The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change

Fernando Valladares,[1,2*,†]
Silvia Matesanz,[2†]
François Guilhaumon,[3,4]
Miguel B. Araújo,[1,3,5]
Luis Balaguer,[6]
Marta Benito-Garzón,[7,8,9,10]
Will Cornwell,[11] Ernesto
Gianoli,[12,13] Mark van Kleunen,[14]
Daniel E. Naya,[15]
Adrienne B. Nicotra,[16]
Hendrik Poorter[17] and
Miguel A. Zavala[18]

Abstract

Species are the unit of analysis in many global change and conservation biology studies; however, species are not uniform entities but are composed of different, sometimes locally adapted, populations differing in plasticity. We examined how intraspecific variation in thermal niches and phenotypic plasticity will affect species distributions in a warming climate. We first developed a conceptual model linking plasticity and niche breadth, providing five alternative intraspecific scenarios that are consistent with existing literature. Secondly, we used ecological niche-modeling techniques to quantify the impact of each intraspecific scenario on the distribution of a virtual species across a geographically realistic setting. Finally, we performed an analogous modeling exercise using real data on the climatic niches of different tree provenances. We show that when population differentiation is accounted for and dispersal is restricted, forecasts of species range shifts under climate change are even more pessimistic than those using the conventional assumption of homogeneously high plasticity across a species' range. Suitable population-level data are not available for most species so identifying general patterns of population differentiation could fill this gap. However, the literature review revealed contrasting patterns among species, urging greater levels of integration among empirical, modeling and theoretical research on intraspecific phenotypic variation.

Keywords

Climate change, climate variability hypothesis, ecological niche models, intraspecific variation, local adaptation, niche, phenotypic plasticity, population differentiation.

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INTRODUCTION

Rapid environmental changes are prompting increased interest in understanding current and future threats to biodiversity (e.g., Pereira *et al*. 2010) and their consequences for ecosystem health and services (e.g., Cardinale *et al*. 2012). However, the areas of enquiry required for understanding the mechanisms driving biodiversity and ecosystem changes progress at different paces thus limiting our ability to make long-term predictions. For instance, while the capacity of organisms to tune

[1]LINCGlobal, Department of Biogeography and Global Change, National Museum of Natural History, MNCN, CSIC, Serrano 115 bis, 28006, Madrid, Spain

[2]Departamento de Biología y Geología, ESCET, Universidad Rey Juan Carlos, Tulipán s/n, 28933, Móstoles, Spain

[3]'Rui Nabeiro' Biodiversity Chair, CIBIO, University of Évora, Largo dos Colegiais, 7000, Évora, Portugal

[4]Laboratoire Écologie des Systèmes Marins Côtiers UMR 5119, CNRS, IRD, IFREMER, UM2, UM1, cc 093, Place E. Bataillon, 34095, Montpellier Cedex 05, France

[5]Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK

[6]Departamento de Biología Vegetal I, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, 28040, Madrid, Spain

[7]CNRS, Laboratoire d'Ecologie, Systématique et Evolution (ESE), UMR 8079, Université Paris-Sud, F-91405, Orsay Cedex, France

[8]CNRS, Centre International de Recherche sur l'Environnement et le Développement (CIRED), F-94736, Nogent-sur-Marne Cedex, France

[9]Université de Bordeaux, UMR 1202 BIOGECO, F-33400, Talence, France

[10]INRA, UMR 1202 BIOGECO, F-33610, Cestas, France

[11]Department of Ecological Sciences, Systems Ecology, Vrije Universiteit, De Boelelaan 1085, 1081 HV, Amsterdam, The Netherlands

[12]Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena, Chile

[13]Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción, Chile

[14]Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, 78457, Konstanz, Germany

[15]Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Montevideo, 11400, Uruguay

[16]Division of Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, Australia

[17]Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, 52425, Jülich, Germany

[18]Forest Ecology and Restoration Group, Department of Life Sciences, Science Building, of Alcalá, Campus Universitario, 28871, Alcalá de Henares, Madrid, Spain

*Correspondence: E-mail: valladares@ccma.csic.es

†These authors contributed equally to this study.

"The authors dedicate this article to the memory of Luis Balaguer, brilliant scientist, coauthor and friend."

their phenotype to changing conditions is widely recognised as an important mechanism to avoid migration or extinction under climate change (Matesanz *et al.* 2010; Nicotra *et al.* 2010), phenotypic plasticity is not generally considered in models of species responses to climate change (e.g., Reed *et al.* 2011; Schwartz 2012). Attempts to include phenology as a plastic response to climate change in models have been made (e.g., Chuine & Beaubien 2001). However, species are usually treated as if individuals from all populations respond equally to environmental pressures (Kawecki 2008; Banta *et al.* 2012). There is ample evidence, though, that populations within a species experiencing different environmental conditions often differ in phenotypic characters and genetic structure (Linhart & Grant 1996). Individuals from different populations may also be characterised by distinct phenotypic responses to environmental conditions (Sultan & Spencer 2002). Differences in genotype and phenotype interact with environmental factors such that fitness can vary among populations as a function of both local adaptation and local environment (Savolainen *et al.* 2007; Leimu & Fischer 2008; Banta *et al.* 2012).

How plasticity and fitness are distributed among populations of a given species is still a matter of ongoing research. At species range edges, where the limits of the distribution are imposed by environmental constraints, individual fitness is generally lower than in the center of its distribution (Kawecki 2008). However, geographically peripheral populations do not always occur in unfavourable habitats (Jump & Woodward 2003; Granado-Yela *et al.* 2013). The fitness decline in populations at the environmental margin will depend on the extent of local adaptation of the populations, their phenotypic plasticity, the steepness of environmental gradients, and gene flow, amongst other factors (Kawecki 2008; Lenoir & Svenning 2013). Features controlling fitness of populations are of particular importance at the margin of a species distribution, especially when they are exposed to climate change (Davis & Shaw 2001; Kokko & Lopez-Sepulcre 2006). Populations and genotypes that experience the greatest extent of variability in a given environmental condition are expected to be most plastic in traits adaptive in those conditions (Van Tienderen 1991; Sultan & Spencer 2002). In the face of change, plasticity may play a key role enabling persistence of remnant individuals or populations (Rubio de Casas *et al.* 2009; Chevin *et al.* 2010; Matesanz *et al.* 2010). Thus, patterns of plasticity of populations at the distribution margin will influence species responses to a changing climate, and will be important in determining species distributions under novel climates.

Ecological niche models (ENMs; Peterson *et al.* 2011) are widely used for exploring the degree of exposure of species distributions to climate change and projecting potential species distributional shifts (Thuiller *et al.* 2008). One prominent feature of ENMs and other models is that the relationship between species distribution and predictive environmental variables is assumed to be constant, thus neglecting the capacity for phenotypic plasticity and natural selection to modulate species responses to changing environments (Reed *et al.* 2011). We argue that patterns of intraspecific differentiation of well-studied species could be used to infer plasticity and niche breadth for species with no available data. Most models

assume that species responses to climate changes are similar across distributional ranges. Few studies have explored strategies to bring intraspecific variation and local adaptation into species distribution modeling. O'Neill *et al.* (2008) and Wang *et al.* (2010) demonstrate the impact of differences in tree growth due to genetic differences between populations that could impact species distributions, and Benito-Garzón *et al.* (2013) incorporated differences in survival between populations into niche models. Oney *et al.* (2013) and Pearman *et al.* (2010) incorporated intraspecific variation into distribution projections leading to less pessimistic distribution projections. However, these studies generally consider intraspecific distribution data, not differences in phenotypic traits or plasticity (Oney *et al.* 2013). Atkins & Travis (2010) modelled the impact of local adaptation on climate change response in a theoretical species and found counter-intuitively that broadly distributed species can have greater range reductions because cooler adapted genotypes may block the potential for range shift by locally adapted genotypes. These studies demonstrate that the predictions of habitat suitability for a given species in future scenarios can be highly affected by intraspecific variation.

