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Species' intrinsic traits inform their range limitations and vulnerability under environmental change

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ABSTRACT

Aim Understanding the factors that govern species' geographical ranges is of utmost importance for predicting potential range shifts triggered by environmental change. Species ranges are partially limited by their tolerances to extrinsic environmental conditions such as climate and habitat. However, they are also determined by the capacity of species to disperse, establish new populations and proliferate, which are in turn dependent on species intrinsic life-history traits. So far, the contribution of intrinsic factors driving species distributions has been inconclusive, largely because intrinsic and extrinsic factors have not been examined simultaneously in a satisfactory way. We investigate how geographical ranges of plants are determined by both extrinsic environmental factors and species intrinsic life-history traits.

Location Europe.

Methods We compiled a database on plant geographical ranges, environmental tolerances and life-history traits that constitutes the largest dataset analysed to date (1276 species). We used generalized linear modelling to test if range size and range filling (the proportion of climatically suitable area a species occupies) are affected by dispersal distance, habitat breadth and 10 life-history traits related to establishment and proliferation.

Results The species characteristics that were most linked to range limitations of European plant species were dispersal potential, seed bank persistence and habitat breadth (which together explained ≥ 30% of deviance in range filling and range size). Specific leaf area, which has been linked to establishment ability, made a smaller contribution to native range limitations.

Main conclusions Our results can be used to improve estimates of extinction vulnerability under climate change. Species with high dispersal capacity, that can maintain viable seed banks for several years and that can live in an intermediate number of habitats have the fewest non-climatic limitations on their ranges, and are most likely to shift their geographical ranges under climate change. We suggest that climate-change risk assessments should not focus exclusively on dispersal capacity.

Keywords
Climate change, dispersal, European plants, range filling, range shift, range size, seed bank persistence, specialist/generalist.

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INTRODUCTION

Understanding which factors determine species current geographical ranges is crucial for explaining biogeographical patterns and predicting future changes in the distribution of biodiversity under climate change. Species ranges are determined by their capacity to disperse, establish new populations and proliferate, which in turn are likely to be dependent on the intrinsic factors of species such as life-history traits (e.g. Lavergne *et al.*, 2004; Van der Veken *et al.*, 2007). Species ranges are also determined by their environmental tolerances, for example the range of climatic conditions and the diversity of vegetation types ('habitats') they exploit (e.g. Thompson *et al.*, 1999; Williams *et al.*, 2007). There is growing interest in the use of species life-history traits to predict the capacity of species to shift their ranges in response to climate change, and thus estimate species vulnerability (Foden *et al.*, 2013; Triviño *et al.*, 2013; Garcia *et al.*, 2014; Pearson *et al.*, 2014). However, there is little empirical evidence that the traits employed play a strong and general role in determining the capacity of species to shift their ranges.

It is widely assumed that dispersal plays a key role in determining species ranges, and thus their range-shift capacity (Bateman *et al.*, 2013), but different studies reach conflicting conclusions (Lester *et al.*, 2007; Normand *et al.*, 2011). For instance, Van der Veken *et al.* (2007) supported the effects of dispersal on range size of forest plant species, Normand *et al.* (2011) showed that both climate and dispersal played key roles in determining species ranges of European plants and Nogués-Bravo *et al.* (2014) detected that the degree of range filling of tree species was influenced by species dispersal. However, other authors have found that dispersal is not a key trait in determining the ranges of herbaceous species (Thompson *et al.*, 1999) or angiosperms (Gove *et al.*, 2009). Apart from the dissimilar study systems analysed, there are several possible reasons for these contradictory results. First, different studies use different metrics for dispersal potential, such as dispersal modes, seed terminal velocity or seed size (Thompson *et al.*, 1999; Van der Veken *et al.*, 2007; Gove *et al.*, 2009; Nogués-Bravo *et al.*, 2014). These proxies can yield different conclusions, and have been argued to be poorly representative of real long-term dispersal ability (Lester *et al.*, 2007; Poschlod *et al.*, 2013). Second, environmental tolerances (e.g. for climate or vegetation) that affect species ranges, might confound the relationship between dispersal and geographical ranges (Thompson *et al.*, 1999; Lester *et al.*, 2007), so they must be analysed jointly. Third, in addition to dispersal, species geographical ranges are likely to be affected by the ability of species to establish new populations and proliferate. However, traits that affect establishment and proliferation have not been studied in concert with dispersal in a comprehensive analysis.

