TITLE: Forecasting plant range collapse in a Mediterranean hotspot: when dispersal uncertainties matter

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ABSTRACT

Aim: The Mediterranean basin is threatened by climate change, and there is an urgent need for studies to determine the risk of plant-range shift and potential extinction. In this paper, we simulate potential range shifts of 176 plant species to perform a detailed prognosis of critical range decline and extinction in a transformed Mediterranean landscape. Particularly, we seek to answer two pivotal questions: 1) What are the general plant-extinction patterns we should expect in Mediterranean landscapes during the 21th century? 2) Does dispersal ability prevent extinction under climate change?

Location: Andalusia: southern Iberian Peninsula; 87,597 km^2; 300 by 520 km.

Methods: We gathered information on the dispersal traits of 176 plant species (dispersal vector, average and maximum dispersal distances, shape of the dispersal kernel). We used these data to feed a stochastic dynamic species distribution model (a combination of a cellular automaton with a ensemble of species distribution models) to simulate plant range-shift under climate change with realistic dispersal under two different warming scenarios. We compared dispersal and no-dispersal simulations to assess the influence that climate change and species-distribution characteristics exert on plant-extinction patterns.

Results: The dispersal simulation showed a lower percentage of extinct (-1%) and quasi-extinct species (-19%) than did the non-dispersal simulation. Summer temperatures of 37 and 33ºC, respectively, accelerated the critical range decline and extinction rates. The average elevation of the plant populations was the variable with the highest influence on extinction probability.

Main conclusions: stochastic dynamic species distribution models proved to be useful when there was lack of data on dispersal distances and population dynamics. Dispersal ability showed minor effectiveness in preventing extinction, but greatly reduced the likelihood of critical range decline for a significant percentage of species.

KEYWORDS: cellular automaton, dispersal kernel, dynamic species distribution models, global warming, range shift

INTRODUCTION

The predicted global warming will probably exceed the migration rate of a great number of plant species (Parmesan 2006), becoming an important driver of species range shift, habitat contraction, and potential extinction. Climate change effects have already been detected in plants inhabiting Mediterranean habitats. For example, Pauli et al. (2012) detected changes in community composition of high mountains during a large-scale monitoring program in Europe, with the Mediterranean mountain ranges being among the most affected habitats. Upward treeline shift and species replacement in mid-mountain ranges have also been reported by Peñuelas and Boada (2003). Such effects are expected to intensify in a future warmer climate, as predicted for the Mediterranean basin in the 21st century (Giorgi and Lionello 2008), and therefore Mediterranean habitats are considered to be among the most threatened by climate change (Giorgi 2006).

In the context of rapid climate change, research to improve species range-shift forecasts and thereby assist decision making is crucial in biodiversity conservation worldwide (Engler et al. 2009, Franklin 2010). Species Distribution Models (SDMs hereafter; Guisan & Zimmermann 2000; Guisan & Thuiller 2005) have been the tool of choice for range-shift modelling, but their limitations (see Pearson & Dawson 2003) have led to the development of dynamic species distribution models (DSDM hereafter; Franklin 2010; Thuiller et al. 2008; Morin & Lechowicz 2008), which are a mixture of SDMs with other spatially explicit simulation methods such as cellular automaton (e.g. Iverson et al. 2004; Smolik et al. 2010). To simulate range shifts with DSDMs requires an empirical or theoretical description on how species disperse across the landscape. It is relatively common to assume fixed dispersal distances for each modelled species (as in Fitzpatrick et al., 2008, or Engler et al. 2009), despite that the uncertainty about dispersal distances for any plant species is often very high (Higgins et al. 2003; Clark et al. 2003). The most straightforward solution is the use of dispersal kernels, as suggested by Franklin (2010) and applied in Dullinger et al. (2012), but this approach is rarely used in range-shift simulation because it is time consuming, and there is a lack of empirical data for the majority of plant species.

The objective of this paper is to design, develop, and analyse the results of an stochastic DSDM used to simulate range shift under climate change of 176 plant species in a Mediterranean hotspot. To do so, we have gathered presence data and information on the dispersal traits of the target species. Our DSDM combines species-distribution models projected over future climatic scenarios and a cellular automaton to simulate the dispersal process. Our model relies on two stochastic components: 1) a pseudo-random generator of dispersal distances based on plant-specific dispersal syndromes and realistic dispersal kernels taken from the literature; 2) binomial trials, used to decide the success or failure of dispersal events. We used this approach in order to answer two questions: 1) What are the general plant-extinction patterns we should expect in Mediterranean landscapes? 2) Does dispersal ability prevent extinction under climate change?

METHODS

Study area

The study area is Andalusia, located in the southern Iberian Peninsula between 36º 00’ N and 38º 35’ N and 1º 35’ W and 7º 35’ W, comprising 87,597 km^2 (300 x 520 km; see Fig. 1). The area harbours about 4000 species of vascular plants and thus being a hotspot within the Mediterranean hotspot (Médail and Diadema 2009). We selected this study area because in the Mediterranean basin, climate warming is expected to be more severe than the global average (Giorgi 2006). Consequently, there is a need for a prognosis concerning the potential effects of climate warming over the Mediterranean flora. Andalusia, being the southernmost position in Europe and having a complete set of high-resolution data available for many plant species makes it a valuable case study.

Presence data, dispersal kernels, and environmental variables

To establish a presence dataset representative of Andalusian flora (see Fig. 1), we combined data from-different sources provided by the environmental administration of Andalusian Regional Government. Forest-species data were compiled from a land-cover map (scale 1:25000, year 2003) and vegetation maps from protected natural areas (scale 1:10,000) whereas threatened-species data were gathered from the Andalusian Programme for Endangered Flora (data taken with GPS precision). The dataset was organized as GIS polygons delimiting the occupancy area of plant populations, and contained presence-only data for 554 species. The presence polygons were converted into 50x50 m raster cells using the v.to.rast module of the GRASS GIS software (GRASS Development Team, 2008). Species with fewer than 100 presence cells were excluded, leaving a total of 176 species. The final dataset consisted of 48 endemic species in Andalusia, 20 in the Iberian Peninsula, 31 in Ibero-Africa, 18 in the western Mediterranean, and 59 in the Mediterranean (see Appendix).

