

Research

Individual fitness is decoupled from coarse-scale probability of occurrence in North American trees

Gabriele Midolo, Camilla Wellstein and Søren Faurby

G. Midolo (<https://orcid.org/0000-0003-1316-2546>) ✉ (gabriele.midolo@natec.unibz.it) and C. Wellstein (<https://orcid.org/0000-0001-6994-274X>), Faculty of Science and Technology, Free Univ. of Bozen-Bolzano, Bolzano, Italy. – S. Faurby (<https://orcid.org/0000-0002-2974-2628>), Dept of Biological and Environmental Sciences, Univ. of Gothenburg, Göteborg, Sweden, and: Gothenburg Global Biodiversity Centre, Göteborg, Sweden.

Ecography

44: 789–801, 2021

doi: 10.1111/ecog.05446

Subject Editor: Kenneth Feeley

Editor-in-Chief:

Jens-Christian Svenning

Accepted 10 January 2021



Habitat suitability estimated with probability of occurrence in species distribution models (SDMs) is used in conservation to identify geographic areas that are most likely to harbor individuals of interest. In theory, probability of occurrence is coupled with individual fitness so that individuals have higher fitness at the centre of their species environmental niche than at the edges, which we here define as ‘fitness–centre’ hypothesis. However, such relationship is uncertain and has been rarely tested across multiple species. Here, we quantified the relationship between coarse-scale probability of occurrence projected with SDMs and individual fitness in 66 tree species native of North America. We used 1) field data of individuals’ growth rate (height and diameter standardized by age) available from the United States Forest Inventory Analysis plots; and 2) common garden data collected from 23 studies reporting individual growth rate, survival, height and diameter of individuals originated from different provenances in United States and Canada. We show ‘fitness–centre’ relationships are rare, with only 12% and 11% of cases showing a significant positive correlation for field and common garden data, respectively. Furthermore, we found the ‘fitness–centre’ relationship is not affected by the precision of the SDMs and it does not depend upon dispersal ability and climatic breath of the species. Thus, although the ‘fitness–centre’ relationship is supported by theory, it does not hold true in nearly any species. Because individual fitness plays a relevant role in buffering local extinction and range contraction following climatic changes and biotic invasions, our results encourage conservationists not to assume the ‘fitness–centre’ relationship when modelling species distribution.

Keywords: centre–periphery, ecological niche model, individual performance, intraspecific variability, meta-analysis, transplant experiment

Introduction

Probability of occurrence estimated with species distribution models (SDMs) is widely used in large-scale conservation assessments to predict range shifts and local extinction rates in response to global environmental changes (Peterson et al. 2002, Thuiller et al. 2005, Pacifici et al. 2015). To improve reliability of SDMs’ projections, recent advances integrate and combine various processes such as eco-evolutionary dynamics

(Cotto et al. 2017), dispersal limitation (Engler et al. 2012) and local adaptation (Benito Garzón et al. 2019, Peterson et al. 2019). However, it is still debated to what extent coarse-scale probability of occurrence reflects underlying ecological and demographic processes related to the concept of environmental niche (Thuiller et al. 2014, Wittmann et al. 2016, Pironon et al. 2018).

In theory, probability of occurrence (sometimes referred as ‘habitat suitability’ in SDMs) is expected to reflect the set of abiotic conditions that maximize the physiological optimum of a species (Guisan et al. 2017). Although SDMs are not designed to model individual fitness or local abundance, areas with higher probability of occurrence in geographic space indicate, in principle, the locations where a species can better establish and maintain populations. Nevertheless, such assumption in SDMs relies on a hypothetical absence of biotic interactions, dispersal limitation and evolutionary change (Pearson and Dawson 2003). In addition, micro-habitat variation unrelated to the coarse scale climate modeled by SDMs could greatly affect species distribution and fitness (Potter et al. 2013).

Understanding relationships between species occurrence and ecological processes is key to evaluate conservation strategies based upon SDMs under present-day and future climate change scenarios (Franklin 2010). To this aim, the reliability of species occurrence obtained from SDMs and other niche modeling approaches can be evaluated testing the ‘centre–periphery’ hypothesis, which states that demographic performance and genetic variation is highest at the centre of the preferred environmental niche and decreases toward the edges (Pironon et al. 2017).

While previous studies focusing on the ‘centre–periphery’ hypothesis are focusing on local abundance (i.e. the ‘abundant–centre’ hypothesis; Box 1) (Dallas et al. 2017, Santini et al. 2019, Osorio-Olvera et al. 2020), a less frequently tested assumption in the niche modeling literature is that individuals have higher fitness at the centre of their species environmental niche than at the edges within their

native range, which hereafter we refer to as the ‘fitness–centre’ hypothesis (Box 1). Because such hypothesis reflects the fundamental ecological theory surrounding the concept of ecological niche (Pulliam 2000), some has proposed that positive coupling can be expected between individual fitness and modeled probability of occurrence in SDMs (Thuiller et al. 2010, Wittmann et al. 2016, Mammola et al. 2019). Indeed, probability of occurrence is commonly used as an ecological niche indicator approximating Grinnellian niche (namely the niche component defined by non-interactive abiotic environmental variables) alongside other metrics of niche-centroid distance (Santini et al. 2019, Osorio-Olvera et al. 2020). Nevertheless, there are multiple reasons to expect weak support of ‘fitness–centre’ hypothesis in SDMs, both biological and methodological.

First, the fitness–centre hypothesis assumes that specimens have the highest fitness under the environmental conditions where they occur more frequently, and that their maximum fitness is reached where these conditions are met. However, due to dispersal limitation and historical factors, species may not be in equilibrium with current environmental conditions, that is, species distribution may be still responding to last glacial period (ca 115–12 ka) and anthropogenic land-use changes and fragmentation (Svenning and Skov 2004, Svenning and Sandel 2013, Wagner et al. 2015). In addition, there is mounting evidence that individuals of a population might not be locally adapted nor express higher individual fitness in local rather than non-local conditions (Svenning and Sandel 2013, De Frenne et al. 2014, Midolo and Wellstein 2020). Such factors do not just disregard the assumption behind the fitness–centre hypothesis, but also bias the estimation of the environmental niche in SDMs (Pearson and Dawson 2003).

Second, individual fitness, like local abundance (Pironon et al. 2015, Santini et al. 2019), may not linearly increase from the centre to the edge of the environmental niche. Instead, performance curves can have abrupt declines

Box 1. List of hypotheses mentioned in this study

Centre–periphery hypothesis (CPH). Biogeographical paradigm stating that genetic variation and demographic performance of species decrease from the centre to the edge of its geographic and environmental range. The CPH is based on the principle that populations and individuals are more isolated near the range limit of the species, resulting in lower demographic (population-level) and fitness (individual-level) performances. Thus, we here consider the CPH as the overarching hypothesis of the ‘abundant–centre’ and ‘fitness–centre’ hypotheses mentioned in the present study. We recommend Pironon et al. (2017) for a detailed overview on the CPH.

Abundant–centre hypothesis. Subhypothesis of CPH referring to the species’ demographic performance, and specifically to the abundance of individuals. The ‘abundant–centre’ hypothesis states that species abundance is higher at the centre of the species range and it decline toward range edges (Sagarin et al. 2006). Such hypothesis has been traditionally proposed as a general macroecological rule, but it is still currently under debate. Recent studies are focusing on abundance variation within the environmental range of the species, using ecological niche indicators to estimate the species environmental range (Dallas et al. 2017, Santini et al. 2019, Osorio-Olvera et al. 2020). The ‘abundant–centre’ hypothesis is not addressed in this study.

