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ΔTraitSDM: species distribution models that account for local adaptation and phenotypic plasticity

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Summary

Improving our understanding of species' ranges under rapid climate change requires application of our knowledge of the tolerance and adaptive capacity of populations to changing environmental conditions. Here, we describe an emerging modelling approach, Δ TraitSDM, which attempts to achieve this by explaining species distribution ranges based on phenotypic plasticity and local adaptation of fitness-related traits measured across large geographical gradients. The collection of intraspecific-trait data measured in common-gardens spanning broad environmental clines has promoted the development of these new models; firstly in trees but now rapidly expanding to other organisms. We review, explain and harmonize the main findings from this new generation of models that, by including trait variation over geographical scales, are able to provide new insights into future species ranges. Overall, Δ TraitSDM predictions generally give a less alarming message than previous models of species distribution under new climates, indicating that phenotypic plasticity should considerably help some plant populations to persist under climate change. The development of Δ TraitSDM opens a new perspective allowing analysis of intra-specific variation in single and multiple traits, with the rationale that trait (co-)variation and consequently fitness can significantly change across geographical gradients and new climates.

1. Introduction

The observed impact of contemporary climate warming on patterns of species migration and range shift has created a high demand for forecasts of biodiversity changes (Urban, 2015). Species distribution models (SDM) are a widely-used tool for generating hypotheses about the potential consequences of climate changes on the natural distribution of species (Urban, 2015), to predict current species richness (Algar *et al.*, 2009), to understand biological invasion (Camenen *et al.*, 2016), to propose locations for protected areas (Koch *et al.*, 2017), to select species for ecological restoration (Gastón & García-Viñas, 2013), and to target areas where endangered species might occur (McCune, 2016). SDM are correlational models of low structural complexity that rely on the statistical relationship between species' occurrence and local climate. However, these models have often been criticized for relying on over-simplistic assumptions and neglecting critical biological processes involved in species' response to a rapidly changing environment (Fordham *et al.*, 2018). Several SDM and mechanistic modelling approaches have recently been developed to better account for key ecological processes such as species' dispersal ability, (meta-)population demography and dynamics, and the role of different biotic interactions (reviewed in Pagel & Schurr, 2012; Wisz *et al.*, 2013; Normand *et al.*, 2014). These refined approaches have considerably improved our understanding of how climate warming could drive changes in the distributions of species and the abundance of populations across their range. However, very few models have to date considered a further key dimension in the response of populations to rapid environmental change: phenotypic variation in functional traits and its consequences for fitness (Valladares *et al.*, 2014; Roches *et al.*, 2018). Here, we review recent developments in this emerging field and unify different approaches that consider phenotypic trait variation under a common header for which we propose the term Δ TraitSDM.

Species ranges are modulated by those biological mechanisms that allow populations to survive and reproduce within their local abiotic and biotic environment as well as those that determine their dispersal capacity (Hargreaves *et al.*, 2014). Under rapid climate change, populations are expected to be extirpated, to track climate through migration (Brito-Morales *et al.*, 2018), or to persist *in situ*

through phenotypic plasticity and evolutionary adaptation (Valladares *et al.*, 2014; Des Roches *et al.*, 2018): the latter two biological mechanisms form the basis of Δ TraitSDM. Phenotypic plasticity refers to the capacity of one genotype to express different phenotypes across environmental gradients, giving individual organisms the flexibility to react rapidly to environmental changes (Nicotra *et al.*, 2010). Evolutionary adaptation involves selection acting on heritable traits, producing fitness differentials that lead to a predominance of individuals with high performance within their local environment (Savolainen *et al.*, 2013). Phenotypic plasticity and local adaptation are ubiquitous in natural populations, and their interplay is important in shaping patterns of geographical variation in phenotypic traits found across the species range (Savolainen *et al.*, 2013; Valladares *et al.*, 2014; Roches *et al.*, 2018). Extensive phenotypic plasticity is often considered favourable for the persistence of populations under rapid climate change (Valladares *et al.*, 2014), although it can delay evolutionary adaptation to new environments in the long term (Wund, 2012). However, few studies have been able to tease apart the roles of plasticity vs. local adaptation for fitness across large environmental gradients (McClean *et al.*, 2014; Richardson *et al.*, 2017; Macdonald *et al.*, 2018). These studies are typically based on common-garden experiments where the genetic origins of the populations are known (Wilczek *et al.*, 2014). Until recently, a poor understanding of the role of phenotypic plasticity and local adaptation in shaping species ranges has critically limited attempts to anticipate how these mechanisms will drive the performance of populations under new climates (Des Roches *et al.*, 2018). This is now changing thanks to the increasing availability of data from common-garden and reciprocal-transplant experiments established along large environmental gradients (Robson *et al.*, 2018), for which reaction norms (i.e., the phenotypic response of a genotype across different environments) have been measured to quantify phenotypic variation of given populations across the species range. These data are fundamental for the development of Δ TraitSDM, emerging models that quantify local adaptation, phenotypic plasticity and their interaction across species ranges to make predictions about the persistence of populations and species under new climates.