For each species, we searched the literature for the dispersal kernel that best matched its dispersal syndrome (see Table 1), and assigned a mean and a maximum dispersal distance according to the review of Vittoz and Engler (2007), specific papers on the biology of each species (see Appendix), and expert knowledge when we could not find reliable data. We were unable to gather long-distance dispersal (LDD) data for our target species, and therefore our simulation considers only short-distance dispersal (SDD) events.

To compile a set of topographic variables relevant to plant distribution (Williams et al. 2012), we resampled the ASTER GDEM (http://asterweb.jpl.nasa.gov) to a 50-m resolution in order to match the spatial scale of the species-presence polygons. Observed climatic records (1971-2001) and downscaled future climate-change simulations —warming scenarios A2 and B2 generated with the model CGCM2 for the period 2010-2100 (IPCC 2007; Flato & Boer 2001; Brunet et al. 2007)— were drawn from the National Meteorology Agency database (AEMET; URL: http://escenarios.inm.es). We selected these scenarios for comparison with other studies on Mediterranean plant extinction under climate change (Benito et al. 2011; Benito-Garzón et al. 2011; de Dios et al. 2009; Benito-Garzón et al. 2008).

The climate data were aggregated yearly and seasonally by arithmetic average in 10-year time slices, and we applied the climatic-mapping method proposed by Ninyerola *et al*. (2000) to interpolate the future climatic maps. Finally, we used climatic (annual and summer rainfall, minimum and maximum winter temperatures, and maximum summer temperature) and topographic variables (terrain curvature, topographic wetness index, topographic position, slope, and mean winter solar radiation) to calibrate the models. The average correlation among the variables was 0.22 (Pearson's correlation index), with a maximum of 0.86 between the minimum and maximum winter temperatures. We also represented land uses unsuitable for natural plant populations from a land-use map, which was applied as a mask to avoid migration over unsuitable land uses.

Stochastic Dynamic Species Distribution Model

Ensemble model forecasting

The choice of a specific SDM method constitutes the main source of uncertainty in range-shift simulations (Nenzén and Araújo 2011), but ensemble modelling approaches have been proposed as a robust solution to minimize this problem (Araújo and New 2007). Thus, considering that we had no true absences to calibrate our models, we selected five presence-only-based modelling algorithms (MaxEnt, GARP, Artificial Neural Networks, Support Vector Machines, and four implementations of ecological distances [similarity/dissimilarity metrics]: Euclidean, Mahalanobis, Manhattan, and Chebyshev) to be ensembled by arithmetic average (Marmion et al. 2009). We assessed the ability of each ensemble to discriminate between presences and absences via AUC (Fielding and Bell 1997, but see Lobo et al. 2008) using k-fold cross-validation (5 groups). The SDMs were projected over the future climatic variables for both climate-change scenarios to represent future habitat-suitability change.

Simulating dispersal, colonization, and local extinction

We designed a generator of dispersal distances that, for each target species, produced 10,000 dispersal values (in multiples of 50, the spatial resolution of the simulation) following a pseudo-random distribution based on the statistical distribution of the species' dispersal kernel (see Table 1). To simulate colonization and local extinction, we applied the following rationale. Considering a given species, its presence cells, and the habitat-suitability values (scaled to [0, 1]) of its current SDM, we computed the cumulative density function which returns the probability of finding a presence record in a cell with a given habitat-suitability value. Such probability values were used as inputs in binomial trials to decide whether a target cell within the dispersal distance was colonized or not, and whether a present cell became locally extinct or not when the habitat suitability changed. In a binomial trial, the probability value of a given cell was compared with a random number, taken from a random map following a uniform distribution in the range [0, 1], which was held constant on each run of the simulation (see the next section for further details). If the probability value given by the density function is lower than the random number, the state of the target cell changes to "absent". This "absent" state has two different meanings depending on the context. In a cell within the dispersal range, it means "no migration" while, in a cell with a "present" state before the dispersal event, it means "locally extinct". This approach follows the hypothesis of species in equilibrium with climate (Araújo and

Pearson 2005), and allowed us to represent the persistence of the species in cells with low probability values but a lower random number (Hampe and Petit 2005).

The 10-year time step or our simulation implies a generation time of 10 years for each plant species in our dataset. We selected this interval length because we needed to maintain the computing requirements within affordable limits, and because we lacked data on generation times for most species in our dataset. Ten years seems to be a reasonable average generation time, considering that annual or biannual species are rare in our dataset (see Appendix).

Cellular automaton and simulation steps

We implemented the rationale explained above in a cellular automaton (Sarkar 2000). To explore different dispersal scenarios, for each species, we performed up to 900 realizations, being each realization one simulation run for a given species over the whole time series of SDMs and both climatic-change scenarios. Each realization was characterized by a dispersal distance given by the generator of dispersal distances and a map of random values to perform the binomial trials to decide whether a cell within the dispersal range was colonized or not. Each realization required the following set of steps, being the steps 2 and 3 repeated once for each time-slice until the year 2100:

1. A dispersal distance is selected and a random map is created to be used throughout the realization.
2. A buffer with a radius equal to the given dispersal distance is drawn around the cells stated as "present", and the state of all cells inside the buffer is immediately set to "present". At this step, we assumed that each species produced enough propagules to reach all the cells within the dispersal range.
3. A binomial trial is applied to all the "present" cells: if the value of the cell given by the density

function is lower than the random number given by the random map in that cell; otherwise the state of the cell is changed to “absent” (which will mean “locally extinct” or “not colonized” depending on the context).

The workflow to execute the simulation (see Fig. 2) was designed and executed in Kepler (Ludäscher et al. 2006; URL https://kepler-project.org/), integrating the software packages MaxEnt (Phillips et al. 2006), OpenModeller (Muñoz et al. 2009), R (R Development Core Team 2009) and GRASS GIS (GRASS Development Team 2010).