Fitness–centre hypothesis. Subhypothesis of CPH referring to the fitness of individuals quantified by functional traits or survivorship. The ‘fitness–centre’ hypothesis defined here states that individual fitness is expected to be higher at the centre of the species range and it decline toward range edges. Like the recent literature on the ‘abundant–centre’ hypothesis, we link the ‘fitness–centre’ hypothesis to the environmental range of the species, using probability of occurrence as an ecological niche indicator. Thus, under the ‘fitness–centre’ hypothesis, a positive coupling is expected between individual fitness and probability of occurrence.

above or below certain thresholds within the climatic envelope of the species. For instance, rapid changes in performance (e.g. photosynthetic rate and frost tolerance) in response to temperature affects plant distribution and elevational zonation (Körner 1999).

Finally, in niche modeling approaches, probability of occurrence is nearly always estimated at coarse-scale resolution using macroclimatic data, while species occurrence and individual fitness may strongly depend on micro-habitat (Suggitt et al. 2011, Greiser et al. 2020). Consequently, low probability of occurrence predicted in a geographical unit may indicate that a smaller fraction of it is suitable rather than the whole unit is less suitable for the species. Such micro-habitat dependency would then confound fitness–centre relationships obtained in SDMs, for instance, in species whose occurrences and fitness are associated with micro-topography (Scherrer and Körner 2011) or slope exposure depending on the latitude (Holland and Steyn 1975).

Previous studies using SDMs to address the fitness–centre hypothesis used various functional traits as surrogates of individual fitness in both animals (Larson et al. 2010, Pellissier et al. 2013, Wittmann et al. 2016, Mammola et al. 2019, Barela et al. 2020) and plants (Elmendorf and Moore 2008, Thuiller et al. 2010, Sangüesa-Barreda et al. 2018, Chardon et al. 2020) and overall reported heterogeneous results. These studies generally tested the hypothesis on single species (but see Thuiller et al. 2010) or normally used few observations of trait data collected in the field (but see Chardon et al. 2020), possibly due to the rarity of the species under consideration (Mammola et al. 2019) or because sampling functional traits at the intraspecific level over large areas is time-consuming and expensive.

Due to data availability restrictions, it is still difficult to draw conclusion on the validity of the fitness–centre hypothesis. However, both forest inventories and common garden experiments represent data sources on plant species occurrences and intraspecific functional traits in SDM-related approaches (Benito Garzón et al. 2019), but have not been applied to test the fitness–centre hypothesis. Specifically, field-observed traits reflect the fitness experienced by the individuals at their local site. In contrast, common gardens remove bias due to differing growing conditions at the site of origin to the ones of the common garden site, allowing for the quantification of adaptive trait variation while filtering out variation caused by site-specific conditions observed at the site of origin, which could confound fitness–centre associations. From this point of view, fitness data obtained from common gardens could show stronger fitness–centre relations than field-collected data.

Here, we tested whether individual fitness traits correlate with probability of occurrence projected with SDMs across 66 tree species native of North America within their native range (Fig. 1). We first compiled two datasets on individual growth rate in forest inventory plots of western United States (hereafter, ‘field’ data), and growth and survival data reported in 23 common garden studies conducted in the United States and Canada (hereafter, ‘common garden’ data). Secondly, we

trained and tested SDMs at 10 km resolution using soil and climatic predictors and presence–absence data from United States and Canada’s Forest National Inventories. Finally, we applied a meta-analytical approach to estimate the mean correlation between individual fitness and coarse probability of occurrence estimated at the sampling location (in ‘field’ data) or at the site of origin of the individuals (in the ‘common garden’ data) across multiple species, and accounted for potential modifying factors like dispersal ability and the climatic niche’ breadth of the species.

We show that associations between individual fitness and coarse-scale probability of occurrence are rare and not affected by species-specific traits or by the precision of the SDMs. We conclude that hypothesized fitness–centre relationships represent an exception rather than the rule when modeling environmental niches in the geographic space. More broadly, our findings reject the universality of centre–periphery hypothesis and pose important constraints in conservation projects based upon such assumption.

Material and methods

We tested the fitness–centre hypothesis across 66 species by calculating the correlation between individual fitness traits sampled within the species distribution range and the coarse probability of occurrence estimated at sampling locations obtained from SDMs. The analysis was performed in three main steps, as summarized in Fig. 1: 1) collection of intraspecific individual fitness data; 2) estimation of probability of occurrence using SDMs for each species; 3) meta-analysis combining the fitness–centre relationships across multiple species and exploration of potential modifying factors.

Individual fitness estimation

We used two datasets on tree species individual fitness containing 1) field data collected in contiguous western United States including the Rocky Mountains, the Great Basin and the Pacific coast states (i.e. in Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming), and 2) common garden data collected from provenance trial experiments located in United States and Canada. We analyzed 66 tree species in total (44 found in the field dataset only, 13 in the common garden dataset only and nine in both datasets). The list of species and details on the number of observations available is reported in the Supporting information.

Species selection criteria

We restricted the analysis to tree species native to United States and Canada (hereafter, Northern America) to reduce variation originating from input data and regions with different biogeographic conditions. Because our presence–absence data used in SDMs were limited to Northern America, we did not consider species with substantial parts of the geographic range located in Mexico to avoid missing occurrences

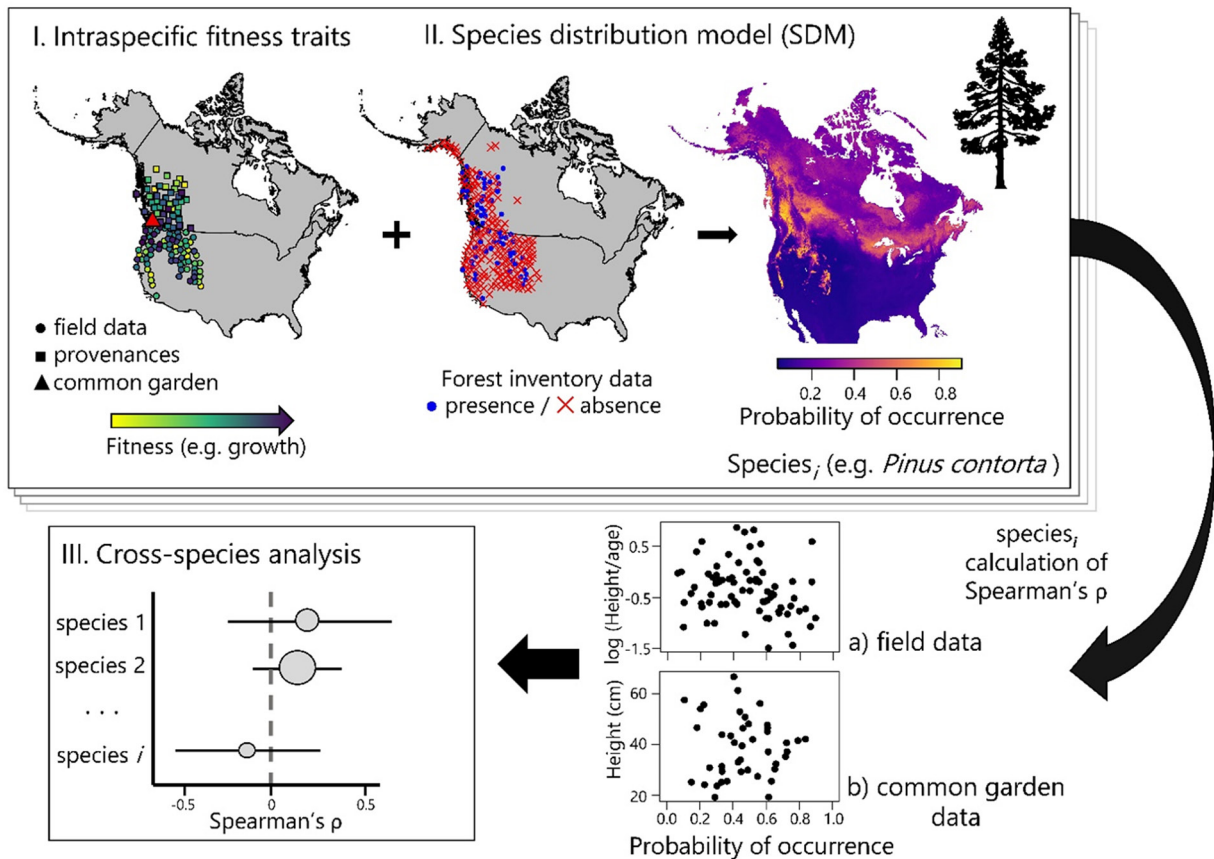


Figure 1. Schematic representation of the methodological steps applied in this study (each step reflects subsections of the ‘Material and methods’ section): (I) for multiple species (in the example, lodgepole pine *Pinus contorta*), we estimated individual fitness from field data (Forest Inventory Analysis of US Forest Service) and/or common garden experiments available from the literature (in the example, data from Mahony et al. 2020, ‘Data sources’ section); (II) we obtained probability of occurrence from species distribution model (SDM) using presence–absence data retrieved from United States and Canada’s National Forest Inventories. After we calculated the correlation between individual fitness at site location and probability of occurrence for multiple species and individual fitness traits, we (III) applied a meta-analytical approach to estimate the mean correlation coefficient across multiple species. Geographic points in the figure are spatially thinned for plotting purposes.