Chevin *et al.* (2010) proposed an alternative approach to ecological niche modeling that explicitly includes the factors that limit population responses to climate change. Their approach is based on evolutionary and demographic mechanisms that determine the critical rate of environmental change beyond which a population cannot persist, and includes phenotypic plasticity and environmental sensitivity to selection. As of yet, no niche model has explicitly considered plasticity and local adaptation due to the complexity and uncertainties involved in such analysis.

Here, we examine the potential impact that population differentiation in thermal fundamental niches and phenotypic plasticity may have on species distributions under a warming climate. We first develop a conceptual model of the relationship between phenotypic plasticity and thermal niche breadth providing five alternative intraspecific scenarios based on patterns observed among plant and animal populations. As the future distribution of species and populations may heavily rely on dispersal opportunities (Dullinger *et al.* 2004), we tested each scenario under the assumptions of unlimited and no dispersal. Secondly, we use ENMs to quantify the impact that each intraspecific scenario has on the distribution of a virtual species distributed across a geographically realistic setting. Finally, we compare the results obtained with an analogous modeling exercise using real data on growth and survival responses to climate of different populations of widespread tree *Pinus sylvestris*.

Patterns of population differentiation

Populations within a single species may differ in trait means across the species range. In a now classical study, Clausen *et al.* (1948) transplanted *Achillea lanulosa* populations from different altitudinal sites to a common garden and demonstrated striking ecotypic differentiation. Since then, numerous examples of such within-species differentiation have been published and attention has more recently turned to the question

of under what circumstances local adaptation is likely to evolve (Kawecki & Ebert 2004; Savolainen *et al.* 2007; Leimu & Fischer 2008; Araújo *et al.* 2013). It is becoming increasingly clear that not only trait means and genetic structure can vary within a species, but also phenotypic plasticity in those traits (Pigliucci *et al.* 1995; Pichancourt & Klinken 2012). Moreover, the mean value and the plasticity of a trait may interact (Auld *et al.* 2010). From the perspective of assessing the contribution of plasticity to persistence and distributional shifts under climate change, it is the adaptive component that is of interest, i.e., plasticity that allows a genotype to maintain high fitness across environmental gradients (Van Kleunen & Fischer 2005; Matesanz *et al.* 2010; Nicotra *et al.* 2010).

Questions are now being raised about how trait means and plasticity vary across a species' range (see e.g. Mägi *et al.* 2011; Molina-Montenegro & Naya 2012). Theoretically, adaptive phenotypic plasticity should be more extensive in species experiencing environmental heterogeneity over the course of a generation and potentially having wider fundamental niches (Balaguer *et al.* 2001; Valladares *et al.* 2007). The climatic variability hypothesis (CVH) states that, as the range of climatic fluctuation experienced by terrestrial organisms throughout a year increases with latitude, individuals at higher latitudes should have broader ranges of thermal tolerance and/or greater physiological flexibilities to cope with more fluctuating environmental conditions (Janzen 1967). Empirical evidence for thermal traits clearly supports the prediction of the CVH since a positive relationship between thermal tolerance ranges and latitude has been reported for many different taxa (see Calosi *et al.* 2008 and studies by Brattstrom, Addo-Bediako *et al.* and Deutsch *et al.* in Naya *et al.* 2012). Evidence for increased physiological flexibilities at higher latitudes is, however, much scarcer, but some studies show a positive relationship between latitude and the amount of flexibility observed for physiological traits in both animals (Naya *et al.* 2012) and plants (Molina-Montenegro & Naya 2012).

Populations at the margin of species' ranges (both the leading and trailing edges) play a crucial role for understanding future changes in species distributions, since it is there that colonisation and extinctions will primarily take place under climate change (Mägi *et al.* 2011; Lenoir & Svenning 2013). It has likewise been predicted that core and margin populations will differ significantly in life-history traits and plasticity patterns, as population genetic structure and selection pressures related to environmental heterogeneity are likely to vary along the distribution range of a species (Purves 2009). However, contrasting hypotheses have been proposed regarding the direction of these differences. Plasticity has been suggested to be lower across the range margins than near range centers due to lack of additive genetic variation, small population sizes, genetic drift or founder effects (Mägi *et al.* 2011). Other hypotheses propose that plasticity should be higher along marginal (or peripheral) populations since these sites are expected to experience high climatic variability and therefore plastic genotypes will be advantageous (Volis *et al.* 1998). Few studies have specifically assessed this question, and while some have found lower plasticity at the margins (Volis *et al.* 1998; Mägi *et al.* 2011), others have found no significant differences in plasticity between marginal and central populations (Stewart & Nilsen 1995; Blacksamuelsson & Andersson 1997).

It is assumed that species abundance and genetic variation decline towards low quality habitats at the range edge (Sagarin & Gaines 2002; Vucetich & Waite 2003). However, peripheral populations may experience favourable conditions, exhibiting higher levels of fitness and phenotypic plasticity. This is the case of the wild olive (*Olea europaea*) at its westernmost limit in the Canary Islands, where phenotypic plasticity in morpho-functional traits and plant size as well as population fitness reach higher values than those exhibited by most of the core populations (Granado-Yela *et al.* 2013). High quality habitats can thus exist in both peripheral and core locations, which is consistent with the observations that species often persist at the marginal rather than at the central parts of their range (Channel & Lomolino 2000). Populations at range limits are structured in metapopulations, constituting a shifting mosaic of source and sink populations held together by migration (Holt *et al.* 2005). Habitat loss, climatic extremes, biotic interactions and limited dispersal can reinforce population isolation (Purves *et al.* 2007; Benavides *et al.* 2013). However, at historical limits, where relict peripheral populations have been confined for long periods of time in habitat refugia, a combination of reproductive isolation, small population size, lower genetic variation, founder effects, and genetic drift often results in genetic divergence (Reisch *et al.* 2003).

Intraspecific variation in plasticity and trait means takes on a new importance in the context of climate change. Populations at the leading edge of the migrating front are expected to remain and track favourable conditions mainly by long-distance dispersal events (Hewitt 2000). Phenotypic plasticity would expand the opportunities for effective migration to the extent that it contributes to niche breadth (Ackerly 2003). Conversely, populations at the trailing edge either go extinct, or experience environmental mismatches that might create opportunities for adaptive evolution (Davis & Shaw 2001; Ackerly 2003). If phenotypic plasticity contributes to persistence of populations under climate change, it does so by providing a buffer period during which niche evolution (i.e. adaptive niche expansion or shift) might occur (Chevin *et al.* 2010). For example, it has been suggested that the expression of phenotypic plasticity enabled survival of remnant lineages of kermes oak (*Quercus coccifera*) under suboptimal steppe conditions during glaciations, which in turn, facilitated adaptive divergence during the Quaternary (Rubio de Casas *et al.* 2009). While the prevailing ecological sorting processes differ between leading and trailing edges, phenotypic plasticity may play a key role in both regions.

In summary, studies of fitness, local adaptation and phenotypic plasticity of populations across the entire range of a species are scant and while important phenotypic differences within species are evident, we lack a comprehensive picture of what the impact of those differences would be on forecasts of species distributions under climate change, and how intraspecific variation in phenotypic plasticity and thermal niche optima affects forecasts.

A CONCEPTUAL MODEL BASED ON OBSERVED ALTERNATIVES FOR INTRASPECIFIC VARIATION

Here, we present a conceptual model in which populations within a species differ in the value of a trait closely related to fitness, thus leading to varying intraspecific responses to climate change. In our conceptual framework fitness is determined by three factors: (1) local adaptation, which involves primarily the genotype, (2) plasticity, which affects in combination with the environment the translation of the genotype into the phenotype, and (3), the strength of environmental selection that leads to a decrease in fitness in proportion to the differentiation of actual phenotype from the optimal one. Our model is based on two main assumptions. First, we assume that plasticity in the trait controlling for tolerance to climate (e.g. temperature) is adaptive. Plasticity is conventionally assessed by describing the response (reaction norm or dose–response curve) of a given genotype under different environmental conditions (Valladares *et al.* 2006). A measure of plasticity (e.g. the slope of the reaction norm) can then be regressed on a fitness proxy to assess the adaptive value of this response (Van Kleunen & Fischer 2005; Nicotra *et al.* 2010). In some cases, it is of interest to understand the pattern of environmental response at higher levels than the genotype, and thus, the reaction norms of several genotypes can be grouped in a composite reaction norm for a specific popula-

tion or a species (Gianoli & Valladares 2012). The reaction norm of the populations can be combined with the trait-fitness relationship in different environments to assess the effect of plasticity on the fitness-environment relationship.