Simulation results

The simulation results were organized following two approaches at the same time: 1) The “species-by-species” approach, which considered the whole set of realizations for each species at once. For each realization, we considered the species to be “extinct” when it reached a 0% of its initial presence, and to undergo a “critical range decline” when it reached the 10% of its initial presence area (Engler et al. 2009). We also computed the probability of critical range decline and extinction for each species by dividing the number of extinction or critical range decline by the total number of realizations. 2) The “trajectories approach”, which considered different “trajectories” of the system. A trajectory is a random combination of 176 realizations, one per species. Every trajectory is an alternative scenario in which the migration of each species has been simulated with a single dispersal distance and a unique random map. We shuffled the realizations to create 10,000 different potential trajectories, which allowed us to explore the uncertainties emerging from the combination of different parameters for each species.

Sensitivity Analysis

We assessed the different sources of uncertainty by performing a sensitivity analysis. To evaluate the spread induced by the binomial trials in the simulation results, we performed a control simulation without dispersal, and running 30 realizations for every species. As a measure of sensitivity to the binomial trials, we computed the arithmetic mean of the standard deviation of the percentage of initial present cells occupied at 2100 across all species. We used the same measure of sensitivity to evaluate how much spread induced variations in dispersal distances. Finally, to assess the influence of the dispersal algorithm in the simulation results, we evaluated the overall differences in percentage of extinct and quasi-extinct species between the results of the 10,000 different potential trajectories produced by the dispersal and the no-dispersal simulations.

Potential extinction patterns

Firstly, we analysed the 10,000 trajectories of the dispersal simulation, to evaluate the percentage of species facing critical range decline and extinction in each scenario. Secondly, we applied beta-regression (R library "betareg"; Cribari-Neto and Zeileis 2010) to assess the influence of the climatic variables in the proportion of species facing critical range decline and extinction. To do so, we used the regional climatic averages for each time slice as independent variables, while the proportion of species facing critical range decline and extinction were taken as dependent variables. Thirdly, we applied conditional inference trees (R library "party"; Hothorn et al. 2006) to evaluate the influence of different species-distribution characteristics and the mode of the dispersal distances applied across the simulation over the species' probabilities of critical range decline and extinction. The selected species-distribution characteristics were: number of starting presence cells, number of presence patches (the actual number of polygons available in the presence dataset), mean patch size, mean and range of elevation of the presence patches. To simplify the analysis we converted the probabilities of critical range decline and extinction into two categories: probabilities lower and higher than 0.5. We also tried to group the data by dispersal syndromes, but the number of cases was not high enough to build reliable conditional inference trees.

RESULTS

SDM evaluation and DSDM sensitivity analysis

The SDMs showed a moderate to high discrimination ability according to the AUC analysis (see Appendix), with an average AUC of 0.849, a minimum of 0.655 (*Ulex eriocladus*) and a maximum of 0.973 (*Festuca clementei*). The binomial trials induced a mean standard deviation of 1.01% of the initial presence cells across all species, time slices, and scenarios. As a consequence of the reduction of suitable habitat through time, the standard deviation declined from 1.38% to 0.38% in the scenario B2, and from 1.48% to 0.75% in the scenario A2. The mean standard deviation induced by the dispersal algorithm was 205.53% of the initial presence cells across all species, time slices, and scenarios. The temporal variation of the mean standard deviation ranged from 203.61% to 197.65% for the B2 scenario (with a peak reaching 231.20 in the year 2060) and from 136.23 to 49.96 for the A2 scenario (with a peak reaching 373.19 in the year 2040).

The comparison between the 10,000 trajectories of the system for the dispersal and no-dispersal simulations showed minimal differences (1,01%) in the percentage of extinct species. The percentages of species facing a critical range decline differed noticeably between the dispersal and no-dispersal simulation: +19.31% for the A2 scenario and +11.93% for the B2 scenario (see Fig. 3 and Table 2).

Critical range decline and extinction

The 10,000 potential trajectories of the system generated, expressed as percentages of extinct and quasi-extinct species, are summarized in the Fig. 3 and the Table 2. The beta regression analysis showed that the better predictor or critical range decline and extinction was the mean summer temperature. All models showed a good fit (see Fig. 4 and Table 3), except the one for extinction in scenario B2. The critical range decline percentages showed a threshold at 33ºC of mean summer temperature, after which the slope of the extinction curve rose appreciably. The threshold in the extinction percentage was at 37ºC, but the extinction rate increased more slowly than in the critical range decline models.

The influence of the species-distribution characteristics on the probability of critical range decline and extinction performed with conditional inference trees showed that the mean elevation of the populations was directly related to higher extinction probabilities. In the A2 scenario, the group of species most prone to extinction occupied an elevation mean above 1866 m and elevation range of less than 1307 m (Fig. 5, Extinction A2, node 6). Another group with high extinction probabilities was that below 1866 m of mean elevation and with an elevation range less than 829 m (Fig. 5, Extinction A2, node 3). Considering the B2 scenario, the mean elevation of the populations was also the most important variable to predict extinction, with a critical value at 2785 m (Fig. 5, Extinction B2, node 3). In both scenarios, dispersal distances were not important for predicting the extinction probability.

The analysis of critical range decline shows that dispersal distance was the most important variable in both scenarios. In the scenario A2, only some 20% of species with dispersal distances higher than 50 m presented critical range decline probabilities higher than 0.5, with that percentage diminishing to 8% in scenario B2 (Fig. 6, critical range decline A2, node 7 and B2, node 3). In the B2 scenario, the 50% of the species without dispersal had a critical range decline probability higher than 0.5.

DISCUSSION

In this paper, we describe an approach that combines an ensemble of SDMs to describe changes in habitat suitability, with a cellular automaton to simulate realistic dispersal and local extinction due to climate change. We used this approach to perform the first assessment of critical range decline and extinction for 176 Mediterranean plant species. Although the results of our simulation have some limitations, they may be a good starting point to select key species with higher extinction and critical range decline risk to be the focus of intensified research that would protect them from the risks associated with climate change.