from the warmest area when estimating the environmental niche (Soberón et al. 2018). Nevertheless, we retained species with the southernmost distribution range located in Mexico in case their occurrence is confined to high-elevation areas where we expected similar climatic conditions of low-elevation areas found at higher latitudes of northern America (e.g. ponderosa pine *Pinus ponderosa*, black cottonwood *Populus trichocarpa*, Douglas-fir *Pseudotsuga menziesii*). Indeed, occurrences of these species showed a linear negative relation between latitude and elevation, at least within northern America (Supporting information). Information on species’ ranges distribution were obtained from the ‘Atlas of United States Trees’ (US Geological Survey 1999) and ‘Plants of the World Online’ (POWO 2019).

Trait data collection

For the field data, we used the United States Forest Inventory Analysis database (FIA) to obtain data on individual growth as a proxy of individual fitness (retrieved from FIA’s datamart:

<<https://apps.fs.usda.gov/fia/datamart>>). To quantify yearly average growth of individuals, we only retained observations where either height or diameter at breast height (DBH) were reported in combination with the age of the individual. Observations reporting age in combination with height or DBH were only available in plots located in continental western United States. Depending on the species and sampling procedure, age was either reported as tree rings from an increment core sample extracted at the root collar (TOTAGE = ‘total age’) or at the breast height (1.37 m above ground) (BHAGE = ‘breast height age’). Thus, to eliminate the effect of stand density and tree age on the size-growth relations (Pretzsch and Dieler 2011), we calculated the median of the ratio between height and/or DBH to TOTAGE and/or BHAGE for each plot and species. We used the median to avoid effects of outliers. Individual height and diameter were standardized by the age to capture vertical and radial tree growth rate. Thus, our metric assigned higher fitness to shorter-lived trees with greater height or DBH compared to

older trees who reached maximum growth rate. In general, individual growth rate is a key component of individual fitness of an organism (Violle et al. 2007). Specifically, growth rate of trees enhances individual competitive ability in natural forest ecosystems (Morgenstern 1996) and can positively influence reproductive success of individuals (Avanzi et al. 2015). In addition, individual growth rate has been previously shown having a positive coupling with SDM-modelled probability of occurrence in grass carp *Ctenopharyngodon idella* (Wittmann et al. 2016). We only retained species with at least 30 plots with calculable individual height or DBH to age ratios. Number of presences (and corresponding absences) per single trait and species selected ranged from 31 to 17 956 (median = 301, SD = 2920) (Supporting information).

For the common garden data, we collected individual fitness from the literature on provenance trial experiments. These studies report data on specimens originating from different locations (i.e. provenances) and simultaneously grown in one or more common garden located within the species range. Data reported are sampled over individuals of the same age sampled at the end of the experiment or throughout it. In February 2020 we searched in Web of Knowledge for primary studies reporting data from common garden experiments conducted in northern America (cf. Supporting information for the search string). Our initial search string yielded 476 results from Web of Knowledge. We also searched for common garden data at the United States Forest Service Research Data Archive. We selected additional sources from studies cited by the articles retained in the search string that were eligible for inclusion. After screening results from the main search string and the Forest Service Research Data Archive, we selected 19 primary studies and four data papers eligible for inclusion ('Data source' section). On average, experiments reported trait data after 13 (SD = 11) growing seasons (range of the year of experiments' start = 1961–2014, and experiments' end = 1979–2016). Each source selected reported at least one of the following mean responses for each provenance and species: height, diameter, survival or growth rate. Height, diameter and survival were reported as the data collected after a certain period or at end of the experiment. Since common gardens were relatively short-running and conducted on coetaneous-transplanted individuals, height and diameter reported at the end of the common garden trials represent growth rate over the period of the common garden trial. Thus, we assumed height and diameter in 'common garden' data to be directly proxies of individuals' growth rates. In addition, we used final height and diameter in the 'common garden' data as proxies of individuals' growth rate as these are commonly used as growth indicators in provenance trials experiments (Taïbi et al. 2014, Warwell and Shaw 2017 in 'Data sources'). Conversely, growth rate was reported by studies as the mean yearly increment of height, biomass or volume of each provenance during the experiment. We collected the geographical coordinates and mean value of the response measures for each study, provenance and common garden' site. Data were retrieved from tables, figures and supporting

information of the study, or provided directly by the authors. Provenances assessed per studies and species ranged in total from 6 to 281 (median = 42, SD = 51.2).

Probability of occurrence estimation

Presence–absence data

We obtained presence–absence data from the USDA Forest Inventory Analysis (FIA) (Burrill et al. 2018) and ground plots of Canada's National Forest Inventory (<<https://nfi.nfis.org>>). These datasets contain geographical coordinates of standardized plots and can be therefore used to train and test SDMs. By relying on forest inventory plots, we used true absence data to fit SDMs rather than randomly generated pseudo-absences.

The United States FIA dataset contained ground plot inventories sampled from 1968 to 2019, each made by four subplots of 168 m² area located within 1-acre sample area (Burrill et al. 2018 for detailed description of sampling design). From these plots we only selected those located in continental United States and excluded those located in artificial forest stands. In addition, we excluded plots located in 'Private' or 'Native American' land, to reduce the effects of cultural management and because these plots' coordinates are swapped with other plots within the same county for legal reasons. Our selection resulted in 103 786 plot locations in total available from the United States. The Canada NFI dataset contained ground plots sampled from 1992 to 2007 with 400 m² and 50 m² area for surveys of large (DBH ≥ 9 cm) and small (DBH < 9 cm) trees, respectively. In total, 985 plot locations were used as background for presence–absence data in Canada.

For each of the 66 species selected for the analysis, we randomly sampled n absence locations 30 times among all the sampled plots, where n was the number of presences available from that species across ground plots data. Given the computationally intensive calculations of SDMs, we used 30 replicates per algorithm applied and species (see Davis et al. 2018 for another use of the same number of replicates for computationally heavy analyses). To sample corresponding absences more uniformly in the study area and to overcome potential different sampling efforts across northern American states, we selected absences within each state up to the equal number of presences available for that state. Such approach allows not to randomly select absences within areas where the species is absent due to historical factors (Guisan et al. 2017). Finally, for each of the 30 replicates, we thinned observations to a minimum distance of 10 km to reduce spatial autocorrelation using the 'ecospat.occ.desaggregation' function of the R package *ecospat* (Di Cola et al. 2017). This distance reflected the resolution of the environmental predictors used in SDMs and it was selected to account for maximum distance uncertainty of presence–absence data in Canada's ground plots (10 km) and to reduce overly close-sampled areas in US.

Coordinates of presence–absence data (i.e. the plot location) used in our analysis had 1.6 km and 10 km uncertainty for United States FIA and Canada NFI data, respectively

(except for 433 plots located in British Columbia, Quebec and New Brunswick, of which exact coordinates were available). For this reason, we explored how coordinate imprecision potentially affected results and conclusion of our analysis due to inaccurate estimate of environmental conditions at locations where the species occurs. We report methodological details and results of this sensitivity analysis in the Supporting information. The sensitivity analysis was performed on the subset of species and presence/absence data did not affect our conclusions.