Second, we assume that the trait mean and its plasticity (slope of the reaction norm) determine the optimum environmental value and the niche breadth, respectively, which can be separated for each population within the species (Fig. 1). In the model, fitness is a function of the trait and climate, and fitness decreases from the center of the distribution to the margins for each population (see Appendix S1 Fig. S1). To illustrate the potential consequences of such within-species variation for changes in species distribution under climate change, we used theoretical and empirical data to simulate the following five different scenarios of intraspecific phenotypic variation based on alternative situations found in the literature (Fig. 1):

(1) *No differentiation.* All populations of a species have the same average trait values and the same reactions norms (magnitude of phenotypic plasticity) and, as a consequence, their fundamental niches are the same and equal the overall fundamental niche of the species (Fig. 1). This is the situation that is implicitly assumed in most currently used species-distribution models of all sorts (Peterson *et al.* 2011; Schwartz 2012).
(2) *Local adaptation, equal plasticity.* All populations consist of locally adapted genotypes with low phenotypic plasticity
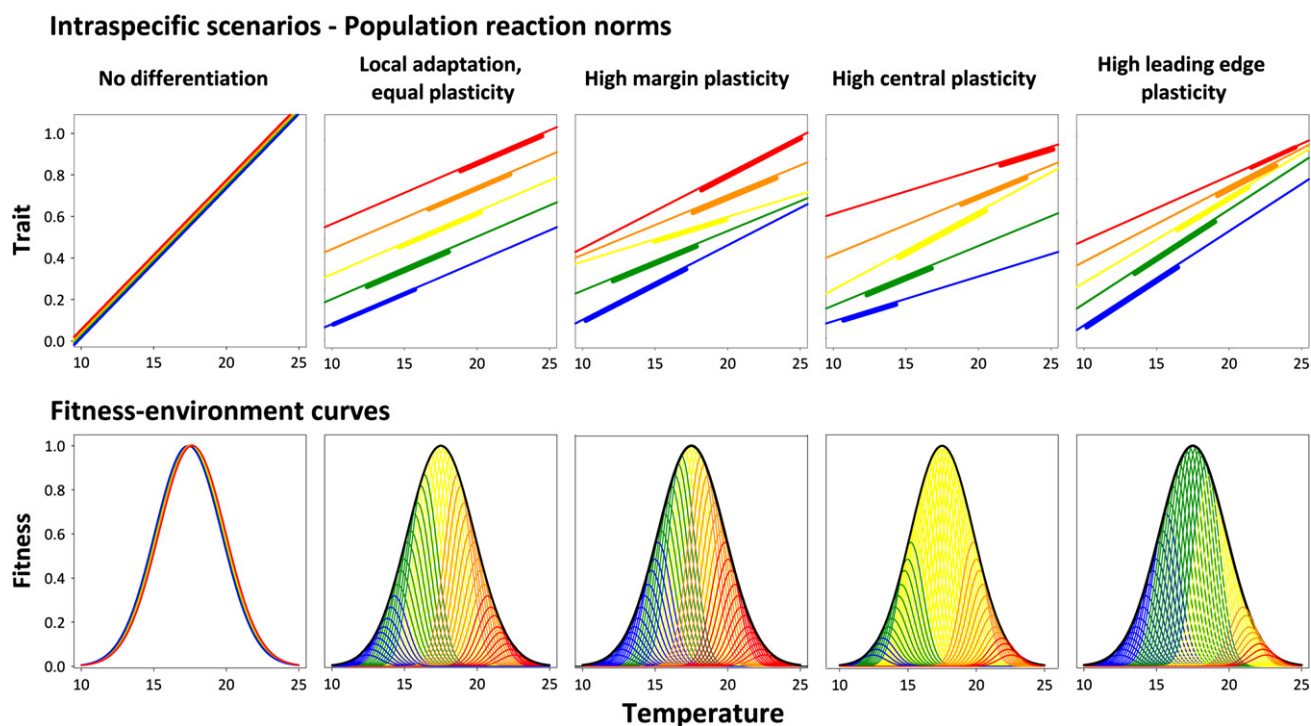

Figure 1 Conceptual model of trait values and fitness vs. environment (temperature) for a virtual species with alternative intraspecific scenarios. Top: Reaction norms of a fitness-related trait in response to temperature for five populations (consisting of different subpopulations) in five different scenarios of intraspecific variation. Trait values are presented in a 0 to 1 arbitrary scale. Thicker sections of each reaction norm represent the section of the environmental gradient corresponding to the range of temperatures experienced by each population. Bottom: Fitness-environment curves for each population; each curve represents the fundamental niche for each population. Fitness is presented in a 0 to 1 arbitrary scale. Reaction norms and fitness-curves were generated for all the subpopulations in each simulation using R (code available in Supporting Information). Reaction norm graphs are for illustrative purposes only; the depicted relationships between reaction norms and the corresponding fitness-environment curves are not based on mathematical equations.

and narrow fundamental niches that fall along different positions within the fundamental niche of the species (Fig. 1). This scenario is supported by studies with plants (Savolainen *et al*. 2007; Leimu & Fischer 2008) and different vertebrates (Bernatchez & Landry 2003; Fischer *et al*. 2011).

(3) *High margin plasticity*. As in scenario 2, all populations consist of locally adapted genotypes, but both plasticity and niche breadth are highest at the range margins and lowest in the center of the distribution (Fig. 1). This pattern has been found in plants (Volis *et al*. 1998), insects (Otaki *et al*. 2010), mammals (Romeo *et al*. 2010), and birds (Sunde *et al*. 2001).

(4) *High central plasticity*. The reverse pattern of scenario 3; plasticity and niche breadth are lowest at the range margins and highest in the center of the distribution. This pattern has been found in a few plant studies (Mägi *et al*. 2011) (Fig. 1).

(5) *High leading edge plasticity*. As in scenarios 3 and 4, all populations consist of locally adapted genotypes and differ in plasticity and niche breadth. However, in this scenario, plasticity and niche breadth increase from the warm range margin to the cold range margin, as predicted under the CVH (Fig. 1). This hypothesis has rarely been explored in plants (Molina-Montenegro & Naya 2012; Araújo *et al*. 2013), but it has been repeatedly addressed and confirmed in different groups of animals (Calosi *et al*. 2008; Kellerman *et al*. 2009; Overgaard *et al*. 2011; Naya *et al*. 2012; Araújo *et al*. 2013).

To ensure that differences among intraspecific scenarios in the modelled species' distribution are exclusively due to within-species phenotypic variation, the overall fundamental niche of the species was maintained equal across scenarios. In order to create different intraspecific scenarios that maintained the overall species niche constant, we simulated fitness-climate curves for a total of 45 sub-populations belonging to five populations (different colours in Fig. 1). In the no-differentiation scenario, all 45 subpopulations had the same fundamental niche (i.e. equal to the overall fundamental niche of the species). In the other four scenarios, the 45 subpopulations had the same niche breadths but differed in temperature optima. Then, to specify the different scenarios, we varied the proportion of subpopulations assigned to each population across scenarios (Fig. 1). The number of subpopulations assigned to each population reflects the amount of phenotypic plasticity expressed by that population, which in turn determines the niche breadth of the population (see Appendix S1 Table S1 for details on the different scenarios).

Data and results from each empirical study case found in the literature were heterogeneous and lacked sufficient detail to be used for parameterising fitness-temperature plots for each population. The plots and the arbitrary distinction of five populations shown in Fig. 1 are used to forecast distribution in a warmer climate must be taken as idealised representations of the alternative cases found in the literature (for the R-code see Appendix S2).