The dependence of Δ TraitSDM on extensive common-garden experiments explains why these models were first developed in forest research (Rehfeldt *et al.*, 1999). Driven by the wish to identify suitable material for afforestation, common-garden experiments with many thousands of trees have been established and monitored over the past decades for a series of economically-important forest tree species. It is hence not surprising that early Δ TraitSDM mostly addressed management-related questions (Rehfeldt *et al.*, 1999). Since then, Δ TraitSDM have been expanded to more broadly consider how phenotypic plasticity and local adaptation affect projections of future species ranges (O'Neill *et al.*, 2008; Benito Garzón *et al.*, 2011; Oney *et al.*, 2013; Sáenz-Romero *et al.*, 2017; Rehfeldt *et al.*, 2018). During the last few years, the use of Δ TraitSDM has also extended to plants other than forest trees with the inception of large-scale experiments designed to separate local adaptation from phenotypic plasticity under controlled environmental conditions (Richardson *et al.*, 2017).

Here, we review, explain and harmonize the use of Δ TraitSDM: species distribution models that, by including phenotypic plasticity and local adaptation of fitness-related traits over geographical scales, are able to provide new insights into the sensitivity to climate change of populations across species ranges.

2. Δ TraitSDM: traits, reaction norms, fitness and species ranges

To account for phenotypic trait variation, Δ TraitSDM capture reaction norms of different provenances (i.e., populations from a specific geographic location) that are planted together in series of common-gardens across a species range (Fig. 1). The rationale underlying this approach is that higher fitness implies a higher probability of population persistence in the local environment. To explain the relationship between trait variation and fitness in Δ TraitSDM, we can make use of SDM as baseline models: in SDM, the occurrence of a species in a given location is implicitly related to its survival capacity (or fitness-related trait values) under certain climatic conditions with fitness represented as binary value (1 = maximum fitness: survival, and 0 = minimum fitness: no survival). In Δ TraitSDM, the binary information on species occurrence is replaced with empirical observations of fitness-related phenotypic traits of controlled genetic origin. This allows Δ TraitSDM to keep the statistical simplicity of SDMs, while (i) making an explicit, empirically grounded link with fitness-related traits; (ii) splitting the phenotypic variation of target traits into the components of local adaptation (i.e., related to the climate of origin of the provenance) and of phenotypic plasticity (i.e., related to the climate of the common-garden site); and (iii) combining multiple traits and assessing their co-variation across species ranges (for which we propose the term multi-trait Δ TraitSDM).

Following this rationale, Δ TraitSDM are developed in three steps (Fig. 1) that are described in the following sections.

2. 1. Gathering phenotypic trait variation from common gardens across large environmental gradients

Δ TraitSDM are based on trait measurements recorded in well replicated common gardens planted with many provenances to capture environmental variation across the species range (Fig. 1A). The choice of an appropriate phenotypic trait is based on its putative relationship with fitness, defined in this context by the capacity of individuals to survive (survival success) and to contribute to the next generation (reproductive success). Data on fitness regarding reproductive success at range-wide scales has been directly measured for some herbaceous species (Wilczek *et al.*, 2014; Wadgymar *et al.*, 2017), although equivalent information has seldom been obtained for trees across large geographical areas. To date, the traits most commonly considered by Δ TraitSDM are those related to growth, spring phenology and mortality. Ecophysiological traits such as: specific leaf area, stomatal anatomy and photosynthesis (Drake *et al.*, 2017; Patterson *et al.*, 2018), wood density (Díaz *et al.*, 2016), and xylem resistance to embolism (Anderegg *et al.*, 2016; Benito Garzón *et al.*, 2018) can affect demography and phenology and may alter fitness across species ranges. Hence, they are good candidates to be integrated in Δ TraitSDM when more information at the intra-specific level becomes available.