Traits that influence establishment and proliferation might be related to resource acquisition or competitiveness, such as specific leaf area (SLA) or plant height (Hamilton *et al.*, 2005). Establishment and proliferation can be also aided by traits that help species to cope with adverse environmental conditions, for example seed bank persistence (Van der Veken *et al.*, 2007), or reproductive strategies that allow rapid recolonization following disturbance, for example the capacity to self-fertilize or to have clonal growth (Bellingham & Sparrow, 2000; Angert *et al.*, 2011).

Here we simultaneously investigate the importance of life-history traits, climatic tolerances and the breadth of habitat a species can occupy for the current geographical ranges of plant species in Europe. We evaluate both species range size and 'range filling' (i.e. the proportion of the climatically suitable geographical area that a species occupies; Svenning & Skov, 2004). In Europe, ranges are largely determined by the degree to which species have been able to expand post-glaciation. Therefore, the life-history traits and habitat breadth that correlate with range size represent the traits that have facilitated post-glacial expansion. On the other hand, range filling is the degree to which species occupy the area that is climatically suitable for them. Consequently, the traits that correlate with range filling indicate the degree to which life-history traits and habitat breadth have acted over and above the limitations of species climatic tolerances (Svenning & Skov, 2004; Dullinger *et al.*, 2012a). The degree of historical range expansion is one of the few indicators as to whether species will be able to shift their ranges under 21st-century climate change (Svenning & Skov, 2007). Therefore, by analysing life-history traits and environmental tolerances simultaneously for a large and taxonomically representative group of plants we can improve our understanding of which life-history traits might allow species to shift their ranges under climate change. In particular, our analyses question whether biodiversity risk assessments under climate change (which predominantly assume that dispersal is the main determinant of the feasibility of climate-induced range shifts; Bateman *et al.*, 2013) should consider other elements of the range-shifting process. Finally, we use a classification scheme for dispersal potential that is based on more complete life-history data than previous proxies but is simple enough to be widely applied. We evaluate whether this scheme captures enough information on dispersal potential to be appropriate for evaluating the role of dispersal in climate-driven range shifts for a wide range of plant species.

METHODS

We used presence data of native European plant species that have been mapped by the Atlas Florae Europaeae (AFE) (Jalas & Suominen, 1972–1994; Jalas *et al.*, 1996), from pteridophytes to the family Brassicaceae. Presence data were on 50 km × 50 km Universal Transverse Mercator grid cells. The study area comprises Europe from −10°9′23″ to 30°43′0″ E and from 34°59′30″ to 70°58′33″ N (see Figure S1 in Appendix S2 in the Supporting Information). Species with fewer presences than 20 grid cells were discarded from analyses to reduce errors associated with extremely narrow-ranged species, for which distribution data are unlikely to reflect climate tolerances (Early & Sax, 2014). The final dataset contained 1276 plant species.

Geographical ranges

Range size was calculated as the number of 50 km × 50 km cells occupied by each species. We estimated range filling as the proportion of the climatically suitable area, i.e. the potential range, that it is occupied (Svenning & Skov, 2004). We first conducted a principal components analysis (PCA) for the following climate variables using all grid-cells in Europe: temperature of the coldest and the warmest months and annual precipitation. These three variables have been shown to perform better in multi-species biogeographical analyses than a larger number of variables, which 'overfit' to species distributions, causing underestimation of a species' climatic tolerance (Early & Sax, 2014). We used the first two axes of this PCA to construct a two-dimensional climate space, on to which we plotted each species' distribution, and calculated the minimum convex hull polygon that included all of the species' occurrences. The grid cells with climatic conditions that fell inside this polygon were considered the potential range, and range filling was the proportion of these grid cells that were occupied ('range filling100') (see Figure S2 in Appendix S2 for a schematic representation). Species occurrences in relatively extreme climatic conditions that are not representative of species environmental tolerances would increase potential species ranges and possibly bias our results. To test for any such effect we also calculated potential range using the minimum convex hull polygon that encloses the 95% most environmentally central species occurrences ('range filling95'). Climatic variables were derived from the climatic research unit (CRU) dataset at 10′ resolution (New *et al.*, 2002) and 10′ climate variables were averaged inside each 50 km × 50 km grid cell.

