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RESEARCH PAPER

Intra-specific variability and plasticity influence potential tree species distributions under climate change

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ABSTRACT

Aim To assess the effect of local adaptation and phenotypic plasticity on the potential distribution of species under future climate changes. Trees may be adapted to specific climatic conditions; however, species range predictions have classically been assessed by species distribution models (SDMs) that do not account for intra-specific genetic variability and phenotypic plasticity, because SDMs rely on the assumption that species respond homogeneously to climate change across their range, i.e. a species is equally adapted throughout its range, and all species are equally plastic. These assumptions could cause SDMs to exaggerate or underestimate species at risk under future climate change.

Location The Iberian Peninsula.

Methods Species distributions are predicted by integrating experimental data and modelling techniques. We incorporate plasticity and local adaptation into a SDM by calibrating models of tree survivorship with adaptive traits in provenance trials. Phenotypic plasticity was incorporated by calibrating our model with a climatic index that provides a measure of the differences between sites and provenances.

Results We present a new modelling approach that is easy to implement and makes use of existing tree provenance trials to predict species distribution models under global warming. Our results indicate that the incorporation of intra-population genetic diversity and phenotypic plasticity in SDMs significantly altered their outcome. In comparing species range predictions, the decrease in area occupancy under global warming conditions is smaller when considering our survival–adaptation model than that predicted by a 'classical SDM' calibrated with presence–absence data. These differences in survivorship are due to both local adaptation and plasticity. Differences due to the use of experimental data in the model calibration are also expressed in our results: we incorporate a null model that uses survival data from all provenances together. This model always predicts less reduction in area occupancy for both species than the SDM calibrated with presence–absence.

Main conclusions We reaffirm the importance of considering adaptive traits when predicting species distributions and avoiding the use of occurrence data as a predictive variable. In light of these recommendations, we advise that existing predictions of future species distributions and their component populations must be reconsidered.

Keywords

Global warming, Iberian Peninsula, local adaptation, phenotypic plasticity, *Pinus pinaster*, *Pinus sylvestris*, species distribution models.

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INTRODUCTION

Species loss as a consequence of recent climate change has been widely documented (Walther *et al*., 2002; Malcom *et al*., 2006; Stork, 2010). Biodiversity patterns and species distributions are expected to change dramatically in response to future rapid climate warming (Araújo & Rahbek, 2006), and generally climate-change modelling predicts that the risks of species loss will increase (Ohlemüller *et al*., 2006). Therefore, improving our understanding of the factors controlling potential species distributions under future global warming scenarios has become a central goal in ecology today.

The contribution of local adaptation and plasticity across populations to the persistence of species under future global warming could be decisive. Local adaptation implies genetic differentiation among populations, as generally occurs in tree species (Rehfeldt *et al*., 2002; Savolainen *et al*., 2007), as a consequence of differential selection pressures and/or population isolation. The response of locally adapted populations to environmental stresses differs from the species' mean response, and this difference may promote or worsen a species' survival under global change. Phenotypic plasticity can be defined as the capacity of a genotype to render different phenotypes under diverse environmental conditions (Garland & Kelly, 2006). Thus, high adaptive phenotypic plasticity would allow species to survive in a broader range of environmental conditions, so decreasing the risk of species loss due to climate change, because the chance of obtaining a phenotype suited to the new environment is improved. Therefore, both local adaptation and phenotypic plasticity would change expectations of species distributions and must be incorporated in estimates of the risk of species loss under climate change scenarios.

Species distribution models (SDMs) are a key tool for predicting species ranges as a function of climate. For example, SDMs suggest that tree species could be strongly affected by global warming at both continental (Thuiller *et al*., 2005) and regional scales (Benito Garzón *et al*., 2008) with severe consequences for habitat preservation and the maintenance of key ecosystem services. However, there is scope for these models to be refined to include a more realistic characterization of the biological processes that govern species responses to climatic changes (e.g. Pearson & Dawson, 2003; Montoya *et al*., 2009). To this end, a number of models have recently been developed that include critical population-level components such as dispersal mode (Purves *et al*., 2007), competition and facilitation (Zavala & Bravo de la Parra, 2008) and species physiological constraints (Kearney & Porter, 2009). Recently some models have incorporated local adaptation and life-history traits (Morin *et al*., 2007, 2008; Bennie *et al*., 2010; Wang *et al*., 2010).

Two of the key assumptions of SDMs are: (1) that there is no intra-specific variability, i.e. all populations of a given species across its distribution range perform similarly; and (2) that species are assumed to produce homogeneous responses to climate variations across their range, i.e. SDMs are usually calibrated with species occurrence or species presence–absence (Hirzel *et al*., 2002; Elith *et al*., 2006) as the only variable factor for a given species over its range.

There is, however, ample evidence against these two underlying assumptions. Firstly, tree species distributions have undergone dynamic reorganization since the Last Glacial Maximum (Hampe & Petit, 2005), which had two main consequences: populations that persisted in different refuges could have evolved independently (Petit *et al*., 2002), leading to locally adapted populations and resulting in current species distributions and diversity patterns that may be correlated with factors beyond current climate (Montoya *et al*., 2007). Secondly, heterogeneous species responses to climate change across their range are directly connected with phenomena such as local adaptation, intra-specific variability and phenotypic plasticity. Local adaptation implies genetic variation between populations, and can be a consequence of species evolution under isolated conditions or differences in selection pressures as suggested by the large variation in functional traits occurring in most natural populations (Savolainen *et al*., 2007). It is likely that predictive models that do not incorporate local adaptation of species would underestimate or overestimate the potential range shift of species due to climate change, since each population has fixed different alleles during evolution and would react differently to changes in environment.