Species distribution models

We modeled and projected current species' probability of occurrence in North America (decimal degrees' longitude: 179° to 52°W; and latitude: 24° to 83°N) using the *sdm* R package (Naimi and Araújo 2016). We applied bioclimatic and soil data at a resolution of 10 km at the equator as predictors. We used 19 climatic variables from WorldClim database (ver. 2.0; <www.worldclim.org>, Fick and Hijmans 2017) and the aridity index, measured as the ratio of mean annual precipitation (estimated by WorldClim database) to the potential evapotranspiration extracted from the CGIAR-CSI GeoPortal (Trabucco and Zomer 2010). In addition, we used six soil variables (i.e. depth to bedrock, bulk density, organic carbon content, soil pH in H₂O, cation exchange capacity and weight percentage of sand particles) obtained from SoilGrids database (Hengl et al. 2017). Soil variables were obtained by averaging estimated parameters within the top 30 cm layer (except for depth to bedrock). To avoid collinearity among predictors, we automatically selected a subset of predictors for each species by iteratively excluding variables with the variance inflation factor (VIF) greater than 10 using the 'vifstep' function of the *usdm* R package (Naimi et al. 2014) and only retained selected variables occurring across all the 30 replicates.

We ran SDMs models using six different algorithms for each of the 30 replicates per species. We used subsampling partitioning using 30% of randomly sampled observations in each run to test the model (Guisan et al. 2017). The algorithms used in modeling were the following: generalized linear model (GLM), generalized additive model (GAM), boosted regression tree (BRT), random forest (RF), multivariate adaptive regression splines (MARS) and support-vector machine (SVM). We used model ensemble to project probability of occurrence by weighting each model by the true skill statistic ('TSS') using the maximum sum of model sensitivity and specificity as cutoff optimization threshold.

Meta-analysis

Effect size calculation

After we obtained the spatial projections of probability of occurrence, we extracted for each species the probability of occurrence at the locations where traits were sampled in ground plots ('field' data), and locations where the provenances tested at the common garden site originated ('common garden' data). Then, because our goal was to assess the

coupling between SDM-modeled probability of occurrence and individual fitness, we used Spearman's correlation coefficient between each trait and the probability of occurrence of the species as the effect-size to quantify the direction and magnitude of the fitness–centre relationship (Santini et al. 2019, Osorio-Olvera et al. 2020). For the 'field' data, we used the 'weightedCorr' function of the *wCorr* R package (Emad and Bailey 2017) to weight correlation coefficients by the number of individuals sampled in each plot. In the case of the common garden data, we computed unweighted correlation coefficients for each common garden site and species assessed by single study, as the number of individuals sampled per provenance was the same within each trial unit.

Nearby sample sites may not be independent and therefore, for each pairwise correlation, we checked for spatial autocorrelation of the residuals obtained from a linear model with trait value as the dependent variable, and probability of occurrence and its quadratic term as the predictors. Before fitting the linear model, we log-transformed growth traits in the field data as these were in most cases positively skewed. Then, we used the 'spline.correlog' function of the *ncfR* package (Bjornstad 2020) over the residuals of the linear model to obtain Moran's *I* correlograms. From these, we identified the minimum geographic distance to which spatial autocorrelation was estimated to be not significant. To remove the effect of spatial autocorrelation, we then calculated 999 times the correlation coefficient between probability of occurrence and trait measurements by randomly thinning each time the sampling locations to the minimum distance threshold estimated for each species and trait. Random thinning was performed using the 'thin' function of the *spThin* R package (Aiello-Lammens et al. 2015). We then took the median of both sample size and correlation coefficients to be used in meta-analysis. Our procedure means that the end-results are influenced by all sample sites available but distant and more independent sample sites are given a higher importance than sample sites showing substantial spatial autocorrelation to nearby sample sites.

We estimated the significance of each correlation coefficient by back-transforming 95% confidence intervals obtained by the Fisher's *z*-transformation, which allow to estimate associated sampling variance of correlation coefficients (i.e. $1/(N - 3)$; where *N* is the sample size) (Borenstein et al. 2009).

Linear mixed-effect models

Using linear mixed effect-models we applied an approach similar to a meta-analysis to estimate the mean effect of fitness–centre relationship across the species and traits analyzed, and to investigate how such relationship is affected by potential modifying factors. We used the 'lmer' function of the *lme4* R package (Bates et al. 2015) for each dataset separately (i.e. field and common garden data). We used Spearman's correlation coefficients as the dependent variable of the fixed component of the model, and the species and the study (namely, the identifier of the common garden study) as crossed random effects in the common garden data (i.e. $(1|\text{species}) + (1|\text{study})$). For the field data, only the species was

used as random effect. We weighted each correlation coefficient by multiplying the sample size of the correlation coefficient by the maximum true skill statistic (TSS) of the SDM obtained from that species. In other words, observations with many sampled locations and with probability of occurrence obtained from more accurate models contributed more to the overall mean estimate.

We first estimated the mean weighted correlation between fitness and probability of occurrence using null models for each dataset. Secondly, we used five predictors we expected to moderate the effect sizes, namely: the different metrics of individual's fitness traits, the main taxonomic group (i.e. angiosperm versus gymnosperm), species dispersal ability and species temperature and precipitation breadth (i.e. the climatic range of the species). We used different metrics of individual's fitness traits as moderator to identify whether different dimension of fitness have intrinsically different relationship with probability of occurrence, or if they overall respond in a similar way. In addition, in the common garden data, we also used the probability of occurrence of the location of the common garden site as predictor.

Dispersal ability affects population isolation and gene flow shaping functional trait variability and local adaptation within the species' range (Sexton et al. 2014, Pironon et al. 2017). Species' seed weight was used as a proxy of species dispersal ability and obtained from the seed information database (SID) of the Royal Botanic Gardens Kew (2020). Two species of poplar (black cottonwood *Populus trichocarpa* and narrowleaf cottonwood *Populus angustifolia*), lacked data on seed weight and for these we used the median of the genus. Similarly, larger climatic variability within the species' range is expected to facilitate intraspecific functional trait variability (Violle and Jiang 2009), thus potentially affecting the probability of detecting such variation within a gradient of probability of occurrence. Temperature and precipitation breadth were estimated as the difference between the 90% and 10% quantile values estimated at the location of the species' occurrences. We used temperature and precipitation average of the warmest year quarter ('BIO10' and 'BIO18' in WorldClim, respectively) at 10 km resolution. We log-transformed seed weight and precipitation breadth due to strong positively skewedness.

We scaled and centered all continuous variables to a mean of 0 and standard deviation of 1 using the 'scale' function of R (<www.r-project.org>), and checked for collinearity prior to modeling. Starting from a full model including all the predictors mentioned above, we performed a stepwise backward selection via likelihood ratio tests.

Finally, we checked whether SDMs' TSS and sample size (namely, the weight assigned to each correlation coefficient used in the mixed-effect models) affected the correlation observed between probability of occurrence and individual fitness. Such approach is comparable to the analysis of publication bias in meta-analysis (Nakagawa and Santos 2012). Thus, we estimated the significance of the intercept of a linear regression model using the residuals of the null mixed-effect model as dependent variable, and the observation's weight

(= sample size \times maximum TSS) as predictor (Nakagawa and Santos 2012). The weight term used in linear mixed effect models had no influence on the variation of correlation coefficients (Supporting information).