Sensitivity Analysis

The variability in dispersal distances induced the highest amount of variability in the simulation outcomes, being around 200 times higher than that produced by the binomial trials, especially for species with larger dispersal distances and restricted known distributions but extensive suitable habitats. Such species showed the greatest spread potential during the simulation, being therefore extremely sensitive to variations in dispersal distances. However, the high sensitivity of such species to changes in dispersal distances was not enough to significantly change the percentage of extinct species between the dispersal and no-dispersal simulations.

When comparing the dispersal and no-dispersal simulations, we found that both diverged by 1% extinct species in the year 2100. This similarity between patterns appeared presumably because of the high proportion of species with short dispersal distances, which were not able to track their suitable habitat in the dispersal simulation. These species are expected to be the first to go extinct in the real world, because they are usually isolated in island-like habitats, lacking the potential to pursue their suitable habitat during a rapid climate change (Skov and Svenning 2004; Meier et al. 2012).

Potential extinction patterns

The percentages of locally extinct species that we found in both warming scenarios (see Table 2) according to the dispersal simulation lie within the ranges reported by other authors for European species, although there are some differences due to spatial and temporal resolution, study area, target species, and the approaches to account for dispersal. For example, Thuiller *et al*. (2005) working with 1350 species of plants in Europe at a resolution of 50x50 km up to the year 2080 found lower extinction values (2% in the worst scenarios), while assuming no migration and total migration. Alkemade et al. (2011), simulating potential plant-diversity changes in Europe until 2100, found that 25% of the species in Southern Europe will disappear by 2100. In the work of Engler *et al*. (2009) the extinction percentages when considering realistic dispersion (SDD) ranged between 4.52% in scenario B2 and 13% in scenario A2. These authors also analysed the critical range decline process, finding values of between 60% in A2 and 40% in B2. This inter-comparison is intended to point out that, despite differences in study areas, target species, climatic data or spatial resolutions, several studies are converging to similar results that are in line with observed range shifts of plant populations and community change, especially in mountain habitats (Peñuelas and Boada 2003; Pauli et al. 2012).

The comparison of the dispersal and no-dispersal simulation did not show remarkable differences in the percentage of extinct species, but when considering the critical range decline process (species occupancy shrinking to 10% of its initial area), an important difference emerged. This result suggests that the study area contains a pool of species which will go extinct, irrespective of the dispersal assumptions made during the simulation. Such species have either poor dispersal ability or inhabit isolated spots without suitable habitats within the species' dispersal range. On the other hand, another pool of species escaped critical range decline due to their good dispersal abilities, added to the availability of suitable habitats within their dispersal distances.

The beta-regression analysis shows that the mean of the percentages for extinction and critical range decline are strongly correlated with the maximum summer temperature. We hypothesise that this robust fit resulted from the inability of the migration process to compensate for the strong effect of the suitability loss caused by the rise in summer temperature beyond a specific threshold. The secondary drivers were probably the patchy distribution of the landscape, the presence of species with distributions restricted to island-like habitats in the species dataset, and the scarcity of species able to disperse over long distances. In these circumstances, and without consideration of other processes in the simulation, such as adaptation or persistence in micro-refuges, the changes in critical climatic drivers will be the most important variables controlling range decline and extinction rate.

Conditional inference trees offered an intuitive way of summarizing the simulation results, pointing out the most important species-distribution characteristics and their relevant values to predict extinction and critical range decline risk. Using this analysis, we found some species-distribution characteristics that are plausible as indicators of critical range decline and potential extinction. The species-distribution characteristic most important in our study area was the mean elevation of the target species' populations. The importance of this indicator in our simulation is consistent with the recent findings of Pauli et al. (2012), who reported that 31% of endemic mountain plant species in Southern Europe were not redetected from 2001 to 2008 during the GLORIA-Europe monitoring program.

Ecological interpretation

Under the scenario B2, 12 plant species (ten of these being endemic to Andalusia) showed an extinction probability higher than 0.5. Of these species, three showed an extinction probability equal to 1: *Boreava aptera* (continental semi-arid habitats), *Anthyllis plumosa* (calcareous mountain habitats), and *Viola crassiuscula* (high-mountain habitats of Sierra Nevada). The majority of species with extinction probabilities between 1 and 0.5 were endemic of the high-mountain habitats of Sierra Nevada (*Trisetum glaciale, Festuca pseudoeskia, Cytisus galianoi,* and *Thymus serpylloides*), but there were also representatives of temperate semi-arid annual grasslands (*Astragalus edulis*) and species inhabiting dolomitic outcrops within calcareous mountains (*Arenaria racemosa* and *Rothmaleria granatensis*). These species were characterized by having a small number of habitat patches within a restricted area (30 by 30 km maximum), and a limited area of suitable habitat around their current populations. Under the A2 scenario, 27 species showed an extinction probability higher than 0.5. Four of these species were endemic to Sierra Nevada (*Arenaria pungens, Draba hispanica laderoi, Moehringia fontqueri,* and *Holcus caespitosus*), and three inhabit calcareous mountain habitats (*Halimium atriplicifolium, Helictotrichon filifolium cazorlense*, and *Juniperus sabina*). Considering these data, and the results of the conditional inference trees, it is clear that the endemic species of the high-mountain habitats of Sierra Nevada are among the most threatened taxa of the Andalusian flora, because such species cannot migrate, due to the lack of suitable habitat in the vicinity of their current distribution (Benito et al. 2011).