This approach, in which species distributions are plotted in the available climate space (i.e. Europe), is the most unbiased way to compare climatic tolerances between species with different range sizes (Broennimann *et al.*, 2012). We chose not to utilize presence–absence/background species distribution modelling due to the large effects of modelling technique and possible false absences on results, which are especially apparent when modelling species across a broad range of geographical range sizes (Garcia *et al.*, 2012).

Species traits

We asked whether 12 species traits related to dispersal, habitat breadth, establishment and proliferation (Table 1) were related to range size or range filling of European plant species. The rationale for each trait is given below, and further information on how each trait was measured and categorized can be found in Appendix S1. Data for these traits were obtained from the databases and studies recorded in Appendix S1.

1. *Dispersal distance*: we classified dispersal distance following Vittoz & Engler (2007). A dispersal distance category was assigned to each plant species according to its dispersal modes (e.g. zoochory, anemochory), dispersal vectors and other life-history traits that influence the efficiency of dispersal, for

Table 1 Results of univariate models for range size and range filling.

	No. of species	Range size	Range filling100	Range filling95
Dispersal distance	618	+*** (11.8)	+*** (11.6)	+*** (12.6)
Dispersal distance^2	618	n.s.	n.s.	n.s.
Seed bank persistence	311	x*** (14.2)	x*** (20.2)	x*** (21.0)
Habitat breadth	551	+*** (4.34)	+*** (4.46)	+*** (3.65)
Habitat breadth^2	551	∩*** (7.27)	∩*** (7.98)	∩*** (7.08)
Vegetative regeneration	217	x** (3.97)	x*** (5.88)	x*** (6.89)
Specific leaf area	398	+* (0.92)	n.s. $P = 0.162$	n.s. $P = 0.089$
Specific leaf area^2	398	∩*** (4.02)	∩** (3.43)	∩** (3.94)
Age of first flowering	537	+* (0.801)	+* (1.08)	+* (0.996)
Age of first flowering^2	537	n.s.	n.s.	n.s.
Plant height	597	+* (0.68)	+** (1.54)	+** (1.46)
Plant height^2	597	n.s.	n.s.	n.s.
Flower pollinator	473	n.s.	n.s.	n.s.
Capacity to self-fertilize	490	n.s.	n.s.	n.s.
Reproductive frequency	1085	n.s.	n.s.	n.s.
Resprouting after fire	100	n.s.	n.s.	n.s.
Seed mass	559	n.s.	n.s.	n.s.
Seed mass^2	559	n.s.	n.s.	n.s.

Range filling100 and Range filling95 are the proportions of a species' potential range (calculated based on the climatic conditions occupied by 100% and 95% of species' occurrences, respectively) that are occupied. +, positive relationship; x, categorical variable; ∩, concave downward relationship of the quadratic term. The percentage of deviance explained by the model is in parentheses. A variable followed by a superscript 2 indicates the quadratic term. Rows shaded grey are the traits with $P < 0.25$ that were subsequently considered in the three-variable models. Units can be found in Appendix S1. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s. $P > 0.25$.

example plant height, growth form or the existence of seed appendages (e.g. plumes or wings).

2. *Habitat breadth*: we compiled the general habitat (e.g. 'woodland') and primary subhabitat categories (e.g. 'coniferous' or 'broadleaved' woodland) within which each plant is associated according to EUNIS (http://eunis.eea.europa.eu/habitats.jsp), a classification scheme designed to be applied in a standard way across Europe. We then calculated a habitat breadth index (see Appendix S1).

3. *Seed bank persistence*: this is a categorical trait which represents the period for which seeds persist in a viable state in the soil, and which corresponds to a species' ability to withstand disturbance (Van der Veken *et al.*, 2007).

4. *Capacity to self-fertilize*: this trait is related to establishment probability or ecological generalization (Angert *et al.*, 2011).

5. *Flower pollinator*: we established two categories – external pollination (insects or wind/water) and self-pollination. The capacity to self-pollinate could improve a species' ability to establish a new population or persist in a small population as it is not dependent on external pollinators (Baker, 1955).

6. *Age of first flowering*: a species with lower age at maturity might be expected to proliferate rapidly (Dullinger *et al.*, 2012b).

7. *Reproductive frequency*: reproductive frequency during a plant's lifetime influences its position along the successional spectrum and responses to environmental disturbances (Boulangeat *et al.*, 2012b).

8. *Resprouting after fire* and 9. *Vegetative regeneration*: these two traits are related to plant colonization following disturbance (Bellingham & Sparrow, 2000; Boulangeat *et al.*, 2012b).