Results

We found poor support for the fitness–centre hypothesis in North American tree species. Pairwise correlation coefficients between individual fitness and probability of occurrence ranged from -0.50 to 0.49 (field data) and -0.64 to 0.56 (common garden data), with mean-weighted-correlation close to zero (Fig. 2). Importantly, only the 12% and 11% of the correlation coefficients were positively significant for the field and the common garden data, respectively. In addition, and contrary to what is expected by the fitness–centre hypothesis, we found few correlations with a negative significant trend (corresponding to the 10% and 2% of observations, for the field and the common garden data, respectively). Thus, in the field data, significant positive associations were detected consistently across all response traits in only six out of 53 species analyzed: Rocky Mountain maple *Acer glabrum*, big-tooth maple *Acer grandidentatum*, red alder *Alnus rubra*, giant chinquapin *Chrysolepis chrysophylla*, foothill pine *Pinus sabiniana* and coast redwood *Sequoia sempervirens*. In the common garden data, Douglas-fir *Pseudotsuga menziesii* was the species showing the highest fraction (38%) of positively significant pairwise correlations across common garden sites and traits examined, while others showed 17% or less.

Overall, mean correlations were not significantly different across the trait measurement types analyzed, suggesting similar responses between survival and various dimensions of individual growth (Fig. 3). Furthermore, none of the species' trait predictors considered in multiple regression (i.e. seed weight, temperature breadth and precipitation breadth) had a significant effect on the variation of the correlation coefficients. In the field data, the mean correlation of angiosperms (estimate = 0.08; SE = 0.03) was significant differently to that of gymnosperms, which was equal to zero. The mean correlation in angiosperms was however too low to indicate a substantial fitness–centre association and no such differences were detected in the common garden data (Supporting information).

Discussion

By combining individual fitness data from forest inventories and common gardens in North America, we showed that individual fitness indicators (growth and survival) are poorly associated with coarse-scale probability of occurrence projected with SDMs. Furthermore, we found the lack of fitness–centre relationships are pervasive across species with different potential dispersal ability and climatic breadth. Finally, we detected no influence of the precision of SDMs (expressed with maximum true skill statistic (TSS) of models

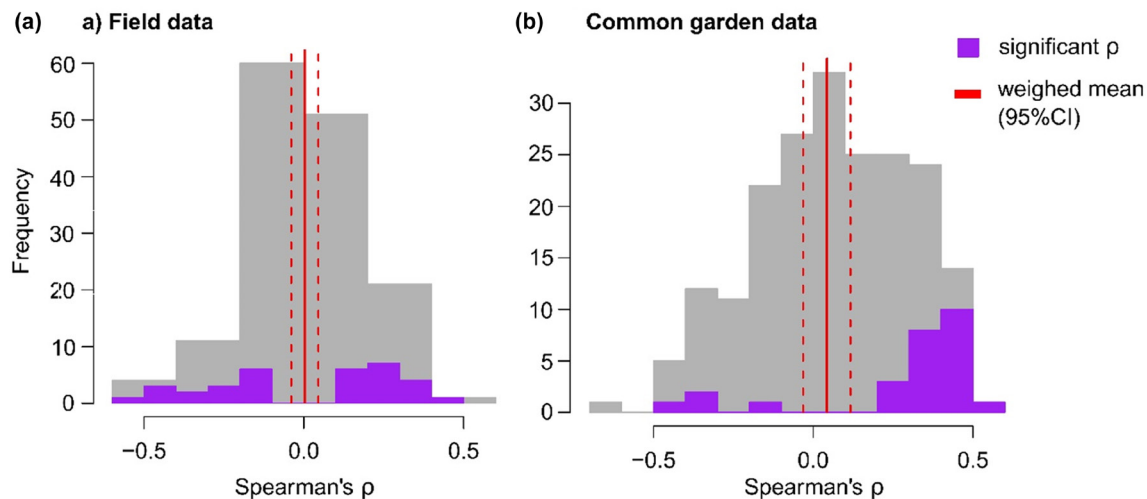


Figure 2. Overall distribution of the Spearman's correlation coefficients (ρ) between species' probability of occurrence and individual fitness sampled in (a) field data (from Forest Inventory Analysis of US Forest Service, FIA) and (b) common garden experiments' data. Purple-shaded bars represent the distribution of significant coefficients (p -value < 0.05). Red vertical lines indicate the mean pooled estimate (solid line) and its 95% CI (dashed lines) obtained from null mixed effect models using species (and study as well, for common garden data) in the random component of the model. Observations in the model are weighted by multiplying the sample size of the correlation coefficient by the maximum 'true skill statistic' (TSS) of the SDM obtained from that species.

used to ensemble the models) on the magnitude and direction of the fitness–centre correlations. Thus, our results reject the fitness–centre hypothesis stating that individual fitness is higher in locations with higher SDM-modeled probability of occurrence.

Why the fitness–centre hypothesis may not hold

The fitness–centre hypothesis has been detected for certain species in previous studies (Nagaraju et al. 2013, Wittmann et al. 2016, Sangüesa-Barreda et al. 2018, Mammola et al. 2019) but not in others (Larson et al. 2010, Barela et al. 2020, Chardon et al. 2020). However, these studies show three main methodological limitations (which we will discuss in detail below). Such limitations concern the restricted number of species analyzed, the amount of observation available to quantify fitness–centre relationships, and the type of trait data used to address the hypothesis.

First, previous studies tested the hypothesis on one or few species. Because our results suggest that fitness–centre correlations across multiple species are normally distributed around the zero, restricting the analysis to only few species makes the hypothesis more likely to be supported by chance alone (Santini et al. 2019). Thus, while positive fitness–centre associations are clear for certain species, these may simply not hold true in other species (Thuiller et al. 2010, Pellissier et al. 2013) or even show a negative relationship (Barela et al. 2020). Indeed, our analysis did not detect an effect of species-specific traits (dispersal ability and climatic breadth) on the fitness–centre relationship, suggesting that correlations are randomly distributed across ecologically different species.

Second, due to sampling limitations, previous studies often used few individual fitness records, which are likely

a poor representation of the full geographic range (but see Chardon et al. 2020). Conversely, our datasets allowed us to address the hypothesis over a significantly larger amount of observations over the entire species range. In addition, we used presence–absence data to train and test SDMs, which is generally a preferable approach than 'presence-only' SDMs (Guisan et al. 2017). Appropriate sampling across the species range allows for better estimation of the covariation between traits and the environmental optimum of the species (Soberón et al. 2018). Indeed, consistent with our findings, Chardon et al. (2020) used a comprehensive set of geographic records of the cushion plant *Silene acaulis* and showed no relationship between individual fitness (plant individual size) and probability of occurrence, even within the same genetic and geographic groups.

Third, while previous studies addressing the fitness–centre hypothesis solely rely on fitness data collected in situ, common garden data reported here were used to quantify survival and to test directly for the association between adaptive trait variation and modeled probability of occurrence. Common garden experiments where individuals are grown in controlled conditions removes in situ individual variation originated from other causes than probability of occurrence. In our case, growth rate of an individual trees can be affected by local biotic interactions with surrounding trees (e.g. light competition), presence of herbivores, parasites and forest utilization (Smith et al. 1997). Our approach showed nevertheless that adaptive trait variation and survival observed at common garden sites are unrelated to the coarse scale predictions of species occurrence.

Our findings agree with recent literature addressing the centre–periphery hypothesis over multiple plant and animal species and revealing no consistent trend (Thuiller et al.