2.2. Integration of reaction norms in a unified model

Reaction norms are calculated by regressing trait values against the climates of the provenance sites and the common gardens (Fig. 1B). Regressions are based on the rationale that (i) individual populations are locally adapted to the climatic conditions of the site where the seed originated,

while (ii) the acclimation response of phenotypic traits occurs in response to the climatic conditions experienced at the common-garden site since the time of plantation (Leites *et al.*, 2012). Two regression methods are typically used to calculate trait reaction norms across species ranges: statistical models such as universal transfer functions or linear mixed-effect models; and machine learning techniques such as random forests or artificial neural networks. Universal transfer functions first fit one equation by provenance and then scale up to all experimental sites in a stepwise process (O'Neill *et al.*, 2008). Linear mixed-effect models combine the provenance and the site effect in a single equation, while including random effects that control for differences among experimental sites that are not related to climate (e.g. soil characteristics) (Leites *et al.*, 2012). Machine learning models are characterized by a greater flexibility as they can use any combination of predictors (i.e., several environmental drivers in complex non-linear relationships); they have a higher predictive power than statistical techniques but do not provide any form of equation. Hence, machine-learning approaches are an interesting option when the complexity of the combination of predictors prevents statistical convergence of other models (Benito Garzón *et al.*, 2011). On the whole, linear mixed-effect models are the most widely used because of their flexibility and capacity to account for the experimental design of common gardens as a random effect.

For linear mixed-effect models, the equation describing the regression between traits and environmental drivers in $\Delta\text{TraitSDM}$ takes the general form:

$$T_1 = a_0 + b_1 CP + b_2 CS + b_3 CP \times CS + \beta + \delta + \varepsilon \quad (\text{equation 1})$$

Where T_1 is the trait value, a_0 represents the slope, b_1 , b_2 and b_3 are the coefficients of the regression, δ is the random effect controlling for variation arising from the common garden experimental design, and ε is the model error. CP represents the climatic variables characterizing the provenances, and CS the climatic variables characterizing the planting site. $CP \times CS$ represents the interaction between the climate of the provenance sites and those of the common garden sites. β can include model co-variables if needed.

Equation 1 allows us to quantify that part of the variance attributable to the genetic effect of each provenance (b_1), to the phenotypic plasticity (b_2) and the interaction between them (b_3) representing the genetic x environment effect.

2.3. Spatial prediction of phenotypic traits.

In addition to quantifying the plastic and genetic components of phenotypic trait variation, $\Delta\text{TraitSDM}$ can also be used to generate spatial projections of trait variation under current or future climate scenarios using the relationship with climate of the fitted equation (equation 1, Fig. 1C). Because traits and their relation with fitness can change across climatic gradients, projections are highly dependent on the trait used. In some cases, higher values of fitness-related traits correspond to species occurrence (Benito Garzón *et al.*, 2011; Chakraborty *et al.*, 2018), but in other cases species occurrence is explained by the complex relationship among various traits over the species range (Gárate Escamilla *et al.*, 2019). For example, phenological traits may delimit species ranges at high latitudes, at least for those species in which photoperiod actively constrains phenology (Way & Montgomery, 2015). Traits related to reproduction are probably more relevant near the leading range-edge where colonization events and population growth prevail, whereas traits related to drought resistance are more likely to be relevant near the trailing range-edge (Hampe & Petit 2005).

Great care is needed in trait selection, to ensure that traits are selected to account for the potential of climate change to reshuffle trait-interaction across species ranges (see Section 4).

