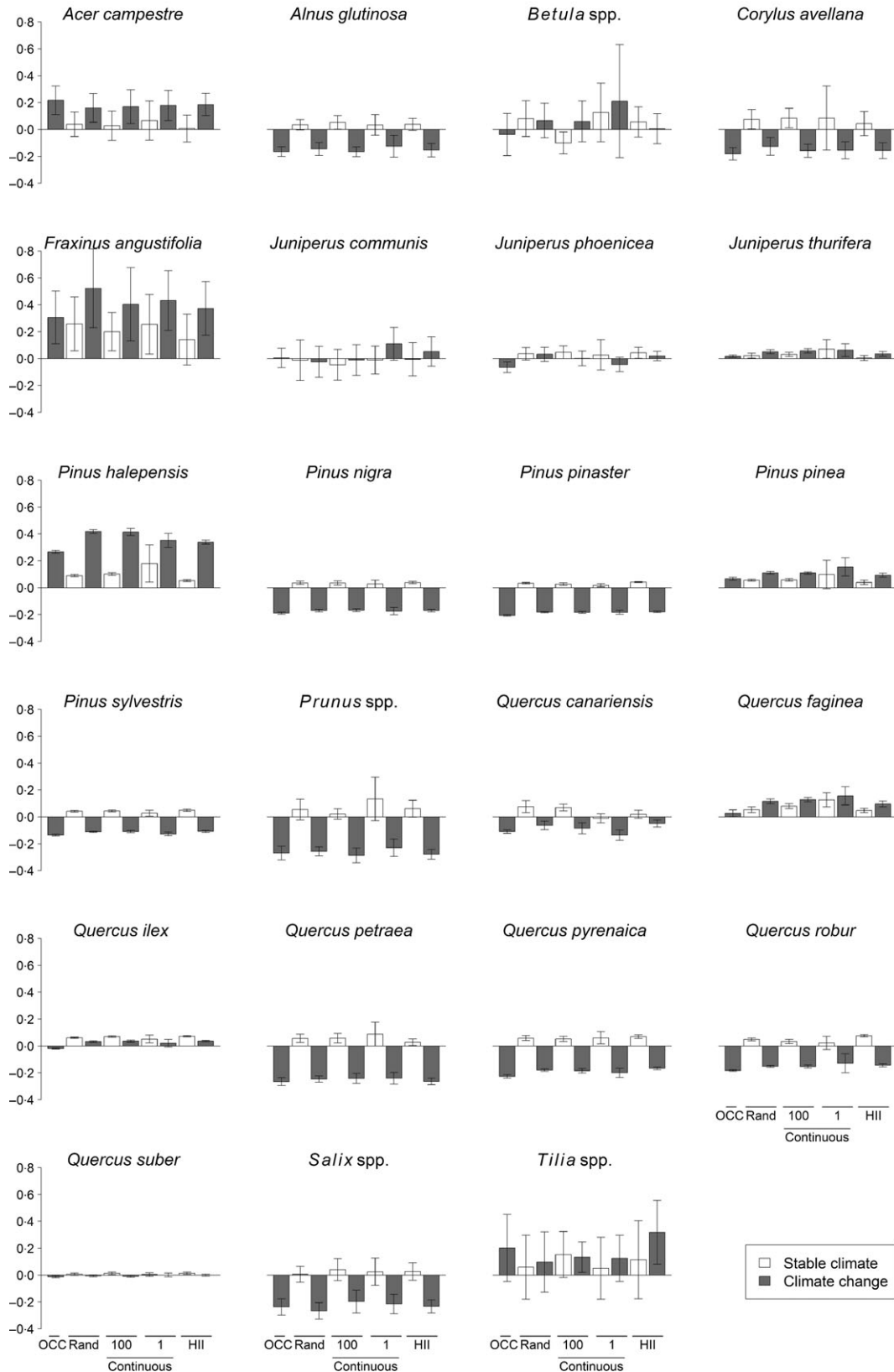
We used tree species local colonization and extinction rates across mainland Spain to simulate the effect of climate and land-use change on their future distributions. We estimated that climate change would reduce the

occupancy of 15 out of 23 species by 2100, relative to baseline projections. If habitats are simultaneously lost during this period, species occupancies would decline even further. However, climate change and habitat loss did not act in synergy, given that their combined effect was slightly smaller than expected if they were additive. Also, habitat creation (i.e. reforestation) was much less effective to offset climate change negative effects than it might have been expected. However, creating new habitat in areas that are currently not impacted by human activities would improve on efforts of mitigating the negative effect of climate change on tree species distributions.