10. *Specific leaf area (SLA)*: species with higher SLA take up nitrogen easily and have a high relative growth rate (Hamilton *et al.*, 2005). SLA is thus used as a surrogate for resource acquisition potential that appears to facilitate establishment in invasive species (Hamilton *et al.*, 2005).

11. *Seed mass*: small-seeded species produce more seeds and the chance that one seed might reach a suitable new site is higher, thus increasing naturalization success (Hamilton *et al.*, 2005). This effect is accounted for in the dispersal classification scheme, but large seeds might also help establishment due to more storage tissue, which allows the seedling to be independent from external resources for a period of time (Jensen & Gutekunst, 2003).

12. *Plant height*: this corresponds to competitive ability, improves naturalization success (Bucharova & Van Kleunen, 2009) and corresponds positively to native distribution size (Lavergne *et al.*, 2004).

Modelling method

We performed generalized linear modelling with range filling and range size as response variables. As both variables showed over-dispersion, we fitted range filling with a quasi-binomial distribution and range size with a negative binomial distribution using the R package 'MASS' (Venables & Ripley, 2002). Data on each trait were not available for all species (Table 1). Therefore, we first performed univariate models for each life-history trait,

testing for linear and unimodal responses. Two variables accounted for more than 10% of explained deviance in the univariate models (dispersal distance and seed bank persistence; see Results). Thus, our second step was to assess whether other variables made important additions to these two variables, and whether the importance of the two variables was maintained when included in models with other variables. We constructed 'three-variable models', in which we entered dispersal distance, seed bank persistence and one of the explanatory variables for which $P < 0.25$ in the univariate models (Hosmer & Lemeshow, 2000). For each three-variable model we performed an information-theoretic approach to obtain values of relative variable importance (RVI) (Burnham & Anderson, 2002). Six variables had RVI > 0.5 in the three-variable models (see Results). Therefore we constructed a combined multivariate model using these six variables. We tested all possible combinations of the six independent variables with the function *dredge* (library *MuMIn*; Bartón, 2012), removing those models that included the quadratic term of a variable but not the linear term of the same variable. A best model subset was identified using $\Delta AICc < 2$ (for range size) (AICc is the Akaike information criterion corrected for small sample sizes) and $\Delta QAICc < 2$ (for range filling) (QAICc is a version of AICc for overdispersed count data where quasi-likelihood adjustments are required). We calculated the RVI of each of the six final variables by summing the Akaike weights over all models in which the variable was present. Finally, we calculated an averaged model using the best model subset (Burnham & Anderson, 2002). We checked Spearman's correlations and multicollinearity (with the variance inflation factor, VIF) between all variables entered into multivariate models.

The combined models (above) were calculated for a subset of species that had information for all six traits retained in the three-variable models ($n = 102$, see Results). To be certain that results for this subset were consistent with results for all species, we performed univariate models using this subset of 102 species, and asked whether the percentage of the deviance explained by each of the final six variables was consistent with the univariate models that were made for a much larger number of species. We also performed models made with two, three, four or five variables in this subset, to evaluate the deviance explained by each additional variable. Statistical analyses were performed in R 3.0.3 (R Core Team, 2014).

Phylogenetic analyses

Because species are phylogenetically related, phylogenetic relationships can result in over-estimation of the degrees of freedom in biogeographical analyses. Therefore, we compared Moran's *I* phylogenetic correlograms for the response variables and the residuals of the combined models (77 species for which data on both phylogeny and predictor variables were complete) including the six predictors selected after the procedure described above (Legendre & Fortin, 1989). This approach determines whether phylogenetic autocorrelation in a response variable has been captured by model predictors. We also compared the significance of model coefficients of the combined models from

generalized linear models and from phylogenetic generalized least squares (PGLS; Freckleton *et al.*, 2002). Details on the sources of the phylogeny and how we estimated branch lengths are given in Appendix S3. Phylogenetic analyses were performed in R using the packages 'ape' (Paradis *et al.*, 2004) and 'caper' (Orme *et al.*, 2012).

RESULTS

Dispersal distance and seed bank persistence were the most significant explanatory variables in the univariate models, each explaining more than 10% of the deviance (Table 1). Other significant variables were habitat breadth, vegetative regeneration, SLA, age of first flowering and plant height. For habitat breadth and SLA, quadratic terms were significant. We entered dispersal distance and seed bank persistence into all three-variable models, and both were always retained with RVI = 1 (Table S1 in Appendix S2). Other variables retained (with RVI > 0.5) were habitat breadth (including the quadratic term), age of first flowering, plant height and SLA (only the linear term in range size and range filling95). Results of the best model subsets and relative importance of the variables averaged across all three-variable models are in Table S1 in Appendix S2.