3. What can we learn from Δ TraitSDM?

Δ TraitSDM are new and have been developed for various different purposes, therefore it is difficult to assess their contribution to understanding phenotypic plasticity and local adaptation patterns across large gradients, and contingent implications for species ranges under current and future conditions. Three major messages emerge from examining the outputs of existing Δ TraitSDM, and from comparing them with SDM outputs as baseline models, for the very few studies that to date have explicitly done this (Tables 1 and 2; Fig 2): (i) phenotypic plasticity is the most important component of intra-specific variation in demographic and phenological traits, (ii) spatial predictions of Δ TraitSDM based on experimental data do not necessarily match current species ranges but rather reflect the adaptive and plastic responses of populations to climate, (iii) spatial predictions using Δ TraitSDM generally depict a smaller contraction of species ranges with climate change compared to forecasts based on SDM. These conclusions are mostly based on trees and may somewhat differ for species with more restricted gene flow or shorter generation times.

Although undoubtedly important, the contribution of local adaptation to phenotypic trait variation across species ranges is lower than the contribution of plasticity for all the species and traits studied to date (Table 1), suggesting that, in trees, phenotypic plasticity is generally the predominant component of intraspecific variability. The initial aim of Δ TraitSDM was in guiding the selection of tree populations for translocation to mitigate the effects of climate change (Aitken & Bemmels, 2016), however this result (Table 1) suggests that moving populations adapted to warmer climates polewards would give only modest benefits towards this aim of increasing their productivity and/or survival. Nevertheless, the relative importance of plasticity vs. local adaptation can differ among traits. Overall, height and radial growth tend to show less local adaptation to climate than traits related to phenology (bud burst and flowering) (Duputié *et al.*, 2015; Richardson *et al.*, 2017). As a consequence, the choice of trait(s) to use in a Δ TraitSDM modulates the predicted response to climate across the range. For instance, growth-related traits are highly plastic, whereas in comparison phenology is constrained by local adaptation to current conditions. Hence, Δ TraitSDM based on growth-related traits would produce predictions of higher tolerance to climatic variation than Δ TraitSDM based on phenology. Nevertheless, phenology has a strong plastic component, suggesting that populations can to some extent accommodate flowering dates to track expected climatic scenarios, as found in *Artemisia tridentata* populations in North America (Richardson *et al.*, 2017). Hence, a natural extension of Δ TraitSDM will be to combine multiple traits and their interactions to account for the different responses of traits to climate (Laughlin, 2018; Gárate Escamilla *et al.*, 2019).

At an evolutionary scale, phenotypic plasticity could slow down genetic adaptation and hence turn into a counter-productive mechanism for the long-term survival of populations (Oostra *et al.*, 2018). However, over the short-time scales imposed by modern rapid climate change, having higher plasticity than local adaptation in fitness-related traits is likely to translate into a positive outcome in terms of survival, at least for long-lived organisms like trees that are experiencing significant environmental change within their lifetime. Δ TraitSDM indicate that many tree populations hold

enough phenotypic plasticity in fitness-related traits to persist *in situ* over the coming few decades under commonly used climatic scenarios (Table 1). This is the case for height growth in *Pinus contorta* (Oney *et al.*, 2013) and in *Abies alba* (Pearman *et al.*, 2008; Fréjaville *et al.*, 2019), showing that Δ TraitSDM predict less-restricted distributions than models that only consider the occurrence of a species. Similar conclusions can be drawn from Δ TraitSDM based on survival of *Pinus sylvestris* and *Pinus pinaster* considering only the southernmost part of their range (Benito Garzón *et al.*, 2011).

A comparison between Δ TraitSDM and SDM predictions under current (Fréjaville & Benito Garzón, 2018) and future climate scenarios (RCP 8.5 GISS-E2-R, Nazarenko *et al.*, 2015) is illustrated by the example of *Fagus sylvatica* (Fig. 2). The SDM (adapted from Stojnić *et al.*, 2018) is based on the occurrence/absence of the species, whereas the Δ TraitSDM (adapted from Gárate Escamilla *et al.*, 2019) is based on young tree mortality measured across a large network of common gardens (Robson *et al.*, 2018). The large differences visible between SDM and Δ TraitSDM outputs can be interpreted as the result of differences in how each model handles fitness. Not surprisingly, the SDM prediction for current conditions perfectly matches the species distribution range that is the basis of the regression. On the contrary, the Δ TraitSDM predicts low survival for young trees in areas within the current range (eastern part of the range) and high survival in areas located outside the current native distribution range of *F. sylvatica* (western part of the range). The former prediction can be interpreted as an early warning: i.e. the species still occurs in that part of the range but with very high mortality. But it may also reflect successful *F. sylvatica* recruitment in climatically favourable years not captured by the trait data. The latter prediction for the western part of the range reflects a long history of active management which has left only a few beech forests remaining in Britain today. These can be considered native (Sjölund *et al.*, 2017) and furthermore where planted *F. sylvatica* is regenerating vigorously in Britain and Ireland (Packham *et al.*, 2012).