Setting the model on stage: intraspecific scenarios for a virtual species

We mapped the simulated fitness-climate curves for the 45 hypothetical subpopulations onto a European template using maximum temperature of the warmest month (TMax) for present time and projected for 2050 (see Appendix S1 Fig. S2). Spatially explicit projections of TMax were obtained for a baseline period (1961–1991) and were derived from data provided by the Climate Research Unit at the University of East Anglia to the European ATEAM project (Schroter *et al*. 2005; available in Appendix S3). The data provides monthly values for 1901–2000 in a 10' grid resolution (ca. 16×16 km). Average monthly temperature in grid cells covering the mapped area of Europe were used to calculate TMax values for 1961–1991 (referred to as 'baseline data'). Future climate projections were derived for 2021–2050 (referred to as '2050 data') from the climate model (HadCM3). The modelled climate anomalies were scaled based on the A1F1 scenario that describes a globalised world under rapid economic growth and global human population that peaks in mid-century and declines thereafter. Concentrations of CO_2 increase from 380 ppm in 2000 to 800 ppm in 2080, and temperature rises by 3.6 °C.

These data were used to generate current and future habitat (climatic) suitability maps for each of the five populations – using the combined data of all the subpopulations assigned to each specific population (see below) – according to the five different intraspecific scenarios (Fig. 1). We assumed a direct relationship between fitness and habitat suitability, i.e. the habitat suitability in a given grid cell was exactly the fitness of the population at the temperature in that grid cell. In the climatic suitability maps, a value of 1 characterises temperature values at the species optimum and 0 characterises unsuitable temperatures. Among these values are intermediate levels of suitability for species occurrence. Distributions predicted under an unlimited dispersal scenario, whereby the populations can colonise any suitable area within the time frame considered, were then compared to the alternative scenario of no dispersal, where populations cannot colonise new suitable areas. While neither dispersal scenario is realistic, the two options characterise the extreme assumptions of dispersal with the truth probably lying somewhere in-between (Thuiller *et al*. 2008).

We illustrated the realised distribution of each population and generated presence/absence maps for current and future climates under the two contrasting dispersal scenarios. We used a conservative threshold of 0.05 for habitat suitability, below which the population was not allowed to be present, to generate a minimum number of presences for the populations with narrow niche breadths and temperature optima located at the extreme of the temperature gradient. The use of this threshold is based on several population viability studies on plant species where the extinction threshold is 0.05 or even lower (see e.g. Nantel *et al*. 1996). Simulations using a different, higher threshold of 0.3 rendered very similar patterns (see comparisons on Appendix S1 Table S2). For the sake of simplicity, we assumed the carrying capacity of each grid cell to be of one population. Several populations may have a fitness value (i.e. habitat suitability) above the 0.05 threshold in a given grid cell and may thus compete for its occupancy. We mimicked a probabilistic intraspecific competitive exclusion process, and drew the population occurring in each grid cell among the 45 possible subpopulations using a multinomial

law parameterised with the fitness of all the subpopulations potentially occurring in that grid cell. Because it is a stochastic process, we repeated the process 1000 times to generate 1000 population presence/absence maps and calculate relative effect sizes (i.e. population range sizes). Under the 'unlimited dispersal' scenario the future population presences/absences were not constrained, and any population was allowed to occupy a grid cell in the future, regardless of its presence in the focal grid cell under current climatic conditions. Under the 'no dispersal' scenario the future population presences/absences were contingent on their occupancy patterns under current climatic conditions, i.e. a population was only allowed to occupy a grid cell in the future if it already occupied the grid cell under current climatic conditions.

Results for simulations with unlimited dispersal

The five intraspecific scenarios led to quite different habitat suitability for the modelled populations (Fig. 2). In the first scenario, there was no population differentiation in plasticity (uniformly high) or niche breadth (filling the niche space) and, therefore, projections of habitat suitability were identical for all five populations (top row). Under climate change (2050 temperature), all populations went locally extinct in portions of the southern part of the range and migrate northward. The projected range size of all populations nonetheless decreased (Figs 3 and 4) as the species reached geographical and ecological limits.

When we simulated populations consisting of locally adapted genotypes with lower phenotypic plasticity (local adaptation, equal plasticity scenario), changes in habitat suitability by 2050 differed markedly among populations. The centrally located populations (green, yellow and orange) lost suitable habitats in the south and centre (yellow-red shades in Fig. 2) but gained suitable habitats in the north (dark blue shades in Fig. 2). The southernmost population (red) showed an increase in overall habitat suitability across the European continent, but only a portion of that area was classified as highly suitable habitat. Each population went locally extinct in parts of their current distribution, but each migrated northward and partially replaced the original resident populations (Fig. 3, second column; Fig. 4). Note that because all the populations had relatively narrow fundamental niches, the overlap between them in their projected future distribution was low (Fig. 3). While the northern and central populations (blue, green and yellow) considerably reduced their range (≈ 40%), the southern populations (red and orange) increased their range size under 2050 climate in this scenario (Figs 3 and 4).

The high-margin-plasticity scenario rendered a case where plasticity and fundamental niche breadth was maximum in the populations at the margins of the distribution. In this scenario, habitat suitability for the population at the warm margin (red population) expanded markedly (Fig. 2, middle row, last column) and as a result the population extended its range (Figs 3 and 4). In this scenario, the reduction in the ranges for the northern populations (blue and green) were largely due to geographical limits set by the sea, but at the species level these declines were compensated for by the expanded distribution of the red population (Fig. 4).

In the high-central-plasticity scenario, where plasticity is highest in the populations at the core of the species range, the central populations (green, yellow and orange) showed both reductions and increases in habitat suitability in different areas (Fig. 2, fourth row). The northern populations (blue and green) showed a marked contraction of range and considerable local extinction, while the orange population considerably expanded as it migrated northward, and therefore showed a large increase in range size (Fig. 4).

Finally, the high-leading-edge scenario modelled the CVH where population plasticity decreases from the cold to the warm margin of the species' distribution. Despite having the highest plasticity and broadest fundamental niche, suitable habitat declined for the northernmost populations (blue and particularly green), simply as a result of geographic limits set by the sea (Fig. 2). The southern populations, although less plastic, still retained a large area of suitable habitat. Consequently, the populations at the warm margin increased their range compared to the other populations (Figs 3 and 4, Appendix S1 Fig. S3).

Results for simulations with no dispersal

The simulation under the assumptions of no dispersal showed declines for all populations under all scenarios (Figs 3 and 4). Indeed, some populations went completely extinct in some scenarios (e.g. population at the warm margin in the high central plasticity and high leading edge plasticity scenarios). The key points worth noticing are the cases where range reduction was minimised due to plasticity: all populations in the no differentiation scenario, and the northernmost population (blue), which showed a smaller decrease in range size in the high margin plasticity and the high leading edge plasticity scenarios. Similarly, when plasticity was highest in the core populations, the central population (yellow) showed a smaller range decrease even without dispersal (Figs 2–4, Appendix S1 Fig. S3).

Species level patterns

All intraspecific scenarios led to similar contractions in overall range size of the hypothetical species (Fig. 5, inset) when the simulations allowed unlimited dispersal. In the models with no dispersal, range reductions were marked, but the reduction was mitigated at the species level when the simulated populations had equal, maximal plasticity and niche breadth (no differentiation scenario). When populations differed in plasticity, the high central plasticity scenario showed smaller reductions in range size (Fig. 5).