When phenotypic plasticity is not incorporated into a SDM, predictions are likely to underestimate species distributions. This is especially relevant at the margins of species distributions, where classical SDMs assume that those populations are equally adapted as those in other territories, even if that is known to be false (Geber, 2008). Under changing conditions plasticity is likely to increase the fitness of organisms within the population by extending the range of its possible responses to new environmental conditions, outweighing any costs incurred by the sensory and regulatory systems that plasticity requires (Ghalambor *et al*., 2007; van Kleunen & Fischer, 2007). In natural forests, a population's phenotypic plasticity for key functional traits can determine whether it persists (Climent *et al*., 2006). This may be especially relevant when considering the plasticity of traits related to climate change, as exemplified in *Betula pendula* grown under increased CO_2 concentrations over 50 years (Wagner *et al*., 1996).

In spite of the importance of genetic differentiation and phenotypic plasticity, there are no studies that directly include these effects in a SDM to explore their influence on potential tree species distributions under current and future climate change conditions.

Here we investigate the role of local adaptation and phenotypic plasticity in shaping potential tree species distributions under a rapidly changing climate. We focus on Scots pine (*Pinus sylvestris* L.) and maritime pine (*Pinus pinaster* Ait.), two key structural components of cool temperate and mediterranean forests. *Pinus sylvestris* has a broad distribution range reaching its southernmost limit in Spain, where genetically different populations have been described (Alía *et al*., 2001; Pyhäjärvi *et al*., 2007; Soto *et al*., 2010). Genetic differentiation in 11 polymorphic enzymatic loci has been also found within the Spanish populations (Prus-Glowacki *et al.*, 2003). *Pinus pinaster* in contrast has a more restricted and fragmented western Mediterranean distribution range, with a large number of haplotypes for the Iberian Peninsula (Gómez *et al.*, 2005). High levels of genetic differentiation between populations, phenotypic plasticity and local adaptation in adaptive traits, stem form, total height growth and survival, have been detected for this species (Matziris, 1982; Alía *et al.*, 1995, 1997; González-Martínez *et al.*, 2002): the differences between populations were suggested to follow an environmental gradient determined by differential adaptation to precipitation, temperature and soil type. We use population survival as a population fitness indicator directly related to climate; however other factors that would affect species survival such as biotic interactions or fecundity have not been incorporated in the analysis.

The main objective of this paper is to assess the effect of local adaptation and phenotypic plasticity on the potential distribution of these two species under future climate changes predicted by the IPCC (IPCC, 2007). Specifically, we ask whether as a result of local adaptation and plasticity species exhibit adaptive responses that can be facilitated by dispersal or assisted migration. For this purpose we calibrate a SDM with survival data measured in common-garden experiments for different Iberian populations of *P. sylvestris* and *P. pinaster*, incorporating plasticity and local adaptation of the species into our modelling approach and overcoming some of the niche modelling caveats.

MATERIALS AND METHODS

Plant material and experimental layout

In this study we took data from two series of provenance tests planted at several experimental sites across Spain for *P. sylvestris* and *P. pinaster* (see Appendix S1 in Supporting Information) (see Alía *et al.*, 1995, 1997, 2001, for more detailed information of the experimental design). The experimental sites were planted in 1992 (*P. sylvestris*) and 1967 (*P. pinaster*). In each experimental site, plants originated from seed collected in different populations (provenances) covering the Iberian part of the distribution range of the species. Plants were arranged in a randomized complete block design with four replicates of 16-tree plots for each provenance. Survival of each tree was assessed annually in the two sets of experiments, and we used data on the survival of 11-year-old trees for both species. Provenances present in all trials (8 for *P. sylvestris* and 26 for *P. pinaster*) were selected for this study. We placed provenances of ecologically and climatically similar origin in four distinct groups for Scots pine (Northern Iberian Range, Central System, Eastern Iberian Range, Nevada Range) and five groups for maritime pine (Atlantic North-western populations, Central Plateau, Iberian Range, Segura Range, Nevada Range).

Survival differences between groups of provenances and experimental sites and their interaction were tested by an ANOVA (differences among sites, groups of provenances and their interaction). Significant differences between provenance groups indicated intra-specific genetic variability, while significant differences between the experimental sites demonstrated the existence of phenotypic plasticity for survival in the two species, whereas a significant provenance–site interaction confirmed the existence of differences in phenotypic plasticity among provenances (Climent *et al.*, 2006).

Climatic information

For each experimental site we used climate data from the closest weather station in the database archive of the Spanish National Meteorology Agency (series 1951–2006). Available data for these weather stations covering the 1951–2006 series were: mean annual temperatures, mean temperature of the warmest month, mean temperature of the coldest month, annual precipitation and summer precipitation.