This example of *F. sylvatica* also illustrates our third conclusion that predictions using Δ TraitSDM generally depict larger future species ranges than forecasts based on SDM (see Fig. 2, Table 2.). Basically, Δ TraitSDM give more conservative predictions of greater similarity in distribution ranges between present and future conditions (Fig. 2). This pattern is consistent across those few studies published to date that employ Δ TraitSDM (Table 1), and it is likely to result from the high plasticity of populations helping them to persist *in situ*. However, we can expect that considering other traits or combination of traits in Δ TraitSDM would lead to different conclusions, particularly under new climates, where it is difficult to predict trait co-variation and the relationship of traits with climate.

4. Towards multi-trait Δ TraitSDM

Although multi-trait approaches are, to date, only conceptually proposed (Laughlin & Messier, 2015; Laughlin, 2018), the flexibility of Δ TraitSDM favors their actual implementation. One possible way to develop multi-trait Δ TraitSDM is by substituting β (equation 1) for a second trait used as a co-variate. For example, a model where a co-variate trait (T_2) that affects T_1 across climatic clines can take the form:

$$\beta = b_4 T_2 + b_5 T_2 \times CS + b_6 T_2 \times CP \quad (\text{equation 2})$$

where T_2 is a trait that co-varies with T_1 ; b_4 , b_5 and b_6 are the coefficients of T_2 and the interactions with climate of the common-garden site (CS) and with the provenance (CP).

Multi-trait Δ TraitSDM draw upon concepts developed in functional ecology that consider weighted-average trait values as a function of species performance to delimit species ranges (Stahl *et al.*, 2014), with the additional strength that they consider intra-specific variation for each of the traits. Trait co-variation can modulate fitness across species ranges (Laughlin & Messier, 2015), and can result in compensatory changes in demographic traits that buffer the negative effects of warming at the trailing range-edge (Peterson *et al.*, 2018). It can also produce relationships between survival and phenology-related traits that vary across species ranges (Richardson *et al.*, 2017; König *et al.*, 2018), and trade-offs between photoperiod and tree growth that might limit species range expansion at the leading edge (Way & Montgomery, 2015).

5. Conclusions, perspectives and limitations of Δ TraitSDM

The Δ TraitSDM approach to understanding the controls on species ranges has been refined over the last decade, producing projected species ranges that are remarkably different from SDM outputs and generally are less alarming with regard to the consequences of climate change for species in the future. These differences emanate from the inclusion in Δ TraitSDM of plasticity, which can differ among populations across species ranges. The broad scope of Δ TraitSDM calls into question why this approach is not more widely used, especially for those forest tree species which are already growing in common gardens. The reason likely reflects technical difficulties in compiling, harmonising and calibrating models using extensive field measurements. Our review shows that future conservation and management programs of tree populations such as assisted migration should look beyond SDM and not neglect the capacity of populations to adapt and acclimate to new conditions.

Δ TraitSDM are based on empirical data measured in large networks of common gardens. This is a great strength of Δ TraitSDM but also its main constraint. Although incomplete data can be used in partial analyses, a poor representation of common gardens and provenances can easily compromise the statistical power of Δ TraitSDM; something that is required to scale-up processes and produce spatial generalisations. This is particularly important in predictive ecology, in which reaction norms inform us about the limits of environmental conditions that populations can withstand. In the context of climate change, one implication of this is straightforward: that new common gardens planted outside the limits of the distribution range of a species are needed to estimate the maximum tolerance of fitness-related traits to new conditions.