We assessed changes in the relative abundance of the five populations by calculating the Shannon diversity index for each scenario, with and without dispersal (Fig. 6). All intraspecific scenarios resulted in a reduction in the diversity index compared to the no differentiation scenario because of unequal shifts in population range sizes. When dispersal was not limited, the local adaptation scenario and the one characterising the CVH showed the lowest loss of diversity. The high central plasticity scenario showed the largest loss of diversity when there was both limited and unlimited dispersal,
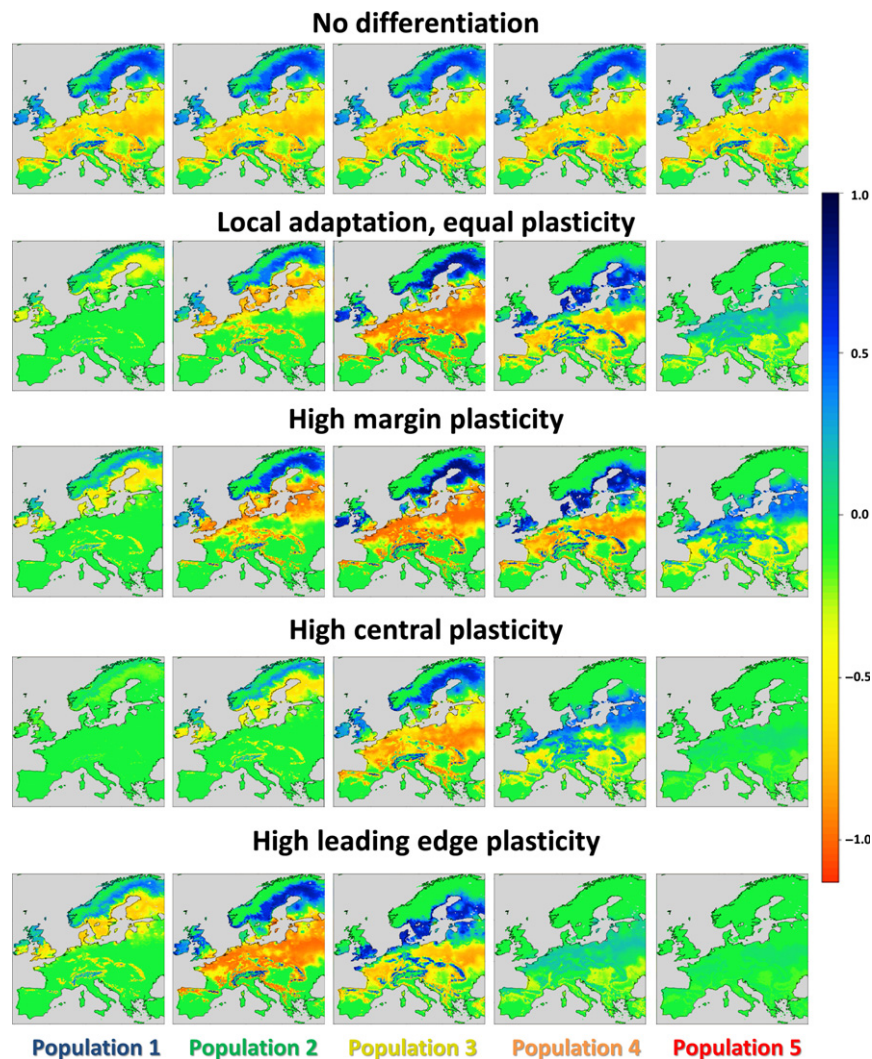
No differentiation

Local adaptation, equal plasticity

High margin plasticity

High central plasticity

High leading edge plasticity

Population 1   **Population 2**   **Population 3**   **Population 4**   **Population 5**

Figure 2 Simulations of differences in climatic suitability (future-current) for five populations of a virtual species occurring in Europe in five intraspecific scenarios differing in population responses to temperature according to Fig. 1. Each row corresponds to simulations for each intraspecific scenario; each column represents a population (group of subpopulations). The model used the maximum temperature of the warmest month projected for the year 2050 as a climatic variable (IPCC scenario A1, model Hadcm3). Reddish colours indicate areas of decreasing climatic suitability, bluish colours indicate increasing suitability. Note that green represents little or no difference in future vs current climatic suitability, which includes two opposing situations: the zone is not suitable for the population (and will remain unsuitable) and the zone is suitable (and will remain equally suitable). See Appendix S1 Fig. S3 for future and current climatic suitability maps.

due to increase in range and representation of the central population (yellow).

MODELLING POPULATION DIFFERENTIATION AND FUTURE DISTRIBUTION IN A REAL SPECIES FROM EXPERIMENTAL DATA

When applying the approach followed by the virtual species to a real one, the usual limitation of finding appropriate population- level data can be partially overcome by using provenance trials for forest tree species, where populations are intentionally translocated from their original site to plantations with different climate, typically established for screening of commercially important trees. These experiments offer a unique opportunity to calibrate ENMs with traits that are

likely to be plastic and/or that may determine fitness, like growth, phenology and survival (Matyas 1994).

We analysed the viability of our theoretical approach by parameterising an ENM for Iberian populations of *Pinus sylvestris*. This species, one of the most widely distributed of the Holarctic tree species, has been shown to be particularly sensitive to climate change (Benavides *et al.* 2013). *Pinus sylvestris* (Scots pine) reaches the Iberian Peninsula in the trailing edge of its distribution, with fragmented, genetically distinct populations that are largely limited to mountains (Reich & Oleksyn 2008; Benavides *et al.* 2013). Previous analyses of *P. sylvestris* provenances at the continental scale show that climate change will compromise growth of this species in the southern populations. Differences in mean annual temperature between the provenance origin and growth site was the most
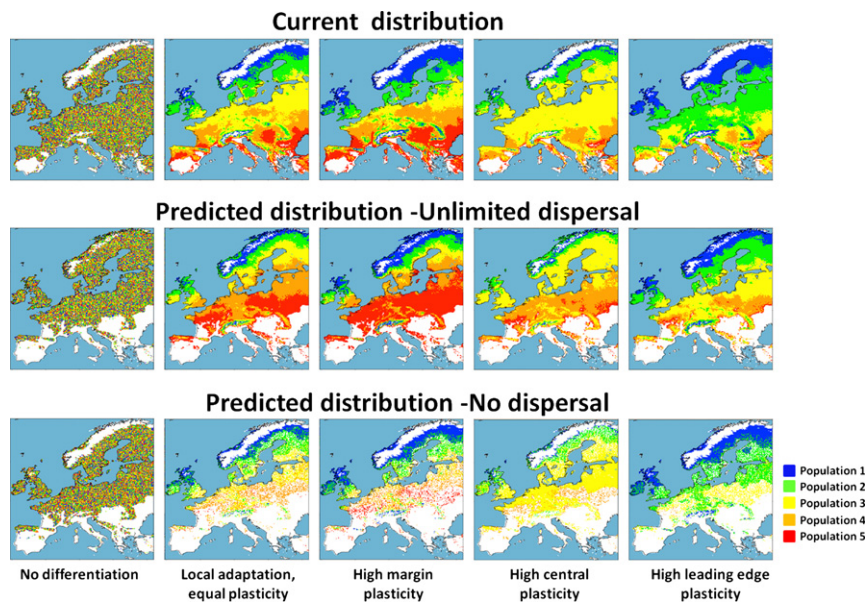
Current distribution

Predicted distribution -Unlimited dispersal

Predicted distribution -No dispersal

No differentiation | Local adaptation, equal plasticity | High margin plasticity | High central plasticity | High leading edge plasticity