Current climate variables for Spain were taken from *The agro-climatic characterization of Spain's provinces* (Sánchez Palomares *et al.*, 1999), covering 17 years and 2605 weather stations, and for Portugal from AGRIBASE (Ministerio da Agricultura, do Desenvolvimento Rural e da Pescas), over 21 years and 60 weather stations. The data were interpolated to 1 km for the whole Iberian Peninsula territory using thin splines (Mitasova & Mitas, 1993). Five climatic variables that have already been demonstrated to act as good predictors for the distribution of Iberian trees (Benito Garzón *et al.*, 2008) were selected: mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, total precipitation and summer precipitation. Because it has been demonstrated that there are differences between the optimal climate of a species and the actual climate it inhabits (Rehfeldt *et al.*, 2002), climatic variables were calculated as a function of the distance from the experimental site to the corresponding provenance, which is a measure of the reaction norm, i.e. the climate variability that a genotype could withstand (see Appendix S2). For each variable, its corresponding climatic index was weighted by the difference in survival of the population in its native site versus its trial site. The index was computed using a climate series of 17 years that covers the period where survival has been measured in the trial sites. We matched each survival point with the variation of each climate variable between the provenance and the trial site, and considered this variation to represent the population plasticity.

Climatic change scenarios were assessed using the A2 HadCM3 global circulation model for 2020, 2050 and 2080. The A2 scenario was chosen because it is one of the most aggressive in terms of future temperature change (IPCC, 2007). The original values were downscaled using climatic anomalies by thin-spline interpolation to 1 km^2 to obtain the fine resolution needed for the model.

Modelling provenance distribution

Modelling was performed for the Iberian Peninsula (Spain and Portugal) at 1 km^2 resolution. We used a SDM to predict the survival of species over time under current and climate change conditions. We used a SDM (Benito Garzón *et al.*, 2006) with survival as the response variable and several climate variables as predictors. To that end, we calibrated our model with tree survival rate for each group of provenances for both species.

The SDM used here works in three main steps: calibration, evaluation and prediction. The original dataset was randomly split into two datasets to independently evaluate the model. Original survival data for each experimental plot were divided into calibration and validation datasets for each group of provenances. Model calibration for each group of provenances was performed with two-thirds of the total survival dataset (training dataset) for each provenance of both species and climate data from the different plantation sites, leaving one-third of the data (evaluation dataset) to validate the model. Finally, model prediction was done over all the climate scenarios, from current conditions to 2080 under global warming.

Model calibration

The model was calibrated with the training dataset using the random forest algorithm (RF), an unsupervised learning algorithm that improves regression trees by using bootstrap aggregation of multiple trees (Breiman, 2001), i.e. the final tree is obtained by combining base models trained on different bootstrap replicate samples of the data. Specifically, we used a combination of 500 trees for regression in the randomForest R library. This algorithm has good generalization properties and has already been proven to predict species distribution under future climate change conditions (Prasad *et al.*, 2006; Benito Garzón *et al.*, 2008). The random forest algorithm can be explained in three main steps:

1. It takes *n* groups of trees in bootstrap from the original data (*n* was set to 500).

2. For each of the tree groups one regression and classification tree is grown. The division between tree nodes is made by randomly taking the number of variables of each division. We tuned the number of variables at each division, optimizing it with the out-of-bag (OOB) error estimates. The mean of squared residuals (MSE_{OOB}) OOB is computed for each tree with the data that remained out of the subgroup.

$$\text{MSE}_{\text{OOB}} = n^{-1}\sum_{1}^{n}\left((y_i - (y_i))^{\text{OOB}}\right)^2$$

where y_i^{OOB} is the mean of the OOB predictors.

3. Each tree is fully grown and not pruned. Tree responses are averaged to obtain the final prediction.

Model validation

The performance of the model was assessed, using the evaluation dataset, by the area under the receiver operating curve (AUC, ROC) technique (McPherson *et al.*, 2004), an accuracy measure based on a confusion matrix.

Model predictions

We estimated the species survival prediction for all scenarios considered (present, A2-2020, A2-2050, and A2-2080). When survival was higher than 0.5 we considered the provenance to be viable and generated occurrence maps. We calculated survival frequencies for each group of provenances across their range for the five climatic indices between provenance origins and trial sites for current and future climate change conditions.

We compared our modelled survival results for present and future conditions with results for the same species using presence–absence data (Benito Garzón *et al.*, 2008) and the same SDM (Benito Garzón *et al.*, 2006). Specifically, we compared the percentage of suitable area predicted for both occurrence and survival data over time. We compared the models for each provenance and the average survival of all provenances together. Under current conditions, the two measures will reveal whether selected species respond homogeneously to local environmental conditions. The model will also identify those provenances most suited to future climate conditions.

RESULTS

Intra-specific differences in survivorship

The existence of intra-specific genetic variability was indicated by statistically significant differences in survival between groups of provenances and trial sites for both *P. sylvestris* and *P. pinaster* (Table 1). A statistically significant difference among trial sites revealed the existence of phenotypic plasticity, and significant differences in the provenance–site interactions indicated the existence of differences in phenotypic plasticity among provenances. Given the significant differences among provenances, trial sites and their interaction, we analysed each species' survivorship as a whole (i.e. including all provenances pooled together) compared with survival of each group of provenances individually (as they could be considered independent ecotypes for modelling purposes).

Mean survival values for both species at the different trial sites and for their provenances are shown in Table 2.

Genetic effects on spatial prediction under current and climate change conditions

Survival prediction differed among groups of provenances, which also differed from survival predicted using all the provenances together for each species, and with spatial prediction using presence–absence information for calibration (Benito Garzón *et al.*, 2008). There were qualitative differences in the geographical patterns of each group of provenances modelled, and in predictions made using presence–absence data (see Fig. 1 for an example). When accounting for adaptation, *P. sylvestris* suffered a decrease in area occupancy but maintained most its range when all provenances were considered together (Fig. 1a, b), which contrasts with the results obtained using presence–absence datasets that present a greatly decreased area occupancy of this species under global warming conditions, restricting its probable territory occupancy to isolated points in North Iberian mountains (Fig. 1c, d). Interestingly, *P. pinaster* Central Plateau provenance (Fig. 1e, f) had more suitable areas available under

Table 1 ANOVA results show significant differences in survival between groups of provenances and trial sites for both *Pinus sylvestris* and *P. pinaster* species.