In our simulation, there were species representing the semi-arid habitats of eastern Andalusia. In this group the probabilities of extinction were low, except for *Astragalus edulis* (0.90 and 0.93 extinction probability in A2 and B2 scenarios, respectively) and *Boreava aptera* (extinction probability equal to 1.0 in both scenarios). Regarding the probabilities of critical range decline, ten species showed high probabilities of critical range decline, especially for the A2 scenario (*Anthyllis cytisoides, Artemisia barrelieri, Lygeum spartum, Stipa tenacissima, Salsola genistoides, Teucrium charidemi, Thymus hyemalis, Vella pseudocytisus pseudocytisus, and Linaria nigricans*). The results for species of semi-arid habitats are far more conservative than those for the species of high-mountain habitats, and this is a result of the spatial configuration of the semi-arid habitats (i.e. ample sedimentary plains without major dispersal barriers) combined with wind-dispersal modes (trichometeorochory and pterometeorochory for the majority of such species), that allows such species to avoid extinction, but not critical range decline.

Finally, considering *Quercus* and *Pinus* species, the tree taxa most representative of the Andalusian Mediterranean ecosystems, our simulation did not predict extinctions or critical range decline, except for the endemic *Pinus sylvestris nevadensis* (A2 probability of extinction = 1.0; B2 = 0.6). Matias et al. (2012) evaluated the specific drought resistance under different habitats for several species from different successional strategies and found that the seedlings *of P. sylvestris nevadensis* were extremely sensitive to drought, an ecological process that is expected to increase under climate warming (Houghton et al. 2001). In the same experiment the authors found that *Quercus ilex* (zero probability of extinction or critical range decline), the most important tree species in Andalusia in terms of its ecological role, abundance and area occupied, was the species least sensitive to drought, together with *Cytisus scoparius*, which, according our simulation, faces a risk of a critical range decline under the A2 scenario (probability = 0.83).

The lack of ecological data for range-shift simulation

Certain progress has been made in the research on range-shift simulations, but there is still a long way to go in order to apply simulation results to decision making in the real world. We are far from predicting the actual responses of plant distributions to climate change, especially in fragmented, heterogeneous, and diverse landscapes. With the aim of contributing to the required improvements in range-shift simulation, in this study we propose a stochastic DSDM approach that is useful for range-shift simulation in situations where dispersal data are lacking. Nevertheless, our approach is only a small step in the refinement of range-shift simulations, and further research is needed on the simulation of ecological processes occurring in the leading and receding edges of the populations.

Migration is methodologically easy to simulate, but extensive gaps persist on how the process occurs, its drivers, and relevant thresholds for each species. The receding edge deserves the same attention as, does the leading edge or even more, (Hampe and Petit 2005) because if current climate change continues as expected, extensive recession will result along the edges of our forested landscapes (Jump et al. 2009). Fortunately, there is an increasing body of work on ecological mechanisms and the climatic drivers acting there. For example, del Cacho et al. (2012) recently found a reduced seed-bank density and a decreased germination potential under drought and warming treatments for short-lived plant species in a Mediterranean shrubland, which could eventually lead to local extinctions. Jump et al. (2009) pointed out that the massive forest dieback observed around the world is related to climate change, and might lead to a regional collapse of tree populations along the receding edges, and Jump et al. (2006) found that population declines on the receding edge of *Fagus sylvatica* populations in Catalonia (north-eastern Spain) strongly correlated with climate warming. Unfortunately, such processes are not explicitly considered in the majority of the current range-shift simulations (including ours, but see Meier et al. 2012). To perform better simulations the research community needs more data on the tolerance of species to changing climatic conditions, on the temperature thresholds that limit seed production and germination, and on the competition dynamics that emerge in the areas where receding and trailing edges of different species overlap. The progressive improvement of methods to simulate range shift under climate change must rely on this biological and ecological knowledge. In this context, stochastig DSDMs constitute a valid choice, but there is an urgent need for ecological data to improve simulation reliability.

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Appendix

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

Appendix: It contains a table with each species' name, life form, dispersal syndrome, species-distribution characteristics, and probability of extinction in each simulation.

BIOSKETCH

Blas M. Benito is a PhD in biology and MD in GIS, highly interested in macroecology, biogeography, and the modelling of past, present and future ecological dynamics. Currently he is focused on the development of Dynamic Species Distribution Models to simulate range shift under environmental change considering realistic dispersal and species interactions.

Author contributions: BMB, JL, JP and LGA conceived the ideas and collected the data; BMB and RPP coded the software to run the simulation; BMB analysed the data; BMB, JL and LGA led the writing.

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TABLES

Table 1: Dispersal syndromes, distances, and dispersal kernels. In the first column the dispersal types according Vittoz and Engler (2007) as reference. References for dispersal kernels: [1] Higgins and Richardson (1999); [2] Clark et al. (2005); [3] Spiegel and Nathan (2007); [4] Vellend et al. (2003); [5] Bullock et al. (2011).

Vittoz 2007	**Group**	**Dispersal syndrome**	**D. average (m.)**	**D. maximum (m.)**	**Distribution of the dispersal kernel**	**Number of species**
1,2,3	a	barochory myrmecochory pterometeorochory-herbs	1	5	not applicable	101
4	b	pterometeorochory-trees	50	150	weibull [1]	11
5	c	trichometeorochory	100	500	Gaussian [2]	19
6	d	ornithochory	400	1500	inverse power [2] weibull [3]	37
6	e	endozoochory-mammals	400	1500	log-normal [4]	3
6	f	epizoochory-mammals	400	1500	power exponential [5]	5

Table 2: Simulated percentages of extinct and quasi-extinct species for the year 2100 for each climate change scenario and simulation. Abbreviations: ext. - extinction; crd. - critical range decline; disp. - dispersal simulation; no-disp. - no dispersal simulation (control).