Figure 3 Simulations of the distribution of a virtual species occurring in Europe with five intraspecific scenarios differing in population responses to temperature according to Figs 1 and 2. Top row: current distribution of each population in the different intraspecific scenarios. Middle row: Predicted distribution of each population in each of the five different intraspecific scenarios with unlimited dispersal. Bottom row: Predicted distribution of each population in the different intraspecific scenarios with no dispersal. Colours used for each population are those used in Fig. 1. Presence/absence data for each population was calculated using a fitness threshold of 0.05 for climatic suitability. In each grid cell, the figure presents the population that occurred the majority of the time across the 1000 replicates of the simulation process (see methods).
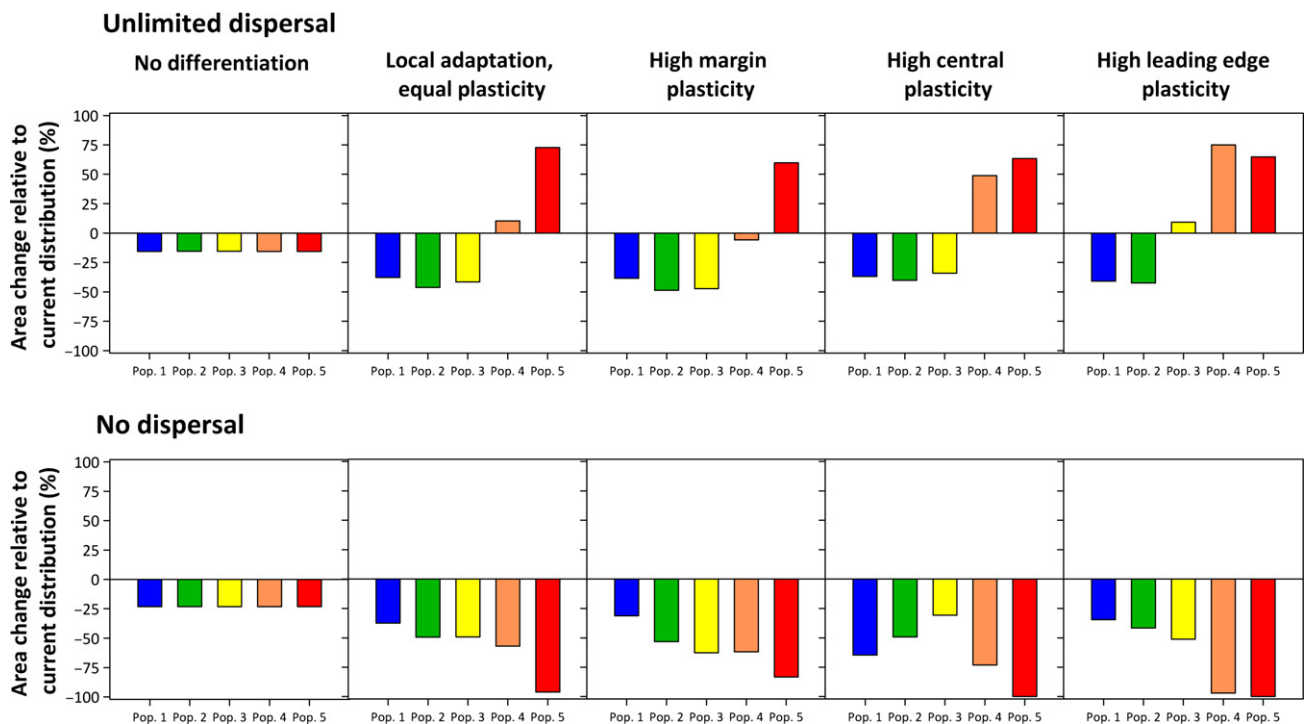

Figure 4 Change in distribution area of five populations of a virtual species occurring over Europe in each of the five intraspecific scenarios of Fig. 1, with unlimited dispersal (top) and no dispersal (bottom) for 2050 relative to current distribution.

important factor explaining this decrease in growth and survival (Reich & Oleksyn 2008). At the regional scale, analyses of Iberian tree species distributions show that tree mortality would increase as a consequence of climate warming, limiting *P. syl-*vestris distribution at the trailing edge (Benavides *et al.* 2013; Ruiz-Benito *et al.* 2013). Using provenance tests on growth and survival of *P. sylvestris* gathered by the Spanish network of genetic trials (GENFORED, http://www.genfored.es/), we
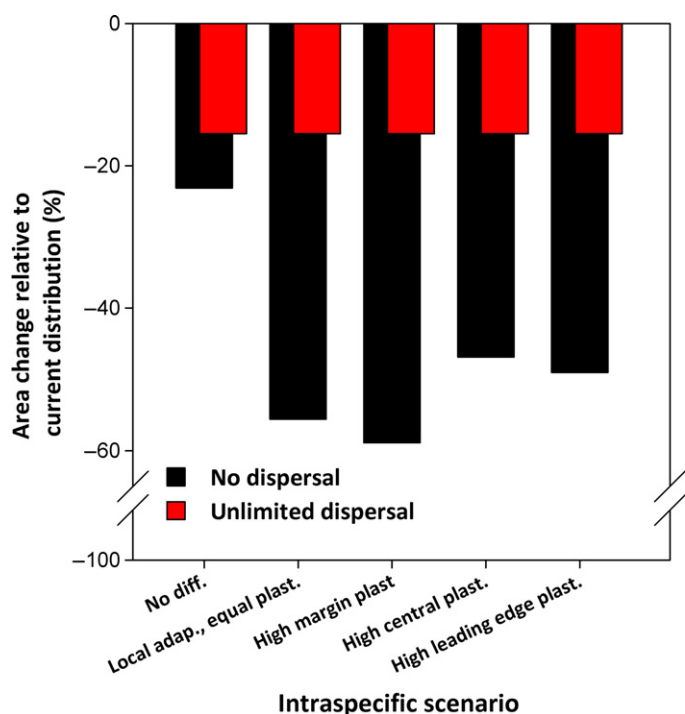
Figure 5 Overall future-to-present change in distribution area for a virtual species occurring over Europe in each of the five intraspecific scenarios of Fig. 1, with no dispersal and unlimited dispersal (inset).

examined how patterns of population differentiation for growth and survival in response to temperature affect potential range shifts in the trailing edge of the species distribution.

Setting up the model

Tree growth is an important fitness component that is determined by plastic traits like wood density, leaf physiology and morphology, which reflects trade-offs in tree life history (Jongejans *et al.* 2010). In GENFORED, *P. sylvestris* growth and survival were measured on 12 provenances grown at four sites (see Appendix S1 Table S3 and S4). In the plantation sites, species growth was measured as the differences in diameter at breast height (ΔDBH) between 2000 and 2005, and mortality as the percentage of trees that died for each provenance for the same period (see Appendix S1 Table S5). One ENM based on tree growth and mortality and climate was calibrated per provenance. This niche model is based on the climatic differences between the provenance and the plantation site, and the combination of growth and survival as determinants of habitat suitability (Benito-Garzón *et al.* 2013). The climatic differences were calculated for five variables that have already proven to determine Iberian tree species distributions (more details in Appendix S1). Prediction of the population suitability for 2050 was performed using the A1F1 HadCM3 scenario of the IPCC, as in the case of the virtual species.

The original growth and survival data was split into training and validation datasets to independently validate the models. The goodness of fit was measured by the generalisation power of the model on the validation dataset (R^2) and by the percentage of the variance explained by the algorithm (see Appendix S1). The model was calibrated with the training dataset using the machine learning technique random forest algorithm (Breiman 2001; see Appendix S1). The random effect of the block structure in average increase in ΔDBH was implemented by comparing a null model (ΔDBH ~ climate data) with a model including the block structure (ΔDBH ~ block, climate data) and comparing the performance of both. Including the random effect of the block structure of the provenance trials only produced a slight increase in the variance explained by the models (see Appendix S1 Table S5). Only when the predictive accuracy of a provenance model as well as the percentage of the variance explained (see Appendix S1 Table S5) was high enough ($R^2 > 0.5$ and % of the variance explained > 40%) did we use
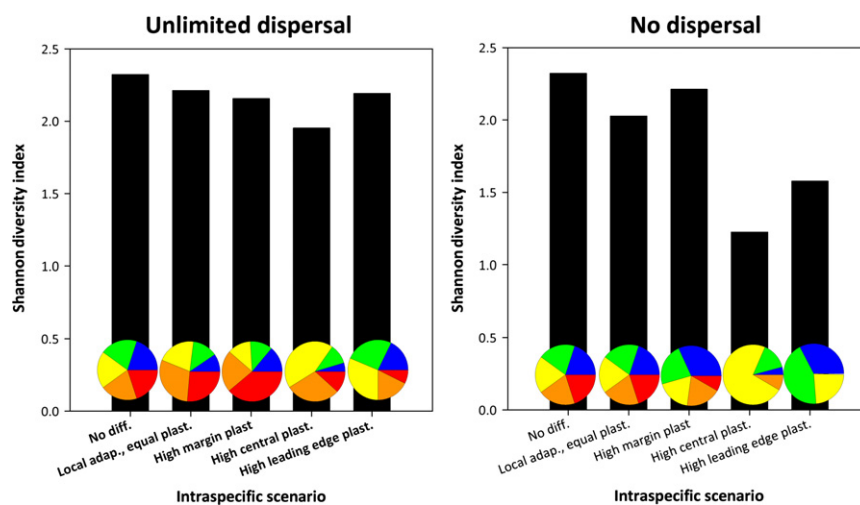

Figure 6 Shannon diversity index of a virtual species occurring over Europe differentiated in five populations. The index was calculated for each intraspecific scenario (see Fig. 1) accounting for the different proportions of the distribution area occupied by each population, which is illustrated with different colours in the pie charts at the bottom of each bar (colours for the populations follow the code of Fig. 1).

the given provenance for prediction purposes. Habitat suitability occurrence was calculated by maximisation of the True Skill Statistics of the combination of growth and survival maps comparing with the EUFORGEN data (Benito-Garzón *et al.* 2013; Appendix S1 Table S6).