## CLIMATE CHANGE

Consistent with a previous study (García-Valdés *et al.* 2013), we estimated that the distribution of many tree

### CREATION OF 20% OF THE HABITAT



**Fig. 3.** Bar-plots of the mean  $\pm$  confident interval (out of 10 simulations) relative difference in species occupancies in the year 2100, between each climate and habitat creation (20%) scenario, and the baseline scenario. OCC stands for only climate change, and the four spatial patterns of habitat creation are random, partially continuous around multiple (100) sites, completely continuous around one (1) single site and biased towards areas currently non-impacted by human activities (HII).

species is currently expanding in mainland Spain and would continue to do so in the absence of climate change (Fig. S1). Hence, their current ranges are smaller, and/or occurrence within their ranges lower, than the equilibrium (Svenning & Sandel 2013). These dynamics may reflect recent agricultural abandonment, decreased traditional silvicultural activities (Debussche, Lepart & Dervieux 1999; Debussche, Debussche & Lepart 2001; Rounsevell *et al.* 2006) or long-term post-glacial dispersion-limited range expansions (Svenning & Skov 2004; Montoya *et al.* 2007; Svenning, Normand & Skov 2008; Baselga & Araújo 2010).

Nonetheless, climate change is likely to modify future range expansions of species, and its effects will differ depending on species characteristics, such as tolerance to drought, current distributions and dispersal ability (García-Valdés *et al.* 2013; see also Nogués-Bravo *et al.* 2014). In general, while a few tree species will be positively affected by climate change, many more will be negatively impacted. This would lead to changes in species distributions and hence changes in forest species co-occurrences and communities, with potentially negative consequences for biodiversity and ecosystem functioning. This predominantly negative impact might occur because many species are already close to the drought-limited southern edge of their ranges in mainland Spain, and thus sensitive to increasing drought (Castro *et al.* 2004; Lloret, Siscart & Dalmases 2004; Arrieta & Suárez 2006; Jump, Hunt & Peñuelas 2006; Peguero-Pina *et al.* 2007). Nonetheless, like previous studies (García-Valdés *et al.* 2013; Svenning & Sandel 2013), our results support the idea that, when exposed to climate change, tree species distributions would not dramatically change over the period of just one century. Instead, discernible consequences of climate change would be expected to manifest themselves over hundreds of years (Botkin *et al.* 2007; Svenning & Sandel 2013). Yet, extreme climatic events such as persistent droughts could lead to rapid and dramatic declines in populations (Allen 2009; Hof *et al.* 2011b).

#### HABITAT LOSS

In our simulations, habitat loss influenced future occupancies by decreasing the probability of future colonizations and increasing the probability of future extinctions. As expected, the frequency of colonizations is significantly reduced during habitat loss in comparison with the baseline scenario. Moreover, colonization rates vary depending on the spatial pattern of habitat loss, demonstrating that varying the spatial arrangement of the remaining habitat allows for different degrees of dispersion. Indirect extinctions, occurring in non-eliminated patches, were more abundant than the direct extinctions occurring in eliminated patches. In addition, different spatial patterns of habitat loss produced varying indirect extinction rates, which can only be explained by different levels of isolation in the remaining populations produced by different degrees of fragmentation of the landscape.

#### Continuous vs. random habitat loss

The present model demonstrates that habitat loss reduces the future occupancy of almost all species and that it causes different effects depending on how it is aggregated (Figs 1 and 2). Fully spatially autocorrelated habitat loss impacts future occupancies less than completely random loss. These findings are consistent with previous results by Travis (2003), who indicated that continuous habitat loss produces landscapes that are less fragmented and thus less prone to extinction (see also Bascompte & Solé 1996; Hill & Caswell 1999; With & King 1999). Interestingly, when continuous habitat loss occurs around multiple sites, the negative impact on future occupancies is even greater than when habitat loss occurs at random. This may be because completely random loss does not eliminate all habitat patches in any given location, allowing for certain degree of connectivity between populations. In contrast, continuous habitat loss around multiple sites eliminates all habitat patches in each location, while occurring in a significant number of places to produce great habitat fragmentation.

#### Human-associated habitat loss

When habitat loss is associated with areas of high human influence, losses in occupancy are projected to be in the mid-range between those of the partially aggregated and the totally aggregated loss. This pattern may occur because the aggregation of the human-impacted patches lies between the other two scenarios or because many tree species primarily occur at sites with relatively low human influence, for example low agricultural land cover (Fig. S7). Consequently, the negative effect of eliminating patches that are impacted by human activities is partially ameliorated because those patches have fewer species.