	A2 ext. disp.	B2 ext. disp.	A2 ext. no-disp.	B2 ext. no-disp.	A2 crd. disp.	B2 crd. disp.	A2 crd. no-disp.	B2 crd. no-disp.
max	19.32	9.66	20.45	10.23	58.52	39.77	75	50
3rd quart	15.91	7.39	17.05	7.52	52.27	34.66	71.59	46.59
median	15.34	6.82	16.48	7.39	51.14	33.52	70.45	45.45
1st quart	14.77	6.25	15.91	6.82	50	32.95	69.89	44.89
min	11.93	3.41	13.64	4.55	44.89	28.41	65.34	40.91

Table 3: Beta-regression model parameters. The parameters correspond to the beta-regression equations formulated on fitting the percentage of extinct and quasi-extinct species against mean summer temperature for two climate-change scenarios (A2 and B2). Abbreviations: ext. - extinction; crd. - critical range decline.

	ext A2	**ext B2**	**crd A2**	**crd B2**
Coefficient	0.22	0.24	0.31	0.48
R2	0.94	0.91	0.88	0.93
AIC	-95.01	-86.57	-46.24	-54.23

FIGURE LEGENDS

Fig. 1: Situation of the study area in Southern Europe and representation of the presence data for 176 species in Andalusia (Spain) aggregated as number of species per cell. The projection employed is UTM with datum ED50.

Fig. 2: Flowchart representing the summary of the steps followed to perform the simulation and analyse its results. The grey boxes represent input data. The rectangular boxes represent methods: modelling, simulation, and analysis.

Fig. 3: Percentages of extinct species and species with critical range decline for the dispersal and no-dispersal simulations on each climate-warming scenario. Each line —there are 10,000 in each scenario— represents a random combination of 176 realizations, one per species. These plots distinguish between trajectories simulated with higher dispersal distances (lines with lower percentages of extinct or quasi-extinct species) with trajectories based on shorter dispersal distances (lines with higher extinction percentages). The density plots represent the distribution of values for each climate-change scenario in the year 2100.

Fig. 4: Fit of the beta regression models applied to predict the proportion of species facing critical range decline and extinction as a function of the mean summer temperature. The dashed line represents a model with a poor fit.

Fig. 5: Conditional inference trees representing the species-distribution characteristics influencing critical range decline and extinction for each climate-change scenario according to the dispersal simulation. Node 6 in the left tree and node 3 in the right tree represent the combination of species-distribution characteristics leading to higher extinction probability. Abbreviations: elev_mean

and elev_range - mean and range of the elevation of the populations; d_mode - statistical model of the dispersal distances applied across the simulation for each species.

Fig. 6: Conditional inference trees representing the species-distribution characteristics influencing critical range decline for each climate-change scenario according to the dispersal simulation. Nodes 4 and 6 in the left tree and node 2 in the right tree represent the combination of species-distribution characteristics with higher quasi-extinction probability. Abbreviations: elev_mean and elev_range - mean and range of the elevation of the populations; d_mode - statistical model of the dispersal distances applied across the simulation for each species.

Figure 1

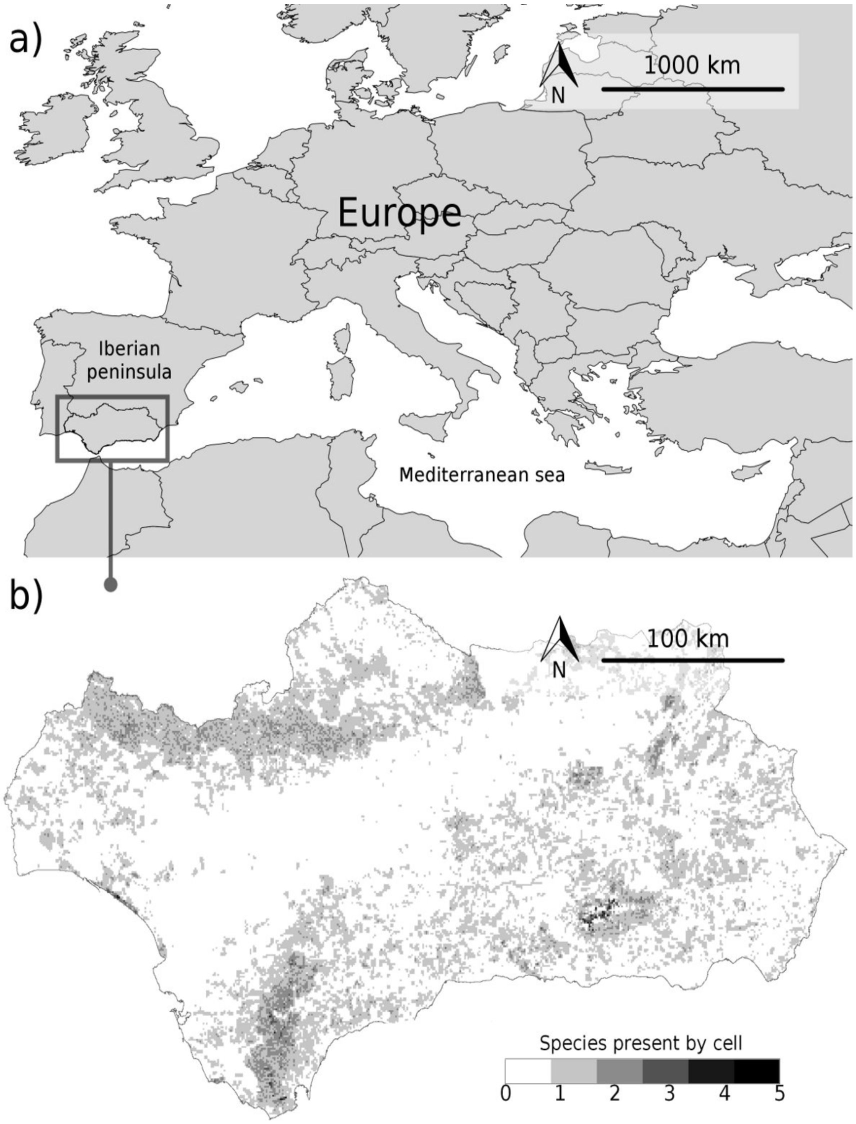

a)
1000 km
N
Europe
Iberian peninsula
Mediterranean sea
b)
100 km
N
Species present by cell
0
1
2
3
4
5