Provenance ranges along the climate versus geographical prediction

Four provenances show high goodness-of-fit in terms of the generalisation power of the models and the percentage of the variance (see Appendix S1 Table S6): Castel de Cabrés, Gúdar, Navafría, and Valsaín. For these four provenances, we first examined variability in growth rate for each provenance as a function of the maximum temperature of the warmest month, which was the most important variable explaining the growth of three of the four provenances. The tolerance range measured in the four plantation sites showed differences for the maximum temperature range among the different provenances (Appendix S1 Fig. S4). In our model for a hypothetical species, we assumed that the trait plasticity to temperature determined the niche breadth for each population. However, this assumption is not fully applicable in our real species model because the niche breadth is determined by several climatic variables in addition to the maximum temperature of the warmest month (see Appendix S1 Table S5). Thus, the provenance with the largest range in maximum temperature did not always correspond to the largest habitat suitability occurrence in the ENM (Fig. 7). The maps generated represent how the climatic suitability would change in the future depending on the provenance used to calibrate the growth and survival models (Fig. 7). The climatic suitability was calculated for each of the four provenances independently, the assembly of all available provenances together to account for the average variability found on the four provenances as representative of the average species response and compared with a classical niche model based on presence/absence of the current distribution of the species in Spain for present climatic conditions and projections for the A1F1 HadCM3 scenario for 2050 (see Appendix S1 Figure S5).
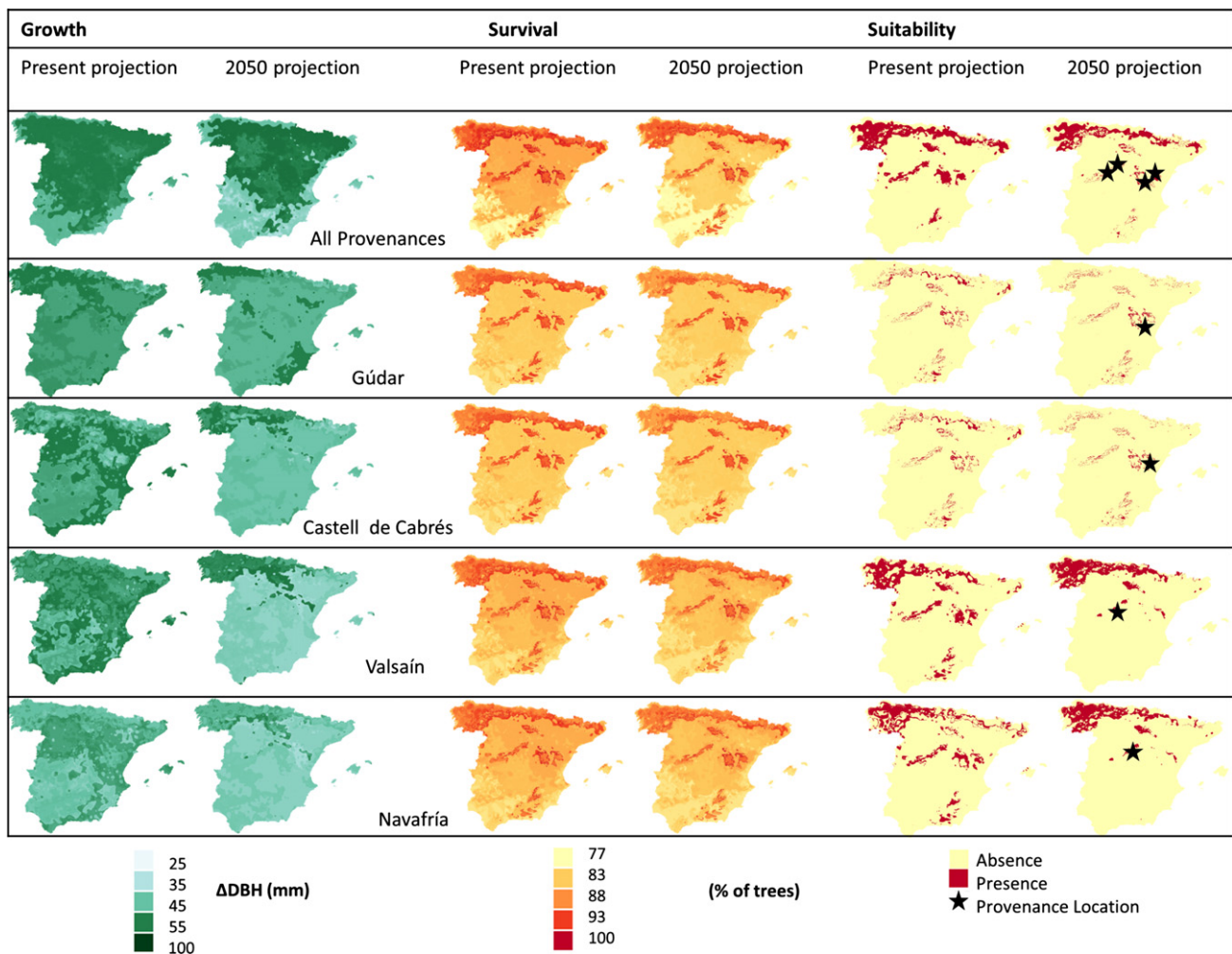

Figure 7 Prediction of growth, survival and occurrence of suitable habitat of *Pinus sylvestris* in Spain for present climate and for A1 HadCM3 scenario using four provenances varying in niche breadth and projection for all provenances together assuming differences in niche breadth among populations. Stars on right-hand panels indicate location of the provenances.

One of the provenances (Gúdar) expressed a wide thermal range with positive growth (taken as indicative of plasticity for growth in response to temperature; Fig S2, temperature part). However, this is not translated into wider habitat suitability occurrence for this provenance in the present (Fig. 7). As expected from our theoretical model, the differences in fitness between provenances due to plasticity are translated into differences in habitat suitability occurrence of the provenances in the present and in their future projections (Fig. 7). Our results suggest that a higher thermal range involving higher plasticity for growth-related traits can support survival of the Southern populations under future climate change projections. This outcome was not detected by the niche model when run for the species without accounting for among-population differentiation in growth responses to temperature (Figure S5 and Table S7). For Scots pine, we found that populations that can live in a wider range of maximum temperatures (Gúdar) are more likely to survive in the rear edge under global warming than provenances with smaller thermal range for positive growth (Navafría, Fig. 7). Generalisations cannot be made for the whole species range, and whether plasticity can contribute to the expansion of *Pinus sylvestris* in the leading edge (Northern European-Asian range) remains unexplored. What we already know is that the leading edge of this species is limited by temperature and photoperiod (Savolainen *et al*. 2011), and therefore climate warming would enhance species growth in the northern edge, provided the limitation by photoperiod is not too severe.