Species	Source of variation	d.f.	Sum of squares	Mean squares	*F*-value	*P*-value
P. sylvestris	Group of provenances	4	0.3	0.1	10.3	<0.0001
	Site	5	0.7	0.2	22.1	<0.0001
	Group of provenances × site	20	1.2	0.1	9.8	<0.0001
	Residuals	649	4.8	0.0		
P. pinaster	Group of provenances	5	1.8	0.5	14.7	<0.0001
	Site	4	0.8	0.2	6.0	<0.0001
	Group of provenances × site	20	1.1	0.1	2.2	<0.0001
	Residuals	314	9.8	0.0		

Significant differences among trial sites demonstrate the existence of phenotypic plasticity, whereas differences between groups of provenances reveal the existence of intra-specific genetic variability. The significant effect of the provenance–site interaction indicates differences in phenotypic plasticity among provenances.

Table 2 Average survival of *Pinus sylvestris* and *P. pinaster* for each site and group of provenances at each trial site.

		Group of provenances				
Species	Site	Northern Iberian Range	Central System	Eastern Iberian Range	Nevada Range	
P. sylvestris	Manzanal	100.0	97.8	95.3	97.2	
	Aragues	90.6	89.2	89.1	89.6	
	Navafria	82.7	93.2	92.6	86.7	
	Baza	89.0	83.3	94.7	92.0	
	Curueno	84.8	81.2	79.6	70.8	
		Atlantic North-western	Central Plateau	Iberian Range	Segura Range	Nevada Range
P. pinaster	Espinoso	65.0	84.5	81.3	77.0	72.0
	Cabañeros	63.0	83.5	76.7	93.3	91.5
	Riofrio	47.0	71.0	77.8	83.4	76.8
	Acebo	61.0	58.8	38.7	66.5	38.7

global warming than under current conditions, which contrasts with the results obtained using presence–absence data to calibrate the model (Fig. 1g, h). In this case predictions using provenance survival data not only differed from the predictions of presence–absence data in terms of decrease in habitat suitability but also in terms of spatial prediction.

Models developed for different groups of provenances explained differential amounts of variance (Table 3). The *P. sylvestris* model for all provenances together explained more variance than models considering each group of provenances separately. For the Nevada Range and Northern Iberian Range groups the variance explained by the model was lower (13.49 and 17.94, respectively) than for the other groups, probably because fewer points were sampled for these groups. For *P. pinaster*, most variance was explained by the model for the Nevada Range group and least for Atlantic North-western group.

Habitat suitability change over time: differences between survival – adaptation models versus SDMs

Probability of survival was predicted for each group of provenances under current conditions, 2020, 2050 and 2080 (Fig. 2), relative to current conditions. Again, we compared these results for predicted occupancy of all provenances (Fig. 2), with predictions obtained from presence–absence data (Benito Garzón *et al.*, 2008). *Pinus sylvestris* suffered a reduction in its predicted range under future conditions when all provenances together were considered, as did the Central System group of provenances in isolation. The Eastern Iberian Range group remained close to its initial percentage of occupancy, whereas the Nevada Range group was predicted to increase its area of suitability under future climate change conditions (Fig. 2a). The reduction in area of *P. sylvestris* under climate change was more drastic when the presence–absence dataset was used to calibrate the