For the combined models (102 species, six variables tested) dispersal distance, seed bank persistence and habitat breadth were retained in all of the models in the best model subset (RVI = 1, Table 2 & Table S2 in Appendix S2). The RVI of SLA, age of first flowering and plant height was between 0.85 and 0.87, 0.23 and 0.26, and 0.24 and 0.33, respectively, depending on the response variable. Seed bank persistence, habitat breadth and dispersal distance (which we denote 'primary variables') explained the most deviance in geographical ranges for the 102 species used in the combined models (Table S3 in Appendix S2).

A model using these three primary variables explained 29% of the deviance in range size, 35% in range filling100 and 34% in range filling95 (in the combined models for 102 species; Table S3 in Appendix S2). The inclusion of SLA, plant height and age of first flowering added 0.8–4.4% to the deviance explained (Table 2 & Table S3 in Appendix S2). These results are consistent with results obtained with all species for which we had information on individual traits (Table 1). Correlation and multicollinearity between explanatory variables entered into multivariate models was low: the maximum absolute value of Rho was ≤ 0.403 (see Table S4 in Appendix S2 for all correlations) and the maximum VIF value was 2.33.

Species with the greatest range filling and largest range size are those with high dispersal potential, with a long-term seed bank and with an intermediate habitat breadth (Fig. 1). The shape of the relationship between range filling100 and each primary explanatory variable, in the context of the other primary variables, is shown in Fig. 2. The quadratic shape of habitat breadth in Fig. 2(c) is maintained even when the two extreme habitat generalist species are removed.

Modelling results were not affected by phylogenetic relatedness among species. The significant phylogenetic autocorrelation in the response variables was absorbed by the six variables included in the combined models, as shown by the phylogenetic autocorrelation in the residuals with non-significant Moran's *I*-values at the first distance class ($I_{range} = 0.126$, $P \le 0.615$; $I_{rfilling100} = 0.102$, $P \le 0.62$; $I_{rfilling95} = 0.261$, $P \le 0.321$) (Fig. S1 in Appendix S3). Finally, comparisons between generalized linear models and PGLS models showed similar *P*-values of model coefficients, and including a phylogenetic correlation structure in the combined models did not change the relative importance or the significance of the predictor variables in any of the models (Table S1 in Appendix S3).

Table 2 Combined models (102 species).

	Range size			Range filling100			Range filling95		
	β	SE	RVI	β	SE	RVI	β	SE	RVI
Intercept	5.14	0.36		−2.25	0.04		−2.48	0.20	
Dispersal distance	0.00007	0.00002	1	0.000104	0.000003	1	0.000112	0.000004	1
Seed bank persistence (short-term persistent)	−0.043	0.125	1	−0.257	0.026	1	−0.296	0.031	1
Seed bank persistence (long-term persistent)	0.324	0.1	1	0.496	0.029	1	0.457	0.033	1
Habitat breadth	1.17	0.30	1	1.89	0.06	1	1.94	0.07	1
Habitat breadth²	−0.236	0.067	1	−0.383	0.029	1	−0.396	0.014	1
Specific leaf area	0.010	0.004	0.87	–	–	–	0.015	0.002	0.85
Plant height	0.006	0.004	0.31	0.0063	0.0005	0.24	0.011	0.001	0.32
Age of first flowering	0.009	0.007	0.25	0.0105	0.0005	0.26	0.015	0.001	0.23
Percentage of deviance explained	33.8			35.8			38.2		