#### CLIMATE CHANGE AND HABITAT LOSS SYNERGY

For most (15 out of 23) species, climate change and habitat loss had negative effects on their distributions, and for some (7–8), climate change increased their occupancies, while habitat loss decreased them. For all of these latter species but one, the negative impact of habitat loss was greater than the positive effect of climate change. The exception is the efficiently dispersed, heat- and drought-tolerant *Pinus halepensis*, which increased its occupancy so much under climate change that even if 20% of its habitat is lost (with a continuous spatial pattern), its occupancy will still increase overall.

When climate change and habitat loss had a negative effect on a group of species, the joint effect was worse than either of the individual effects. However, in contrast with the theoretical findings of Travis (2003), the combined effect was semiredundant (or subadditive, i.e. slightly smaller than the addition of the two). Likewise,



Cabral *et al.* (2013) found no additive or multiplicative effects of these two factors on the distribution of woody plants (Proteaceae) in South Africa (see also Hof *et al.* 2011a). In the study by Travis (2003), habitat loss removed habitat patches and prevented migration of species from areas that had become unsuitable into regions that had become suitable due to climate change. Although our SPOM simulates a process similar to the one used by Travis (2003), the extinction and colonization dynamics followed by our targeted species were very slow, and our model captures these processes realistically. Thus, distributional shifts in response to climate change will occur over several centuries or more (see also Vanderwel & Purves 2014). Nonetheless, we had anticipated manifestation of this negative synergy by the year 2100 (Fig. 2), but found that a 'deadly anthropogenic cocktail' of climate change and habitat loss (Travis 2003) was not noticeable at this geographical and temporal scale.

#### HABITAT CREATION

The SPOM simulations indicate that the negative effects of a given amount of habitat loss would be greater than the positive effects of a similar amount of habitat creation. Our results show time-lagged responses to both, climate change and change in habitat cover. Hence, there seems to be a qualitative asymmetry of the consequences of habitat loss and creation that might not come as a surprise, because the positive effects of reforestation require time for establishment and growth, whereas the negative effects of habitat loss take place instantly in most cases. Our model also provides quantitative estimates of this asymmetry of habitat changes. In particular, a 20% increase in habitat only resulted in a 4–5% averaged gain in occupancy after 100 years in comparison with the baseline (Fig. 2), while a loss of 20% of the habitat would decrease occupancies by 16–25%. Moreover, complete mitigation of climate change effects by 2100 would require reforestation on scale of 80% of the current habitat (Fig. S6). Such habitat creation would have a greater positive impact on species threatened by climate change if territories that are less influenced by human activities (more pristine) are prioritized.

#### CONCLUSIONS

Climate change and habitat loss, acting together or alone, are going to limit the expansion of tree species in mainland Spain, with likely deleterious impacts for forest biodiversity. In general, climate change and habitat loss may have complex, synergistic effects depending on the species and communities. However, over the time-scale of one century, geographical distributions of long-lived species, such as the trees studied here, may respond to these two factors in a relatively simple manner, producing a subadditive effect that depends on the spatial pattern and amount of lost habitat. Finally, illustrating an important

time-lag between habitat creation and environmental benefits, the effects of reforestation will generally compensate for the negative effects of climate change only to a minor extent.

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#### Data accessibility

Inventory data: (Villaescusa & Diaz (1998); Villanueva (2004)). [http://www.magrama.gob.es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2\\_descargas.aspx](http://www.magrama.gob.es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2_descargas.aspx), and [http://www.magrama.gob.es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3\\_bbdd\\_descargas.htm.aspx](http://www.magrama.gob.es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx). Climate data: Fordham *et al.* (2012).

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## Supporting Information

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

**Appendix S1.** Model description and parameterization.

**Appendix S2.** Parameter posterior distributions.

**Appendix S3.** Model limitations and future improvements

**Table S1** Species list and their principal dispersal vector.

**Fig. S1.** Comparison against current occupancies.

**Fig. S2.** Colonizations and extinctions with stable and changing climate and with stable and 20% of change in habitat.

**Fig. S3.** Percentage of indirect/direct extinctions, and of colonizations of old/new patches.

**Fig. S4.** Histograms of the relative difference in species occupancies between the joint impact of climate change and habitat loss and the addition of the two separated threats.

**Fig. S5.** Change in 40% of the habitat.

**Fig. S6.** Change in 80% of the habitat.

**Fig. S7.** Relative differences in mean human influence index in each species occupied plots in relation to the mean human influence index in the unoccupied plots.