INCORPORATING PHENOTYPIC PLASTICITY INTO MODELS OF SPECIES DISTRIBUTION

Ecological niche models are increasingly used to estimate potential distributional ranges at varying spatial and temporal scales and they have several well-known strengths and limitations as discussed elsewhere (e.g., Araújo & Peterson 2012; Schwartz 2012). Here, we demonstrated how alternative scenarios of intraspecific variation of phenotypic plasticity and local adaptation affect forecasts of species distributional changes under climate change. Specifically, we show that forecasts of range reduction can vary significantly depending on the assumptions regarding phenotypic plasticity. Assuming no variation and uniformly high plasticity among populations across a given species results in a relatively low area loss calculated by the models. The simulations also demonstrated that peripheral populations can be important for the persistence of species under climate change. This can be seen, for example, comparing the high margin plasticity and high central plasticity scenarios for the simulations with the virtual species. As shown by Dullinger *et al*. (2004) for tree line shifts, dispersal had a significant impact on patterns of species distribution in a climate change scenario. In this regard, further modelling approaches may be enriched by incorporating the consequences of migration and gene flow on local plasticity patterns and overall adaptation to climate change (Sultan & Spencer 2002).

A major limitation introducing phenotypic plasticity into ENMs is the lack of plasticity data covering a significant fraction of the entire distribution of the species. The span of reaction norms may be either underestimated or overestimated if appropriate and complete climate data is not used for the design of experiments quantifying plasticity. This is particularly important when the section of the reaction norm that is missing has a major contribution to fitness. Another important limitation for including plasticity in assessing the consequences of climate change on species distributions is that valuable information sources such as those coming from laboratory experiments, reciprocal transplants, provenance tests and common garden experiments generally exist for a few selected species (Kawecki & Ebert 2004; Wang *et al*. 2010; Naya *et al*. 2012). Besides, it is not always easy to predict which traits will be most important for species persistence in the future (Kawecki & Ebert 2004; Hänninen 2006; Crispo *et al*. 2010). It is noteworthy that while plasticity can act as a quick buffer for climatic changes, it might also slow down or hamper evolutionary adaptation and might thus have negative consequences for species survival in the long term, so a dynamic component of ecological and evolutionary responses to these changes might render valuable insights. Finally, climate change, apart from affecting the phenotype of the target species, may influence its interaction with co-occurring species, and the interplay between the interacting species and the environment may ultimately determine the success of adaptation to the environmental shift (Valladares *et al*. 2007). Both *et al*. (2009) have shown that the degree of matching between consumers' phenology with that of predators and of their food resource may explain why some organisms do adjust their phenology to climate change, while others do not. Also, it has been demonstrated that herbivore damage in plants may modify their reaction norms to the abiotic environment (Gianoli *et al*. 2009).

If suitable data are not available, or cannot be collected for most species, finding global patterns of population differentiation in performance and plasticity across environmental gradients and geographic ranges and generalising them across phylogenies could contribute to filling the gap (Molina-Montenegro & Naya 2012). One of the best substantiated patterns of variation in plasticity across species is that occurring along latitudinal gradients, as described under the CVH (i.e. high leading edge plasticity scenario in our conceptual model). For the hypothetical species, higher plasticity in the northern populations was important for species persistence under no dispersal, while under unlimited dispersal it was the central and southern populations that showed an ability to maintain their ranges under climate change. It must be noted, however, that our hypothetical species was very widely distributed and it was limited to the north by geography. For more narrowly (or southerly) distributed species the patterns arising from the CVH could lead to increased ability to persist and shift range into new habitats. Incorporation of plasticity into distribution models highlights the relevance of migratory barriers at the leading edge to establish the realised range size (as opposed to the potential range size *sensu* Banta *et al*. 2012). Importantly, phenotypic plasticity is not fixed, so the same rationale applied to the spatial differentiation across populations applies to the temporal differentiation (evolution) of plasticity, which can be quite rapid (Nussey *et al*. 2007; Matesanz *et al*. 2010). It has been shown that plasticity has evolved in

response to anthropogenic factors, with significant interactions between taxon and trait type: while invertebrates exhibit evolution of increased plasticity for life-history traits and decreased plasticity for morphological traits, plants seem to show no clear trends in the direction of plasticity evolution (Crispo *et al.* 2010).

Including population differentiation within the representation of both the fundamental niche and plasticity resulted in more pessimistic predictions compared to business-as-usual, ecological niche forecasts of climate change effects on species distributions. This was found in the simulated future distribution of a virtual species exhibiting alternative patterns of population differentiation matching those observed in different plant and animal studies. This result has important implications: if current ENMs assume low or no plasticity, predictions may be exaggerated relative to a situation where plasticity and niche breadth vary across the species. If, however, ENMs assume uniformly high plasticity then the result of the current work indicates that impacts of warming on species distributions may be underestimated.

We note that a seemingly different result was obtained in the simulated distribution of a real tree species showing population differentiations in the range of temperatures for survival and growth. In our real species simulations we did find the pattern of less pessimistic forecasts when population differentiation is accounted for, which was an expected possibility (e.g., Pearman *et al.* 2010; Oney *et al.* 2013). Pearman *et al.* (2010) ran species distribution models both with and without considering subtaxa for ten animal species and they found larger projected future distributions when intraspecific variation (i.e. subtaxa) was considered for seven of them. Oney *et al.* (2013) found similar results when they considered intraspecific variation in *Pinus contorta*. The latter two studies seem to contradict the results of our conceptual model. These apparent discrepancies are due at least in part to the fact that we used fundamental niches for our species and that in all scenarios the fundamental niche of the species remained the same, while Pearman *et al.* (2010) and Oney *et al.* (2013) worked with realised niches estimated from the current distributions. When relating the current distributions to environmental variables, a model that does not consider intraspecific variation may smooth across fitness-environment curves of the individual subtaxa (populations), and, consequently, may not capture the intraspecific niche diversity very well. Atkins & Travis (2010) showed in a simulation model that when there is local adaptation (and restricted dispersal), a species may fail to survive a period of climate change, even when there is an overlap between its range prior to climate change and the area where climate is predicted to be suitable following climate change. This agrees well with our conceptual model.

Our real species simulation was focused on a number of southern provenances of a widespread species. The southern populations in our virtual species also benefitted from plasticity. Thus, differences between our virtual species simulation and our study case are likely to result from three factors: first, in our uniform population simulation the virtual species exhibited high plasticity across its entire range, second, northern populations of our virtual species were geographically constrained, and, finally, if we compare only the southernmost

virtual populations we support the prediction of plasticity buffering climate change effects. We would argue that it is more realistic for modeling scenarios to incorporate variation in plasticity in at least some parts of the species distribution. Thus, while population differentiation can buffer against impact of climate change as indicated by our study case, by previous studies, and by results for the southern populations of our virtual species, forecasts may still be more pessimistic than current ENMs if the reference for comparison involves uniformly high levels of plasticity.

Previous analyses of uncertainties in ENMs have resulted in a bias towards overestimating extirpation vulnerability driven by climate change (Schwartz 2012; see also Araújo *et al.* 2013), but these models could be still underestimating the actual area loss by assuming no variation among populations. Available study cases do not show a coherent pattern of population differentiation on performance and plasticity across wide environmental or geographic gradients. On the contrary, dissimilar fitness and plasticity trends across populations were found for different species. This is problematic because the forecast for species distribution with models assuming intraspecific uniformity and parameterised based on one or a few populations could render contrasting results depending on which scenario fits better the actual population differentiation. For example, taking the entire species into consideration, the fitness and plasticity of the central population will render forecasts that are too optimistic when the species fit the high central plasticity scenario, while the reverse is true if we use for the model the same values of the central population but the species fits the high margin plasticity scenario.

Collectively, our results indicate that beside the challenges in the theoretical and methodological domains, one of the main difficulties for improving forecasts of species distributions under future climate change scenarios falls in the empirical domain. More observational and experimental studies on local adaptation and plasticity of contrasting species are still needed, and the important genetic and phenotypic variation within populations requires urgent attention. To meet the challenge of improving forecasts of species distribution on a warming climate, we suggest one way forward: empiricists, theoreticians and modellers have to work in a more concerted way accounting for intraspecific genetic and phenotypic variation.

AUTHORSHIP

All authors collected references and key data and contributed to the development of the conceptual model, FV and SM wrote the first draft of the manuscript and all authors contributed substantially to revisions, MBA and FG performed modeling of the virtual species, MBG and MAZ carried out the simulations for *Pinus sylvestris* with provenance data.

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