For each set of variables, results are averaged across the best model subset (i.e. models where ΔAICc < 2 for range size, ΔQAICc < 2 for range filling). Range filling100 and Range filling95 are the proportions of a species' potential range (calculated based on the climatic conditions occupied by 100% and 95% of species' occurrences, respectively) that are occupied. β, model-averaged coefficients; SE, standard errors across best model subset; RVI, relative variable importance. Units of variables are detailed in Appendix S1. Specific leaf area is not included in range filling100 because it did not pass the threshold of RVI > 0.5 in the three-variable models (see Methods and Table S1 in Appendix S2).
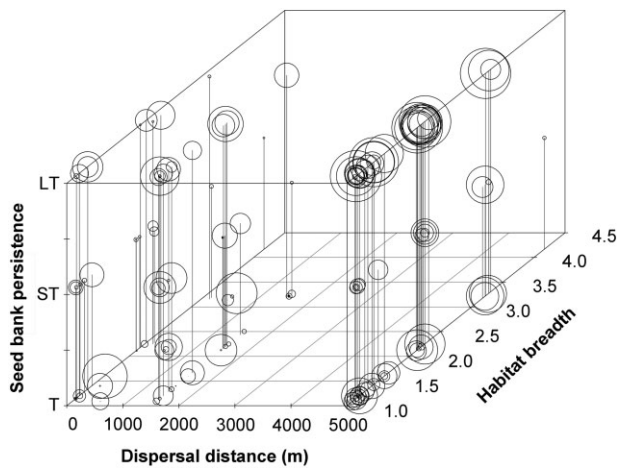
Figure 1 Scatter plot of the three primary variables (dispersal distance, habitat breadth and seed bank persistence). The size of the circles corresponds to range filling100, i.e. larger circles indicate higher range filling. Range filling100 is the proportion of a species' potential range (calculated based on the climatic conditions occupied by 100% of species occurrences) that is occupied. Categories of seed bank persistence are: T, transient seed bank; ST, short-term persistent seed bank; LT, long-term persistent seed bank. Species with the greatest range filling are those with high dispersal potential, with a long-term seed bank and with an intermediate habitat breadth.

DISCUSSION

We asked how geographical ranges are determined by species intrinsic life-history traits and environmental tolerances. Of the tested factors, the most important for explaining range size and range filling of native European plants were dispersal potential, seed bank persistence and habitat breadth. Results were consistent across the subsets of species analysed and across analytical methods (Tables 1 & 2). These three 'primary' traits together explained more than 30% of the deviance in range filling and 29% in range size (Table S3 in Appendix S2), a high value in comparison with other macroecological studies of life history and geographical ranges (Van der Veken *et al.*, 2007; Laube *et al.*, 2013). Both the consistency of the primary traits and the percentage of deviance explained are probably due to: (1) the large number of species for which we gathered information (Table 1), which is unusual in studies relating current ranges or range shifts with life-history traits (Van der Veken *et al.*, 2007; Angert *et al.*, 2011); (2) the inclusion of a variety of life-history traits along with dispersal; (3) the use of a composite metric of dispersal distance rather than a simpler proxy (Lester *et al.*, 2007) (see Appendix S1); and (4) the use of range filling as a response variable that allows us to quantify the factors other than climate that limit species distributions. The explanatory variables for both range filling and range size were similar, demonstrating that for plants the same traits underlie both the likelihood of being widespread and of being frequent within the geographical distribution. Our approach does not consider intraspecific plasticity or variation of traits, which can

be substantial (e.g. Kostikova *et al.*, 2013). However, this information is not publicly available for many species, so it would not be possible to develop a comprehensive analysis on the effect of intraspecific variation on range filling for plant species. Growth form does not appear to play a role in range filling. Shrubs and trees (which constitute *c.* 30% of our study species in the combined models) are not concentrated in a specific class of dispersal or habitat breadth, nor do they perform differently for range filling than other herbaceous species (Fig. S3 in Appendix S2).

Species current occupied ranges are much lower than their potential ranges (on average species occupied just 25% of their climatically suitable range). In Europe this is probably due to limitations on post-glacial dispersal, and our results corroborate those of other studies suggesting that dispersal potential substantially limits range expansion, even over thousands of years (Svenning & Skov, 2004, 2007; Lester *et al.*, 2007; Normand *et al.*, 2011; Dullinger *et al.*, 2012a). In our dispersal classification, the longest distance dispersal category is due to human dispersal (5 km; Vittoz & Engler, 2007). Although dispersal by humans is a highly stochastic process, it appears to have played an important role in the distribution of European plant species (Clark *et al.*, 1998). However, when considering species ability to range-shift under climate change we recommend that human dispersal is not included, because the effect of human transport on species future distributions is unlikely to be the same as the effect since the Last Glacial Maximum. Both the potential for long-distance transport by humans and the restrictions on introduction of regionally non-native species are greater now than during the last 10,000 years. Additionally, most range-shift studies aim to assess a species' intrinsic capacity to cope with climate change without the help of human dispersal.