Figure 2

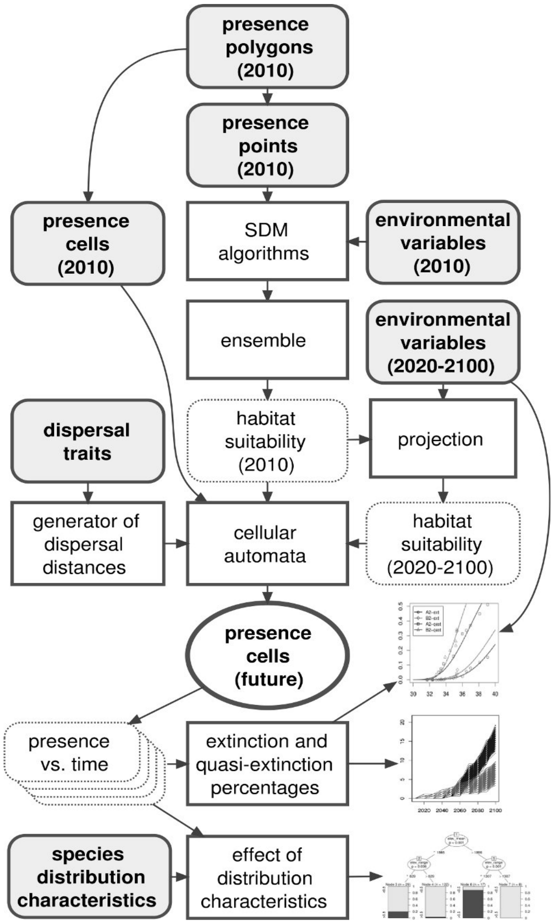

presence polygons (2010)
presence points (2010)
presence cells (2010)
SDM algorithms
environmental variables (2010)
ensemble
environmental variables (2020-2100)
dispersal traits
habitat suitability (2010)
projection
generator of dispersal distances
cellular automata
habitat suitability (2020-2100)
presence cells (future)
presence vs. time
extinction and quasi-extinction percentages
species distribution characteristics
effect of distribution characteristics

Figure 3

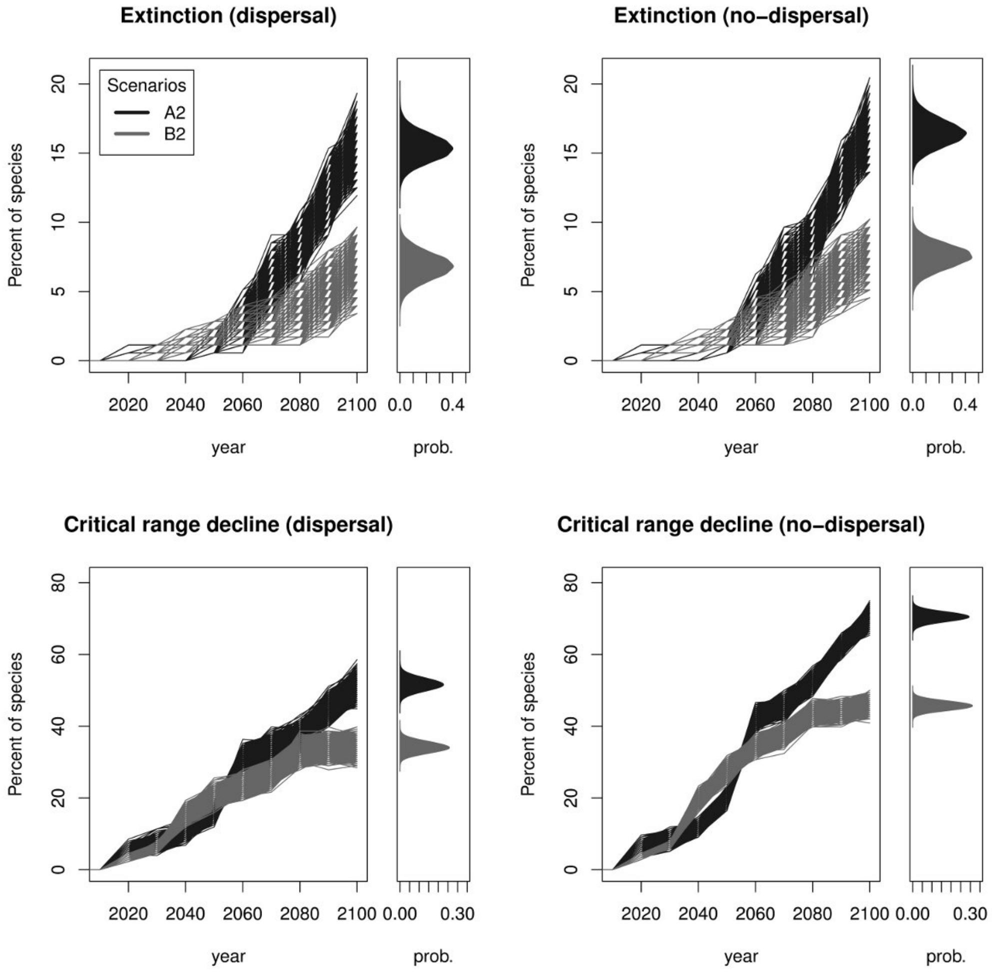
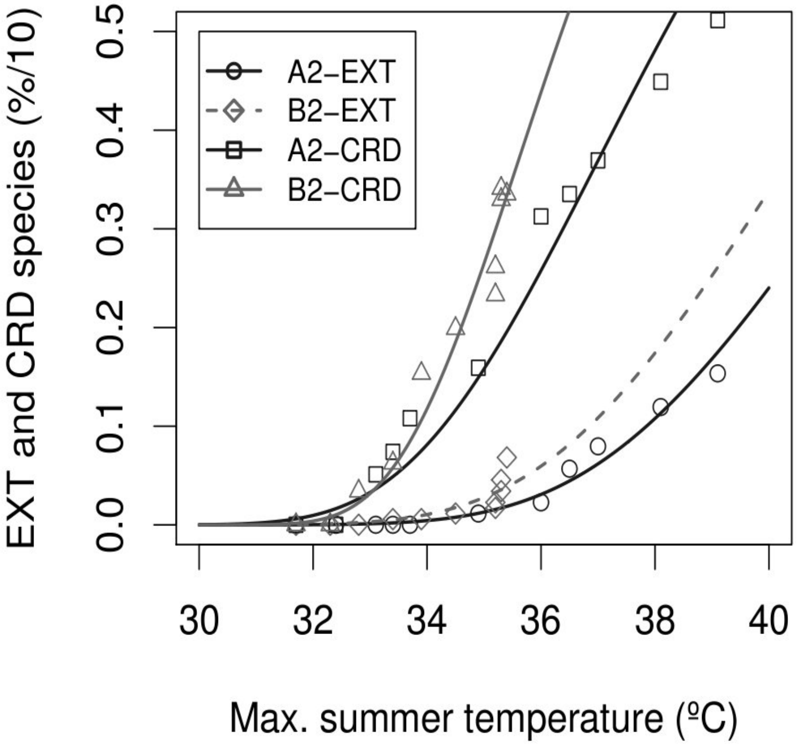