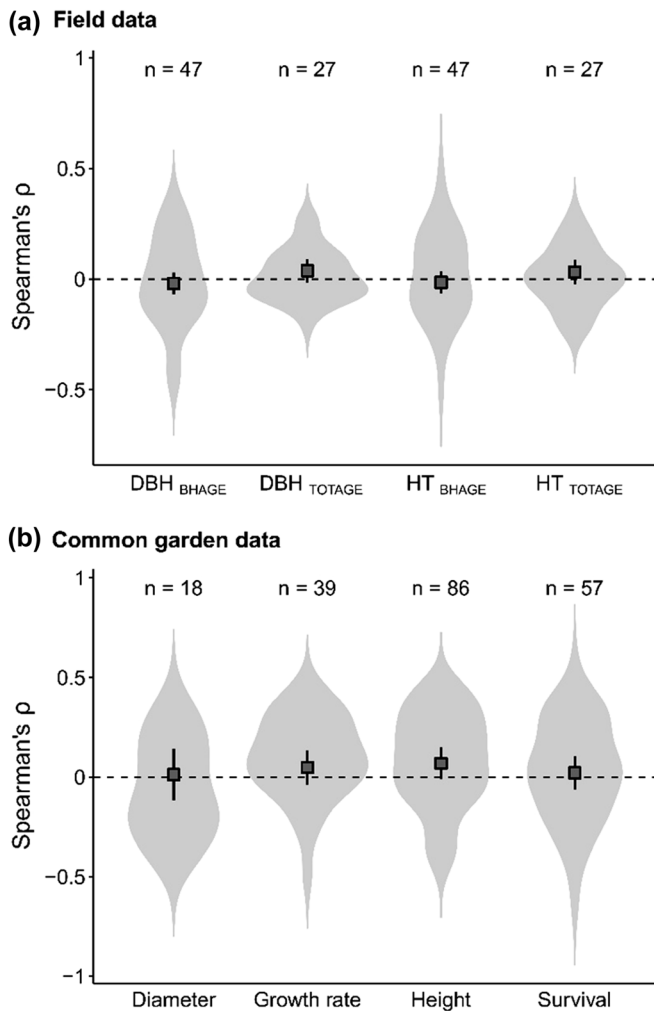


Figure 3. Distribution of Spearman's correlation coefficients (ρ) between species' probability of occurrence and individual fitness across different response traits analyzed (violin plot) for (a) field data (from Forest Inventory Analysis of US Forest Service, FIA) and (b) common garden experiments' data. No significant difference was detected across different response traits analyzed in both datasets. Grey squared points indicate mean pooled effect (and 95% CI) obtained from mixed-effect models using response trait type as predictor (n = number of pairwise correlations). Horizontal dashed line indicates Spearman's correlation equal to zero. Response traits in field data are diameter at breast height (DBH) and tree height (HT) standardized to age estimated at the root collar (TOTAGE) or at the breast height (BHAGE).

2014, Dallas et al. 2017, Pironon et al. 2017, Santini et al. 2019; but see Osorio-Olvera et al. 2020). Overall, recent simulations on artificial landscapes have showed support to the centre-periphery relationships only when certain conditions are met (i.e. deterministic population growth, high dispersal, low competition), which rarely occur in the reality of natural systems (Dallas and Santini 2020). Particularly, Dallas et al. (2017) showed that abundance of tree species (as well as birds, fishes and mammals) in the United States

does not correlate with distance to the environmental centroid reporting mean abundance-distance correlation coefficients close to zero. Similarly, Thuiller et al. (2014) found uncertain relationship between probability of occurrence and tree populations' dynamics (population growth rate, carrying capacity and population density) in Northern America and Europe. Like our study, Thuiller et al. (2014) included data from forest inventory plots located in western United States; yet, their analysis focused on population-level traits (i.e. basal area) related to local abundance rather than individual tree growth.

Pironon et al. (2017) and Santini et al. (2019) report various arguments for which centre-periphery hypothesis might not hold true that are transferable to our hypothesis tested here: 1) individual fitness can show abrupt rather than linear declines from the centre to the edge of the environmental niche; 2) fitness might depend on biotic interactions, which are not accounted for in SDMs; 3) occurrences of specimens and their individual performance might not be in equilibrium with the environment.

In addition, we also highlight that coarse-scale modeling approaches cannot capture microhabitat properties where individuals live. Since important factors affecting plant growth depend upon micro-habitat (Suggitt et al. 2011) and topography (e.g. slope aspect) (Cantlon 1953, Holland and Steyn 1975), the lack of support for the fitness-centre hypothesis found here and elsewhere needs to be circumscribed to the coarse-scale level only. Under this point of view, more advanced niche modeling approaches accounting for micro-habitat conditions (Lembrechts et al. 2019) and biotic interactions through joint distribution models (Clark et al. 2017) would be more likely to detect a consistent trend between individual fitness and probability of occurrence. In general, additional uncertainties other than coarse-scale resolution to detect such trends could be present when SDMs fail to properly model species distribution under certain circumstances, such as missing relevant environmental variables for certain species or wrong model structures.

We acknowledge that tree fitness in the field data were potentially affected by noise caused by temporal variation in sampling growth rate of different individuals at different times that do not match environmental conditions of bioclimatic predictors used to obtain SDMs. We further note that unaccounted temporal fluctuation of individual fitness in space (e.g. caused by pests' outbreaks and forest utilization) could produce additional noise to field data retrieved from forest inventory data (Thuiller et al. 2014). Yet, we also underline that climatic data used in our SDMs represented the historical averaging climatic conditions (1970–2000) matching the time period in which individuals were sampled in the field data and that such cross-individuals temporal fluctuation is virtually absent in common garden data, where individuals are simultaneously grown and sampled.

Finally, we here mainly focused on growth rate data (except for survival assessed in the common garden data). Yet, a combination of indicators other than growth rates, like fecundity

and seedling survival, could potentially be more closely correlated to probability of occurrence modeled by SDMs than individual growth rate, as these are key determinant of plant persistence in space.

General implications

Addressing the validity of the fitness–centre hypothesis has important implications for conservation and applied biodiversity management. Indeed, several conservation studies are based upon estimations of coarse modeled habitat suitability based on occurrence records to predict areas where species will most likely harbor individuals of that species (Peterson et al. 2002, Fitzpatrick et al. 2008, Zhang et al. 2020). However, a lack of the underlying fitness–centre relationship alters our interpretation of how modeled probability of occurrence is linked to the ability of specimens to survive and grow in a given location, affecting decisions on where to prioritize conservation efforts. Based on our results, areas with lower probability of occurrence might be occupied by individuals with higher fitness compared to those located in areas estimated with higher probability of occurrence. In such cases, the fitness of individuals located in areas with lower probability of occurrence are likely to be either positively affected by certain biotic and micro-habitat conditions neglected by SDMs, or locally adjusting through adaptation and plasticity, for instance, in response to climate change (Nicotra et al. 2010). In addition, eco-evolutionary processes in response to range shifts occurring in areas with lower probability of occurrence could help maintaining high genetic variation enhancing individual fitness, as long as climate change or other factors do not enhance isolation and restrain gene flow from populations nearby (Pironon et al. 2017, Nadeau and Urban 2019).

We suggest that using data on intraspecific variability of fitness-related traits in concert with SDMs could improve conservation planning. Indeed, mapping functional traits in space can be used as a tool to evaluate the output of SDMs and its biological meaning. For instance, identifying populations with greater longevity and dispersal ability located in areas with high probability of occurrence could help to trace most suitable biological corridors facilitating range shifts. Conserving high-fitness individuals occurring in most environmentally suitable areas could also produce more economically effective conservation plans when resources are limited.

Concluding remarks

Here, we determine that spatial variation in individual fitness within the species distribution range is not explained by the output of SDMs, contrary to what showed by some previous analyses. Although our results were limited to a single system (i.e. tree species in North America) our results clearly highlight that a strong pattern cannot safely be assumed to work in any system unless there is specific evidence of a fitness–centre coupling for a certain system. In that regard, we

highlight that we could not find any evidence of dispersal capacity and climatic breath to influence the overall results. Thus, the main takeaway from our study is that while the fitness–centre is supported by theory surrounding the concept of environmental niche (Pulliam 2000), it does not hold true in nearly any species. Because individual fitness plays a relevant role in buffering local extinction and range contraction following environmental changes and biotic invasions (Anderson 2016), our results imply that conservation projects relying on the assumption of the fitness–centre hypothesis should be revised. We thus recommend assessing how individual fitness vary within the current species range along modeled probability of occurrence before inferring conclusions on present and future range contractions based on SDMs.