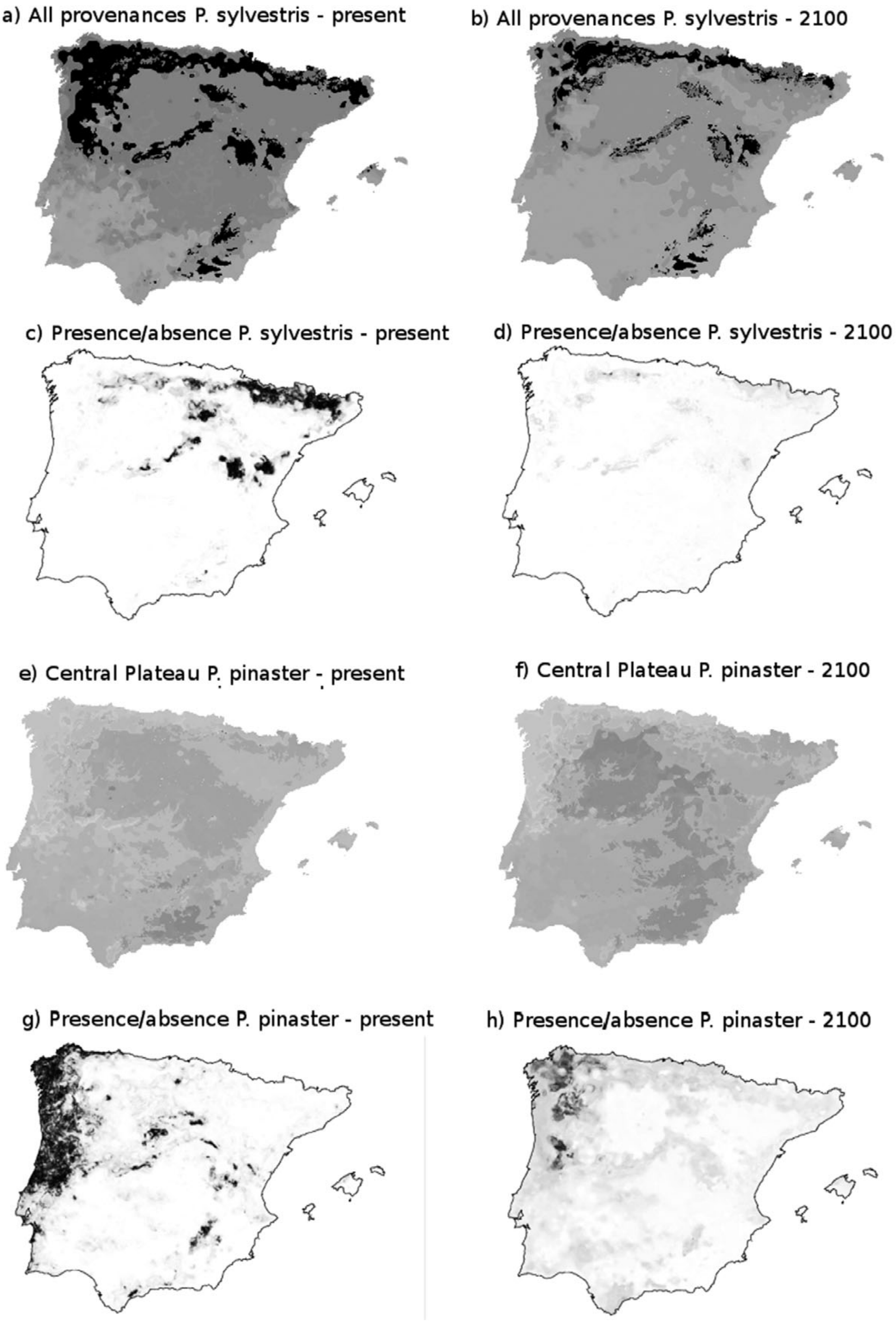
a) All provenances P. sylvestris - present
b) All provenances P. sylvestris - 2100
c) Presence/absence P. sylvestris - present
d) Presence/absence P. sylvestris - 2100
e) Central Plateau P. pinaster - present
f) Central Plateau P. pinaster - 2100
g) Presence/absence P. pinaster - present
h) Presence/absence P. pinaster - 2100

Table 3 The random forest algorithm estimates the accuracy of the prediction by the percentage of the total variance explained in the model by the explicative variables.

Species	Model	% Variance explained
P. sylvestris	All provenances together	82.4
	Northern Iberian Range	18.0
	Central System	70.3
	Eastern Iberian Range	70.0
	Nevada Range	13.5
P. pinaster	All provenances together	43.1
	Atlantic North-western	29.1
	Central Plateau	38.0
	Iberian Range	36.1
	Segura Range	24.2
	Nevada Range	63.0

Here the percentage of the variance explained by the species distribution models generated for all provenances and for each group of provenances is shown, ranging from 13.5 to 82.4%.

model than when models were calibrated with survival data (Fig. 2a). Total range of *P. pinaster* was increased when considering all populations together, and when considering the Central Plateau group of provenances alone. The Segura Range group maintained a similar area over time but the Atlantic North-western group suffered a large decrease in its range (Fig. 2b). The reduction in *P. pinaster* area under climate change was also different between occurrence and survival data, and this was especially evident when all populations were considered together (Fig. 2b). The Atlantic North-western group was predicted to be most affected by climate change conditions, as its occupancy was drastically reduced by 2080. The other groups of provenances were predicted to maintain their suitability under climate change or even to increase (Fig. 2b).

Phenotype changes under climate change predictions

Summer precipitation was the most important variable for almost all populations of *P. sylvestris* and *P. pinaster* in the model calibration. Therefore, we present the predicted occupancy frequencies for each *P. sylvestris* and *P. pinaster* group with respect to a summer precipitation gradient from the present until 2080 under the A2 scenario (Fig. 3). For *P. sylvestris*, the Northern Iberian Range group displayed much lower survival rate values than the other *P. sylvestris* provenances. This group was also the most affected by climate change in terms of territory occupancy (Fig. 2a). For *P. pinaster*, the Iberian Range and Nevada Range groups were predicted to increase by 2020 (Fig. 3), whereas the other groups of provenances decreased their phenotypic occurrences but maintained their climatic range.

DISCUSSION

In this study we assessed the importance of local adaptation for species distributions under future climate change, considering that these mechanisms can buffer or exacerbate processes leading to extinction risk and should be incorporated in SDM models. Hypotheses concerning the adaptability of tree species to global warming are difficult to test experimentally due to the long life cycle, high reproductive age and slow rates of speciation and extinction of trees (Petit & Hampe, 2006). In light of this, we were able to demonstrate that data from common-garden experiments can provide critical information concerning tree responses along an environmental gradient and should be incorporated into SDMs to realistically improve their predictions.

Intra-specific variability and plasticity in survival data

Phenotypic plasticity allows an organism to live across a wider range of environments than those with stable phenotypes (Ghalambor *et al.*, 2007; van Kleunen & Fischer, 2007). Generally, tree species are considered to express moderate to high plasticity in their responses to environmental stress (Wagner *et al.*, 1996; Climent *et al.*, 2006), and studies in *P. sylvestris* suggest that plasticity can be highly trait dependent (Magnani, 2009). Differentiation between populations across generations could lead to locally adapted populations, and there is widespread evidence of such adaptation in several adaptive traits in wild forest populations (Petit *et al.*, 2002; Rehfeldt *et al.*, 2002; Savolainen *et al.*, 2007).