Extinction (dispersal)
Extinction (no−dispersal)
Critical range decline (dispersal)
Critical range decline (no−dispersal)
Scenarios
A2
B2
Percent of species
0
5
10
15
20
0
20
40
60
80
2020
2040
2060
2080
2100
0.0
0.4
0.00
0.30
year
prob.

Figure 4



A2−EXT
B2−EXT
A2−CRD
B2−CRD
EXT and CRD species (%/10)
0.0
0.1
0.2
0.3
0.4
0.5
30
32
34
36
38
40
Max. summer temperature (ºC)

Figure 5

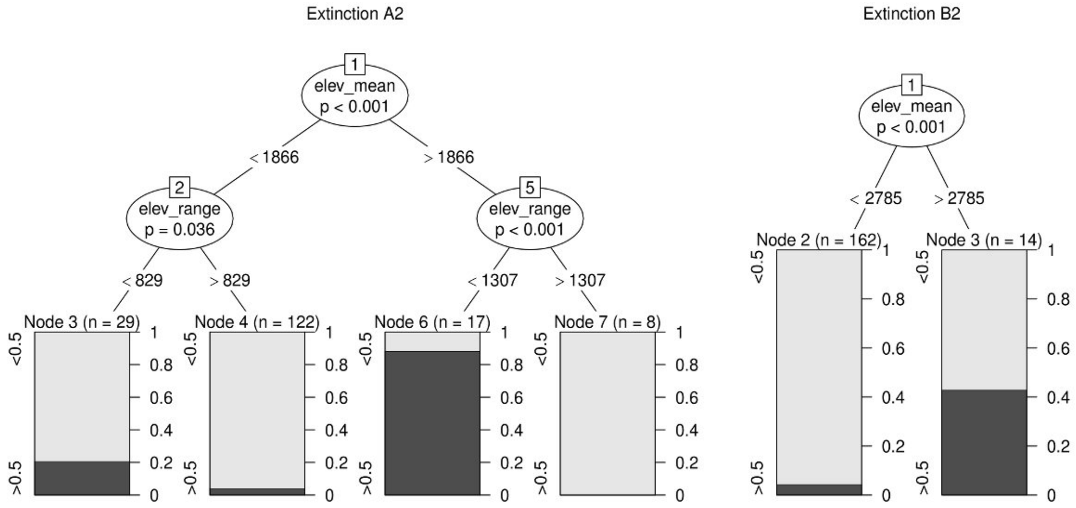
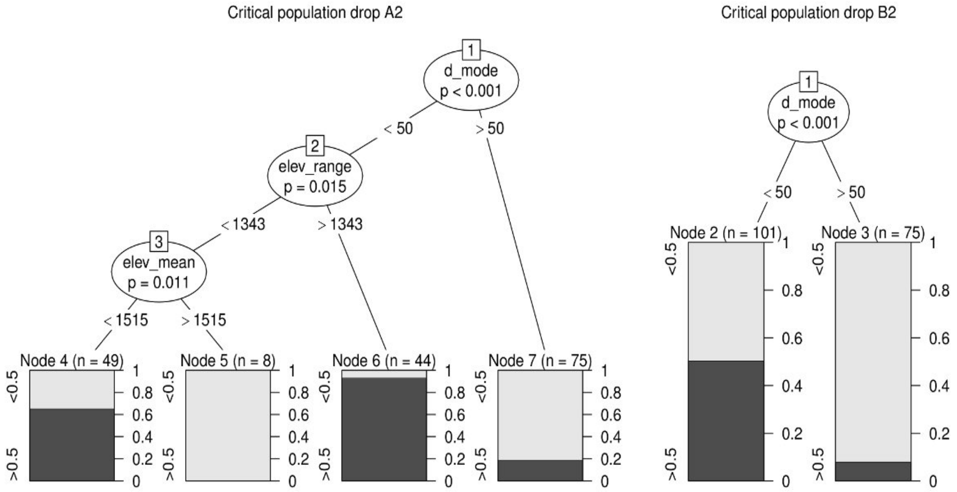

Extinction A2
1
elev_mean
p < 0.001
< 1866
> 1866
2
elev_range
p = 0.036
< 829
> 829
5
elev_range
p < 0.001
< 1307
> 1307
Node 3 (n = 29)
Node 4 (n = 122)
Node 6 (n = 17)
Node 7 (n = 8)
<0.5
>0.5
1
0.8
0.6
0.4
0.2
0
Extinction B2
1
elev_mean
p < 0.001
< 2785
> 2785
Node 2 (n = 162)
Node 3 (n = 14)

Figure 6


Critical population drop A2
1
d_mode
p < 0.001
< 50
> 50
2
elev_range
p = 0.015
< 1343
> 1343
3
elev_mean
p = 0.011
< 1515
> 1515
Node 4 (n = 49)
Node 5 (n = 8)
Node 6 (n = 44)
Node 7 (n = 75)
<0.5
>0.5
1
0.8
0.6
0.4
0.2
0
Critical population drop B2
1
d_mode
p < 0.001
< 50
> 50
Node 2 (n = 101)
Node 3 (n = 75)