In addition to dispersal, we hypothesized that species ranges are determined by their ability to establish and proliferate in new areas. Indeed, the length of time for which seeds are maintained in a viable state in the soil was even more important than dispersal in our analyses. No correlation between seed bank persistence and range filling or range size, at a continental scale, has previously been demonstrated. However, seed bank persistence has previously been shown to be important for species distributions at small scales (e.g. within fields; Poschlod *et al.*, 2013), and in one case a 'cautious' link between seed bank persistence and range extent has been made at a multinational scale (Van der Veken *et al.*, 2007). Our results suggest that seed bank persistence has been crucial to the range expansion of species from glacial refugia and/or has helped species to persist in refugia across a broad geographical region during glaciations. One likely mechanism for this effect is that persistent seed banks allow populations to survive in seasonally or occasionally disturbed habitats (Poschlod *et al.*, 2013) or during short periods of unsuitable environmental conditions. Thus, a persistent soil seed bank may act as a reservoir for recolonization after disturbance. Persistence under unsuitable conditions can help species shift their ranges under fluctuating climate change (Early & Sax, 2011). It is concerning that climate change may itself reduce

Figure 2 Regression lines for the effects of dispersal distance, habitat breadth and seed bank persistence on range filling100. Range filling100 is the proportion of a species' potential range (calculated based on the climatic conditions occupied by 100% of species occurrences) that is occupied. Regression coefficients were obtained by modelling all three explanatory variables simultaneously for 171 species. The deviance explained of the model is 30.51%, significance is < 0.001 for dispersal distance and seed bank persistence, and < 0.01 for habitat breadth. (a) Dispersal distance for species with transient and short-term persistent seed banks ($n = 112$), (b) dispersal distance for species with long-term persistent seed banks ($n = 59$), (c) habitat breadth for species with transient and short-term persistent seed banks ($n = 112$), (d) habitat breadth for species with long-term persistent seed banks ($n = 59$).
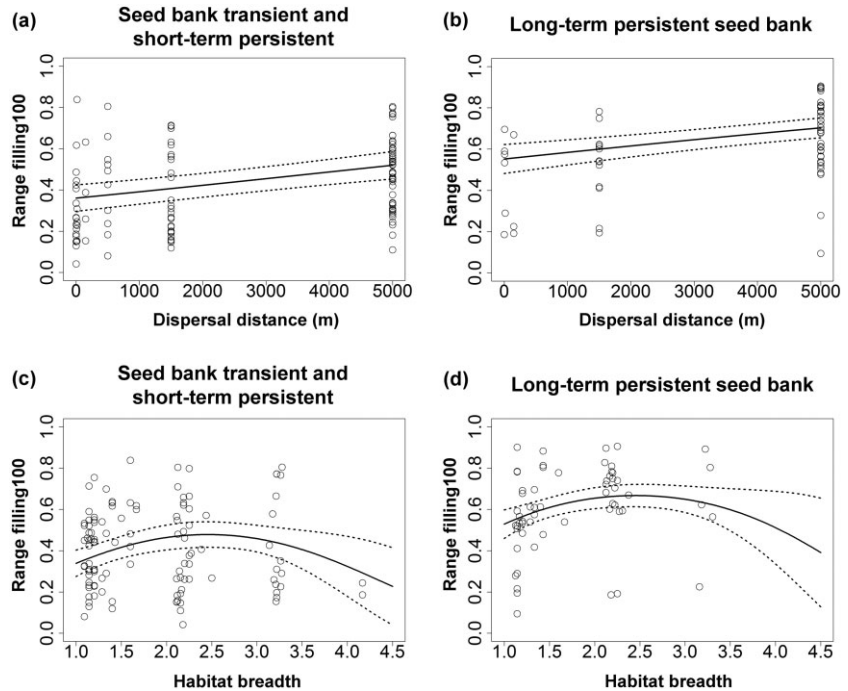
the persistence of soil seed banks (Poschlod *et al.*, 2013). Species for which climate change will reduce their potential geographical range will be more vulnerable to extinction if climate change also has a negative impact on their seed bank.