Interestingly, the differences in response we obtained among provenances and site–provenance interactions for both *P. sylvestris* and *P. pinaster* mean that both phenotypic plasticity and genetic diversity made a contribution to survival. These results are supported by studies of growth in the same species (Oleksyn *et al.*, 2003) and provenanced material (Alía *et al.*, 1997, 2010; Alía Miranda *et al.*, 2001). These differences among provenances result from clear genetic structure in each species as shown by molecular markers (Prus-Glowacki *et al.*, 2003; Gómez *et al.*, 2005) and quantitative traits (González-Martínez *et al.*, 2002).

Populations are locally adapted when they have their highest relative fitness at their provenance sites and lower fitness in

Figure 1 The maps show the prediction of probability of survival for all *Pinus sylvestris* provenances considered together for present and future conditions (a and b, respectively), and the spatial probability prediction calibrating the model with presence–absence data for the same climate conditions (c and d, respectively). The figure also shows the prediction of probability of survival for the *P. pinaster* Central Plateau provenance under present and future conditions (e and f, respectively), and the spatial prediction calibrating the model with the *P. pinaster* presence–absence dataset for the same climate conditions (g and h). Dark colours indicate a high probability of occupancy, with black being the maximum probability (1) and white the minimum (0).

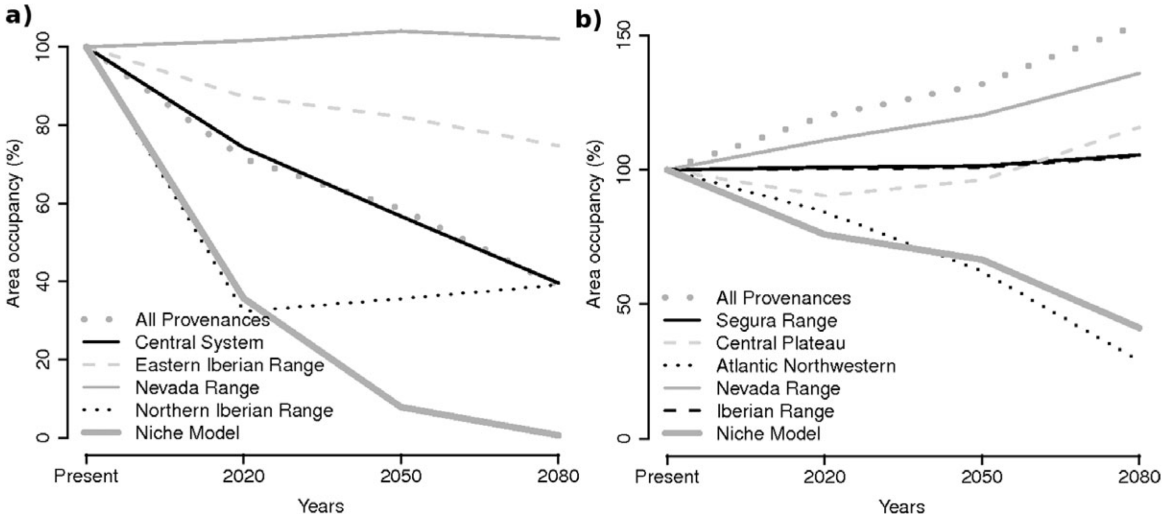

Figure 2 Percentage of occupancy area for *Pinus sylvestris* (a) and *P. pinaster* (b) from current (100% of its potential area occupied) to 2080 under the A2 HadCM3 scenario. The area is shown for all the provenances together, for each of the groups, and for niche modelling using presence–absence of the species to calibrate the model (Benito Garzón *et al.*, 2008).

other parts of their range (Savolainen *et al.*, 2007). Our results for survival differences show that populations do not always present higher average fitness when grown under environmental conditions similar to those in their original provenance region (Table 2). Therefore, although local adaptation for these species has been reported (Alía *et al.*, 1997), this cannot be considered to be a general rule for all populations. However, other local factors that were not considered in this study, such as slope and soil type, would also condition local species adaptation.

The role of plasticity and intra-specific variability when modelling species distributions

A number of studies have highlighted the importance of considering whole species ranges when modelling species distributions, arguing that for large-scale species distribution modelling, tree populations are in pseudo-equilibrium with environmental conditions (Araújo & Pearson, 2005) and can respond homogenously to climate change across their range. However, by discounting different ecotypes across species ranges these studies may reach spurious conclusions, because the inclusion of plasticity and genetic diversity among populations has a substantial effect on model outcomes.

The first indication of SDM inconsistencies can be detected when comparing species distributions generated by SDM for the whole of Europe (Thuiller, 2003) with species distributions predicted within a given geographical region (Benito Garzón *et al.*, 2008). Intra-specific variation across populations has been demonstrated by genetic analysis of European tree populations (Petit *et al.*, 2002; Cheddadi *et al.*, 2006) mainly arising from the movement of populations since the last glaciation (Hewitt, 1999; Petit *et al.*, 2003). Overall, many factors prevent species responses to climate from being considered homogeneous for their entire range, such as life history of a species leading to many different subpopulations, and differential phenotypic plasticity (Morin & Thuiller, 2009). Our models for each of the provenances demonstrate the importance of considering plasticity and genetic diversity among populations when predicting species distributions.