Data availability statement

We report references of common-garden studies in the ‘Data source’ section. Data on the correlation coefficients used in the meta-analysis are available at the Figshare data repository <<https://doi.org/10.6084/m9.figshare.13637633.v1>>. Raw data on forest inventories are available online for United States (<<https://apps.fs.usda.gov/fia/datamart>>) and upon request to the Canadian Forest Service (<<https://nfi.nfis.org/en/datarequest>>).

Acknowledgements – We thank C. D. Bacon for proofreading the draft of the manuscript; M. V. Warwell, G. E. Rehfeldt, H. Cooper, A. Hamann and R. Marchin for providing data on common gardens; B. Smiley for ground plot data; and S. Midolo for remote server support.

Funding – This work was supported by the Swedish Research Council (2017-03862) and Carl Tryggers Stiftelse för Vetenskaplig Forskning (CTS18:105) to SF. The authors thank the Department of Innovation, Research and University of the Autonomous Province of Bozen/Bolzano for covering the Open Access publication costs.

Conflicts of interests – The authors have no conflicts of interests to declare.

Author contributions

Gabriele Midolo: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Project administration (equal); Visualization (lead); Writing – original draft (lead). **Camilla Wellstein:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (supporting); Supervision (lead); Writing – review and editing (equal). **Søren Faurby:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

References

- Aiello-Lammens, M. E. et al. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. – *Ecography* 38: 541–545.
- Anderson, J. T. 2016. Plant fitness in a rapidly changing world. – *New Phytol.* 210: 81–87.
- Avanzi, C. et al. 2015. Individual reproductive success in Norway spruce natural populations depends on growth rate, age and sensitivity to temperature. – *Heredity* 124: 685–698.
- Barela, I. et al. 2020. Relationships between survival and habitat suitability of semi-aquatic mammals. – *Ecol. Evol.* 10: 4867–4875.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Benito Garzón, M. et al. 2019. Δ TraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. – *New Phytol.* 222: 1757–1765.
- Bjornstad, O. N. 2020. ncf: spatial covariance functions. – R package ver. 1.2-9. <<https://CRAN.R-project.org/package=ncf>>.
- Borenstein, M. et al. 2009. Introduction to meta-analysis. – Wiley.
- Burrill, E. A. et al. 2018. The Forest Inventory and Analysis Database: database description and user guide Ver. 8.0 for Phase 2: Gen. Tech. Rep. RMRS-GTR-245. – US Dept of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, p. 946.
- Cantlon, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey. – *Ecol. Monogr.* 23: 241–270.
- Chardon, N. I. et al. 2020. Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. – *Ecography* 43: 60–74.
- Clark, J. S. et al. 2017. Generalized joint attribute modeling for biodiversity analysis: median-zero, multivariate, multifarious data. – *Ecol. Monogr.* 87: 34–56.
- Cotto, O. et al. 2017. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. – *Nat. Comm.* 8: 1–9.
- Dallas, T. A. and Santini, L. 2020. The influence of stochasticity, landscape structure and species traits on abundant–centre relationships. – *Ecography* 43: 1341–1351.
- Dallas, T. A. et al. 2017. Species are not most abundant in the centre of their geographic range or climatic niche. – *Ecol. Lett.* 20: 1526–1533.
- Davis, M. et al. 2018. Mammal diversity will take millions of years to recover from the current biodiversity crisis. – *Proc. Natl Acad. Sci. USA* 115: 11262–11267.
- De Frenne, P. et al. 2014. Plant movements and climate warming: intraspecific variation in growth responses to nonlocal soils. – *New Phytol.* 202: 431–441.
- Di Cola, V. et al. 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. – *Ecography* 40: 774–787.
- Elmendorf, S. C. and Moore, K. A. 2008. Use of community-composition data to predict the fecundity and abundance of species. – *Conserv. Biol.* 22: 1523–1532.
- Emad, A. and Bailey, P. 2017. wCorr: weighted correlations. – R package ver. 1.9.1. <<https://CRAN.R-project.org/package=wCorr>>.
- Engler, R. et al. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. – *Ecography* 35: 872–878.
- Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. – *Int. J. Climatol.* 37: 4302–4315.
- Fitzpatrick, M. C. et al. 2008. Climate change, plant migration and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. – *Global Change Biol.* 14: 1337–1352.
- Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. – *Divers. Distrib.* 16: 321–330.
- Greiser, C. et al. 2020. Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. – *Ecography* 43: 637–647.
- Guisan, A. et al. 2017. Habitat suitability and distribution models. – Cambridge Univ. Press.
- Hengl, T. et al. 2017. SoilGrids250m: global gridded soil information based on machine learning. – *PLoS One* 12: e0169748.
- Holland, P. G. and Steyn, D. G. 1975. Vegetational responses to latitudinal variations in slope angle and aspect. – *J. Biogeogr.* 2: 179.
- Körner, C. 1999. Alpine plant life. Functional plant ecology of high mountain ecosystems. – Springer Science & Business Media.
- Larson, E. R. et al. 2010. Decoupled conservatism of Grinnellian and Eltonian niches in an invasive arthropod. – *Ecosphere* 1: 1–13.
- Lembrechts, J. J. et al. 2019. Incorporating microclimate into species distribution models. – *Ecography* 42: 1267–1279.
- Mammola, S. et al. 2019. Associations between habitat quality, body size and reproductive fitness in the alpine endemic spider *Vesubia jugorum*. – *Global Ecol. Biogeogr.* 28: 1325–1335.
- Midolo, G. and Wellstein, C. 2020. Plant performance and survival across transplant experiments depend upon temperature and precipitation change along elevation. – *J. Ecol.* 108: 2107–2120.
- Morgenstern, E. K. 1996. Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. – UBC Press, Vancouver.
- Nadeau, C. P. and Urban, M. C. 2019. Eco-evolution on the edge during climate change. – *Ecography* 42: 1280–1297.
- Nagaraju, S. K. et al. 2013. Do ecological niche model predictions reflect the adaptive landscape of species? A test using *Myristica malabarica* Lam., an endemic tree in the Western Ghats, India. – *PLoS One* 8: e82066.
- Naimi, B. and Araújo, M. B. 2016. sdm: a reproducible and extensible R platform for species distribution modelling. – *Ecography* 39: 368–375.
- Naimi, B. et al. 2014. Where is positional uncertainty a problem for species distribution modelling? – *Ecography* 37: 191–203.
- Nakagawa, S. and Santos, E. S. A. 2012. Methodological issues and advances in biological meta-analysis. – *Evol. Ecol.* 26: 1253–1274.
- Nicotra, A. B. et al. 2010. Plant phenotypic plasticity in a changing climate. – *Trends Plant Sci.* 15: 684–692.
- Osorio-Olvera, L. et al. 2020. Relationships between population densities and niche-centroid distances in North American birds. – *Ecol. Lett.* 23: 555–564.
- Pacifici, M. et al. 2015. Assessing species vulnerability to climate change. – *Nat. Clim. Change* 5: 215–224.

- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Pellissier, L. et al. 2013. Suitability, success and sinks: how do predictions of nesting distributions relate to fitness parameters in high arctic waders? – *Divers. Distrib.* 19: 1496–1505.
- Peterson, A. T. et al. 2002. Future projections for Mexican faunas under global climate change scenarios. – *Nature* 416: 626–629.
- Peterson, M. L. et al. 2019. Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. – *Global Change Biol.* 25: 775–793.
- Pironon, S. et al. 2015. Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? – *Global Ecol. Biogeogr.* 24: 611–620.
- Pironon, S. et al. 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. – *Biol. Rev.* 92: 1877–1909.
- Pironon, S. et al. 2018. The 'Hutchinsonian niche' as an assemblage of demographic niches: implications for species geographic ranges. – *Ecography* 41: 1103–1113.
- Potter, K. A. et al. 2013. Microclimatic challenges in global change biology. – *Global Change Biol.* 19: 2932–2939.
- POWO 2019. Plants of the World Online. – Facilitated by the Royal Botanic Gardens, Kew. <www.plantsoftheworldonline.org/>, retrieved on April 2020.
- Pretzsch, H. and Dieler, J. 2011. The dependency of the size-growth relationship of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on long-term site conditions, drought events and ozone stress. – *Trees* 25: 355–369.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. – *Ecol. Lett.* 3: 349–361.
- Royal Botanic Gardens Kew. 2020. Seed Information Database (SID). Ver. 7.1. – <<http://data.kew.org/sid/>>, retrieved on April 2020.
- Sagarin, R. D. et al. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. – *Trends Ecol. Evol.* 21: 524–530.
- Sangüesa-Barreda, G. et al. 2018. Delineating limits: confronting predicted climatic suitability to field performance in mistletoe populations. – *J. Ecol.* 106: 2218–2229.
- Santini, L. et al. 2019. Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. – *Ecography* 42: 696–705.
- Scherrer, D. and Körner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. – *J. Biogeogr.* 38: 406–416.
- Sexton, J. P. et al. 2014. Genetic isolation by environment or distance: which pattern of gene flow is most common? – *Evolution* 68: 1–15.
- Smith, D. M. et al. 1997. The practice of silviculture. Applied forest ecology. – Wiley.
- Soberón, J. et al. 2018. A comment on 'Species are not most abundant in the centre of their geographic range or climatic niche'. – *Rethinking Ecol.* 3: 13–18.
- Suggitt, A. J. et al. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. – *Oikos* 120: 1–8.
- Svenning, J.-C. and Sandel, B. 2013. Disequilibrium vegetation dynamics under future climate change. – *Am. J. Bot.* 100: 1266–1286.
- Svenning, J.-C. and Skov, F. 2004. Limited filling of the potential range in European tree species. – *Ecol. Lett.* 7: 565–573.
- Taïbi, K. et al. 2014. Testing Aleppo pine seed sources response to climate change by using trial sites reflecting future conditions. – *New For.* 45: 603–624.
- Thuiller, W. et al. 2005. Climate change threats to plant diversity in Europe. – *Proc. Natl Acad. Sci. USA* 102: 8245–8250.
- Thuiller, W. et al. 2010. Variation in habitat suitability does not always relate to variation in species' plant functional traits. – *Biol. Lett.* 6: 120–123.
- Thuiller, W. et al. 2014. Does probability of occurrence relate to population dynamics? – *Ecography* 37: 1155–1166.
- Trabucco, A. and Zomer, R. J. 2010. Global soil water balance geospatialdatabase. CGIAR consortium for spatial information. Available from the CGIAR-CSI GeoPortal <www.cgiar-csi.org>.
- US Geological Survey. 1999. Digital representation of 'Atlas of United States Trees' by Elbert L. Little, Jr. United States Geological Survey Professional Paper 1650.
- Violle, C. and Jiang, L. 2009. Towards a trait-based quantification of species niche. – *J. Plant Ecol.* 2: 87–93.
- Violle, C. et al. 2007. Let the concept of trait be functional! – *Oikos* 116: 882–892.
- Wagner, S. et al. 2015. History of *Larix decidua* Mill. (European larch) since 130 ka. – *Quat. Sci. Rev.* 124: 224–247.
- Wittmann, M. E. et al. 2016. Confronting species distribution model predictions with species functional traits. – *Ecol. Evol.* 6: 873–879.
- Zhang, Z. et al. 2020. Future climate change will severely reduce habitat suitability of the critically endangered Chinese giant salamander. – *Freshwater Biol.* 65: 971–980.

Data sources

- Akalusi, M. E. and Bourque, C. P. A. 2018. Effect of climatic variation on the morphological characteristics of 37-year-old balsam fir provenances planted in a common garden in New Brunswick, Canada. – *Ecol. Evol.* 8: 3208–3218.
- Bresnan, D. F. et al. 1994. Black walnut provenance performance in seven 22-year-old plantations. – *Silvae Genetica* 43: 246–252.
- Bresnan, D. F. et al. 1996. Variation among green ash of differing geographic origins outplanted in Kansas. – *J. Arboricult.* 22: 113–116.
- Cooper, H. F. et al. 2019. Genotypic variation in phenological plasticity: reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. – *Global Change Biol.* 25: 187–200.
- Ding, C. et al. 2017. Post-glacial biogeography of trembling aspen inferred from habitat models and genetic variance in quantitative traits. – *Sci. Rep.* 7: 4672.
- Friedman, J. M. et al. 2011. Genetic and environmental influences on leaf phenology and cold hardiness of native and introduced riparian trees. – *Int. J. Biometeorol.* 55: 775–787.
- Huang, Y.-N. et al. 2015. White oak growth after 23 years in a three-site provenance/progeny trial on a latitudinal gradient in Indiana. – *For. Sci.* 62: 99–106.
- Ledig, F. T. et al. 2015. Postglacial migration and adaptation for dispersal in pitch pine (Pinaceae). – *Am. J. Bot.* 102: 2074–2091.
- Mahony, C. R. et al. 2020. Evaluating genomic data for management of local adaptation in a changing climate: a lodgepole pine case study. – *Evol. Appl.* 13: 116–131.

- Marchin, R. M. et al. 2008. Population-level variation of *Fraxinus Americana* (white ash) is influenced by precipitation differences across the native range. – *Tree Physiol.* 28: 151–9
- McKown, A. D. et al. 2014. Geographical and environmental gradients shape phenotypic trait variation and genetic structure in *Populus trichocarpa*. – *New Phytol.* 201: 1263–1276.
- McLane, S. C. and Aitken, S. N. 2012. Whitebark pine *Pinus albicaulis* assisted migration potential: testing establishment north of the species range. – *Ecol. Appl.* 22: 142–153.
- Mylecraine, K. A. et al. 2005. Rangewide provenance variation in Atlantic white-cedar *Chamaecyparis thyoides*: early survival and growth in New Jersey and North Carolina plantations. – *For. Ecol. Manage.* 216: 91–104.
- Rehfeldt, G. E. 2011. ‘Genetic variation in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*)’. Obtained through personal communication with M.V. Warwell. – U.S. Dept of Agriculture, Forest Service, Rocky Mountain Research Station (unpubl.).
- Savva, Y. et al. 2007. Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada. – *For. Ecol. Manage.* 242: 636–647.
- Sebastian-Azcona, J. et al. 2019. Survival, growth and cold hardness tradeoffs in white spruce populations: implications for assisted migration. – *For. Ecol. Manage.* 433: 544–552.
- Soolanayakanahally, R. Y. et al. 2009. Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). – *Plant Cell Environ.* 32: 1821–1832.
- Steiner, K. C. et al. 1988. Juvenile performance in a range-wide provenance test of *Fraxinus pennsylvanica* Marsh. – *Silvae Genetica* 37: 104–111.
- van Haverbeke, D. F. 2005. Data product containing tree heights, survival and genetic variation for ‘Genetic variation in ponderosa pine: a 15-year test of provenances in the great plains’. – Forest Service Research Data Archive.
- van Haverbeke, D. F. 2006. Data product containing 16-year tree heights, survival and genetic variation for ‘Genetic variation in blue spruce: a test of populations in Nebraska’. – Forest Service Research Data Archive.
- van Haverbeke, D. F. and King, R. M. 2006. Data product containing 5-year tree heights, survival and genetic variation for ‘Genetic variation in great plains *Juniperus*’. – Forest Service Research Data Archive.
- Warwell, M. V. and Shaw, R. G. 2017. Climate-related genetic variation in a threatened tree species, *Pinus albicaulis*. – *Am. J. Bot.* 104: 1205–1218.
- Xie, C. Y. et al. 1996. Genetic variability and performance of red alder *Alnus rubra* in British Columbia. – In: Ecology and management of B.C. Hardwoods. Workshop proceedings, 1–2 December 1993, Richmond, B. C. Edited by Comeau, P. G. et al. FRDA report No. 225. Co-published by Canadian Forest Service and B.C. Ministry of Forests, Vancouver, B.C., pp. 147–156.