The importance of habitat breadth in determining geographical ranges has been disputed (Lambdon, 2008). However, our results provide comprehensive evidence to support this relationship. This could occur either because within a species' climatically suitable distribution there is simply more habitat available to be occupied, or because increased habitat availability provides more routes for expansion from glacial refugia. A species that occupies a broad range of habitats could do so because it is adapted to a broad range of physical environmental factors such as soil type or light availability. Alternatively, the species could be a good competitor. Boulangeat *et al.* (2012a) found that generalist species tend to be competitors, whereas species classified as stress-tolerant tend to be specialists. Our results show that the greatest range filling is achieved when a species can live in two general habitats and different subhabitats (Figs 1 & 2). The unimodal response to habitat breadth could be caused by a similar trade-off between tolerance to stress and competitive ability. We suggest that, subject to trade-offs, species that are unspecialized to a single general habitat type and that are not extreme generalists will be well positioned to occupy a large proportion of their potential distribution. Furthermore, our results demonstrate that fragmented habitat will restrict climate-driven range shifts, particularly for habitat specialists, and merits more consideration in climate change risk assessments.

SLA appears to be a relevant trait for determining geographical ranges of European plant species, although it does not have a consistent relationship with each of the three response variables

analysed. For range filling100 SLA did not pass the threshold of RVI > 0.5 in the three-variable models (Table S1 in Appendix S2), and therefore SLA was not included in the combined models. However, in the case of range size and range filling95 SLA had a high RVI (*c.* 0.85) in the combined models (Table 2). The importance of SLA for the establishment ability and range expansion of native species is in accordance with that previously obtained for naturalization success in introduced species (Hamilton *et al.*, 2005). This finding appears to be because high SLA corresponds to a high relative growth rate and rapid resource acquisition. The positive relationship between plant height and range size/filling supports the hypothesis that the competitive ability of taller plants might increase range sizes (Lavergne *et al.*, 2004). Contrary to findings for woody plants by Van der Veken *et al.* (2007), this variable has very low explanatory power. Therefore competitive ability conferred by plant height does not appear to be a major driver of distributions for plants in general. Age of first flowering was also marginally important for range size/filling. Contrary to our expectations, this relationship was positive. One explanation for this result might be that establishment ability is higher for species that reproduce later in life since early reproducing species are ruderal rather than competitive species (Grime, 1977).

Our results could be affected by the spatial resolution of the analyses (i.e. 50 km × 50 km grid cells), as climate conditions were calculated as the averaged value of the 10′ grid cells that fall inside each 50 km^2 grid cell. The 50-km^2 climate values will be more intermediate than those obtained at a finer resolution, where more extreme climatic conditions will be more apparent. Additionally we performed our analyses in Europe, which does not encompass the full geographical ranges of most species, so the degree of global range filling for a species could differ.

Despite these potential drawbacks, our results are comparable between species and reveal limitations on species ranges at a spatial extent and resolution that is frequently used for estimating range filling (Svenning & Skov, 2004; Nogués-Bravo *et al.*, 2014) and for assessments of the impacts of climate change (e.g. Araújo *et al.*, 2011).

Implications for range shifts under climate change

Forecasts of climate-driven range shifts that attempt to incorporate the range-shift capacity of species focus almost exclusively on dispersal potential (Bateman *et al.*, 2013). However, we demonstrate that traits related to processes of establishment and proliferation are equally, if not more, important for range filling. This suggests that evaluations of the likely effects of climate change on species distributions should account for such traits. For plants, seed bank persistence and habitat breadth are prime candidates for inclusion, and data on these traits are widely available. Trait-based assessments of extinction vulnerability under climate change are increasingly common and are potentially very useful tools (Foden *et al.*, 2013; Triviño *et al.*, 2013; Garcia *et al.*, 2014; Guisan, 2014; Pearson *et al.*, 2014), but we argue that any such assessment should be underlain by empirical analyses of the relevance of the traits used. In conclusion, our analysis suggests that species with a high capacity to disperse, that can maintain viable seed banks for several years, that can live in an intermediate number of habitats and to a lesser extent those that have higher competitive ability will be more likely to shift their geographical ranges under climate change.

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NOTE: Additional references to the data sources can be found in Appendix S1.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Description of species traits and sources used to compile them.
Appendix S2 Additional figures and tables.
Appendix S3 Phylogenetic analyses.

BIOSKETCH

Alba Estrada is a post-doctoral researcher working in macroecology and biogeography. She is interested in understanding the factors that determine species distributions and in detecting changes in large-scale biodiversity patterns under climate and land-use change. The research team forms part of the European BiodivERsA Project: European Conservation for the 21st Century (EC21C: http://cibioue.uevora.pt/projects/biodiversa-ec21c), which aims to predict when and where shifts in species distributions will disrupt European communities and ecosystems, and to evaluate methods for reducing this disruption.

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