Future climate change can be considered as a selection pressure, and consequently population structure is expected to determine species behaviour. In this case, the use of plasticity and genetic differentiation among populations would be critical to accurately predict species extinction risk under conditions of global warming. Previous models in the Iberian Peninsula, based on occurrence data developed for the same species (Benito Garzón *et al.*, 2008), overestimate the decrease in the suitable area for species under global warming (Fig. 2) when compared with models developed here that take species survival into account.

Since the incorporation of intra-population genetic diversity and phenotypic plasticity in our SDM significantly altered its outcome, we recommend that existing predictions of future tree species distributions and their component populations must be reconsidered. Specifically, we report large phenotype changes for Iberian populations of *P. sylvestris* and *P. pinaster* when using IPCC climate change scenarios, leading to decreases in survival values for almost all populations. Following our approach, under future climate change conditions provenances would not behave as previously predicted, so leading to different habitat suitability distributions for each provenance.

Genetic effects on Mediterranean forest distributions under global warming

Our results based on data-driven models indicate that *P. sylvestris* and *P. pinaster* populations from southern Spain would have higher relative survival in northern territories (that will be warmer) under future climate scenarios than under current con-

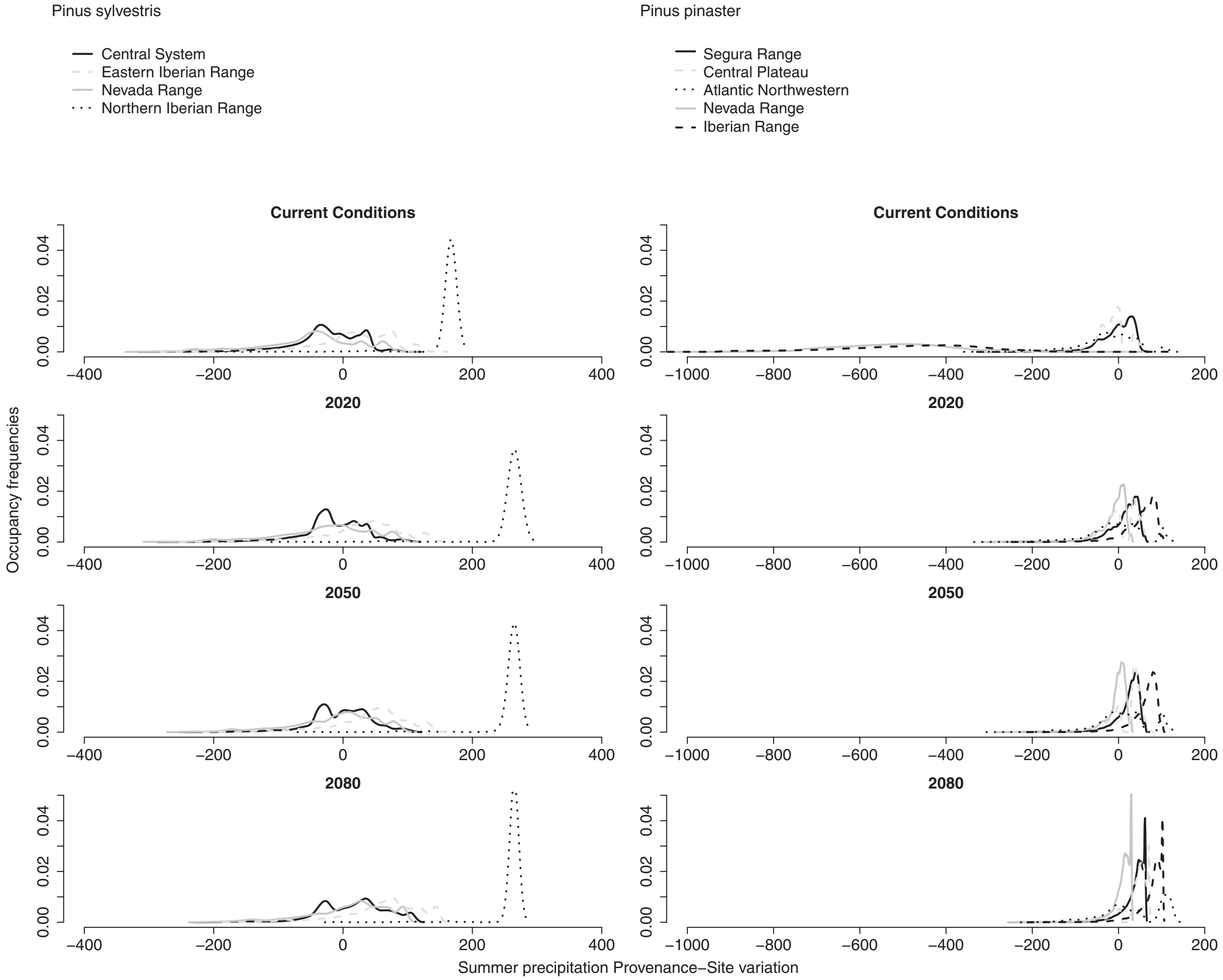

Figure 3 Occupancy frequencies for *Pinus sylvestris* and *P. pinaster* across their distribution range for summer precipitation variation between provenance and trial site for each provenance. Occupancy is considered positive when the predicted survival probability is higher than 0.5. The figure shows the occupancy frequency for each group of provenances considered for current predicted conditions and 2020, 2050 and 2080 summer precipitation variation between provenances and trial sites.

ditions (Fig. 2), suggesting pre-adaptation of these populations to warmer climates. In this case, locally adapted provenances to warmer conditions would benefit from climate change at the expense of other provenances.

For example, the *P. sylvestris* Northern Iberian Range group (northernmost population) has the largest predicted decrease in area occupancy (Fig. 2a), and also the narrowest survival frequencies over different climatic conditions of all the groups of provenances (Fig. 3b–d). Consequently, this phenotype would not be adapted to global warming in the Iberian Peninsula. These results are expected since northern *P. sylvestris* populations are likely to be adapted to a colder climate than southern ones. For *P. pinaster*, Atlantic North-west provenances continue to decrease in both predicted occupancy (Fig. 2b) and survival frequencies irrespective of climatic conditions (Fig. 3e–h), whereas the other provenances maintain or slightly increase their habitat suitability under the global warming scenarios and are able to maintain their survival levels up to 2050. In fact, some authors have considered two different subspecies of *P. pinaster*, one for Atlantic Spain, Portugal and France and another mediterranean subspecies that covers the rest of its range in the Mediterranean Basin (Costa Tenorio *et al.*, 1998). Relatively low drought tolerance in the North-western provenance group may be responsible for its maladaptation to future climate change, particularly in light of the predicted increase in aridity for the Iberian Peninsula. Drought tolerance is considered a key trait for future local adaptation of populations (St. Clair & Howe, 2007).

Our results agree with studies on local adaptation of the mediterranean species *Quercus suber* in the same region. Ramírez-Valiente *et al.* (2009) find that not all Iberian *Q. suber* populations are equally vulnerable to climate change and suggest that northern populations are less adapted to drier conditions than southern populations. This means that local adaptation could also be detrimental to survival under future climate change conditions, where populations have evolved traits adapted to local stress factors other than increased drought and temperature. For some species local maladaptation has been demonstrated by planting northern populations to the south of their original provenance region (Savolainen *et al*., 2007). If southernmost populations are adapted to harsh conditions, and would survive *in situ* under expected climate changes, the new conditions would also be likely to favour their northwards migration. However, it is unlikely that tree species could naturally migrate quickly enough to keep up with the rapid pace of expected future climate change. For instance, *P. sylvestris* pollen can disperse beyond 200 m per year in some Iberian populations (Robledo-Arnuncio & Gil, 2005), but this would not be enough to allow the species to colonize new northern territories under climate change.

In some cases, such as the Nevada Range and Northern Iberian Range groups of *P. sylvestris* provenances, the low explicative value of the models should be taken into account when drawing conclusions (Table 3). The low explicative variance may be due to sample size, since experimental data were less abundant for some groups of provenances than others. The amount of variance explained by the models also depended on the species considered. The relatively greater plasticity of *P. pinaster* (e.g. Chambel *et al*., 2007) and differences in the original environmental conditions at the experimental sites may both partially contribute to the differences between the species. The *P. pinaster* experimental sites were all located in central Spain, and some climatic provenances, such as the north-west or most southerly, are therefore not represented by the trial sites. In contrast, *P. sylvestris* was planted in sites close to the origin of some of its provenances, hence these were climatically similar.

Further work

To fully understand effects of genetic diversity on future species distributions under the selection pressures resulting from climate change, models should include intra-population genetic variability. Survival under changing conditions is expected to increase with intra-population diversity, as many different alleles provide the capacity to produce a greater variety of responses to selection pressures, allowing different individual survival rates for each population. For instance, this is suggested in the case of *B. pendula*, in which as conditions change, within-population genetic diversity may allow pre-adapted alleles to increase their frequencies in the population (Kelly *et al*., 2003).

Beyond the scope of our study, some other important factors controlling species adaptability may further improve modelling of future tree distributions. Evolving *in situ* is one possible solution for species facing future climate change (Jump & Peñuelas, 2005), but the characteristics of most tree species preclude this option. For example, Savolainen *et al*. (2004) have shown that the rate of evolution of *P. sylvestris* will be too slow to keep pace with predicted climate changes, but other populations might display higher genetic variance for adaptive traits. Besides, pines have the capacity for long-distance pollen dispersal (Robledo-Arnuncio *et al*., 2005) that could allow gene flow from southern populations already adapted to drought conditions to introgress in northern populations being affected by climatic change.

The climate change scenario selected for use with the model will affect the strength of the responses obtained. We used a strong impact scenario (A2) that probably has a relatively large effect on the ecotype distributions, compared with other socio-economic scenarios. Under a less aggressive scenario in terms of temperature increase, more moderate responses from selected provenances and narrower differences between present and future provenance distributions would be expected.

The existence of plasticity and genetic variability in survivorship is demonstrated by our study, as well as a significant genotype–environment interaction among provenances and trial sites. Furthermore, we make SDM models more realistic by incorporating survival data. Similar approaches could include calibrating our model with other experimental variables such as the species' reproductive output. We reaffirm the importance of considering adaptive traits when predicting species distributions and avoiding the use of occurrence data as a predictive variable. Finally, our approach confirms the value of linking experimental trial data with modelling approaches to help determine the suitability of provenances under future climate change conditions.

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SUPPORTING INFORMATION

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

Appendix S1 Provenance and trial site location used in this study for both *Pinus sylvestris* and *Pinus pinaster*.
Appendix S2 Example of climatic index calculation as a function of the provenance–site climate differences for each survival point used to calibrate the modes.

BIOSKETCH

M.A.Z. and M.B.G. conceived the initial idea. All authors contributed to discussion of the ideas and writing of the paper. The experimental database was provided by R.A. M.B.G. analysed the database.

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