To date, Δ TraitSDM have mostly been based on a limited variety of traits that are largely related to the survival component of fitness. Although growth and phenology can indirectly impact seed production, therefore affecting fitness through reproduction, direct measurements of reproduction are still missing from Δ TraitSDM. This is mainly because reproduction is largely unexplored at the range-wide scale in common gardens. More generally, we still know little about how well phenotypic traits measured under the experimental conditions of a common garden can represent phenotypic variation and its relation with fitness in natural populations.

Natural selection boosts genetic differentiation among populations but reduces within-population genetic variation by fixing alleles (local adaptation). The potential of populations to adapt to new climates depends on the extent of within-population genetic variation at evolutionarily relevant loci; something that has not yet been addressed by Δ TraitSDM. This variation is however associated with climate across large gradients (Bay *et al.*, 2018). Hence, linking genomics to phenotypic and environmental variation is the natural next step in Δ TraitSDM that will help us explain populations' potential for adaptation under new climate conditions across species ranges.

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AUTHOR CONTRIBUTIONS

MBG designed and wrote the first draft. MBG, TMR and AH wrote the final manuscript.

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FIGURE LEGENDS

Figure 1. Conceptual framework of Δ TraitSDM: A) Experimental design of common-garden networks across different climates (coloured oval shapes), where trees originate from different provenances (indicated by three colours: blue, red and yellow). Tree performance is represented by tree size. B) The graphs on the left represent different possible reaction norms calculated from the various provenances (indicated by their colour) across common gardens (three left panels); the corresponding graphics on the right represent the conversion of these reaction norms into trait breadth, that is, the relationship between the phenotype – e.g. height or survival - and fitness. C) Spatial prediction of a given fitness-related trait. The example shows the output of a Δ TraitSDM for *Fagus sylvatica* based on survival of young trees (adapted from Gárate Escamilla *et al.*, 2019) estimated from the BeechCOSTe52 network of common gardens (Robson *et al.*, 2018). The dashed envelope shows the current distribution of *Fagus sylvatica* (<http://www.euforgen.org/species/fagus-sylvatica/>).

Figure 2. Spatial predictions of habitat suitability (>0.5) from a SDM (left) and probability of young tree survival according to common-garden data (>0.5) from a Δ TraitSDM (right) under current (top) and future conditions (bottom) based on mortality measurements. The maps compare the models' predictions with the current species range. Blue areas identify a perfect match between model predictions (habitat suitability/recruit survival) and species occurrence. Orange areas show regions with high suitability/recruit survival (>0.5) predicted by the models where the species is currently absent. Green areas indicate low suitability/recruit survival (<0.5) where the species is currently present. Habitat suitability was calculated using the occurrence/absence of the species according to EUFORGEN (<http://www.euforgen.org/species/fagus-sylvatica/>) and by adapting the SDM developed in (Stojnić *et al.*, 2018) to match the same climatic variables as those used by the Δ TraitSDM. Probability of recruit survival was estimated by a Δ TraitSDM based on individual survival of young trees (adapted from Gárate Escamilla *et al.*, 2019) measured in the BeechCOSTe52 network of provenance tests (Robson *et al.*, 2018). Future predictions are based on RCP 8.5 (Representative Concentration Pathway 8.5) Scenario from the NASA Goddard Institute for Space Sciences coupled general circulation model for an increase in temperature ranging 3.5–4.5°C in 2100 (Nazarenko *et al.*, 2015).

TABLES

Table 1. Comparison between Δ TraitSDM and SDM outputs for those cases where both types of models exist or where local adaptation and phenotypic plasticity have been quantified across species ranges.

	Δ TraitSDM					SDM	Δ TraitSDM - SDM – PBM Comparison
Species	TPVE	PVEP	PVEG	Traits	References	References	
<i>Abies alba</i>	42			Tree height	(Fréjaville <i>et al.</i> , 2019) ¹	(Pearman Peter B. <i>et al.</i> , 2008)	SDM show a more restricted distribution than Δ TraitSDM, particularly at the periphery of the distribution.
<i>Artemisia tridentata</i>	79	46	33	Flowering phenology	(Richardson <i>et al.</i> , 2017)		
<i>Fagus sylvatica</i>	45 (PVEP+ PVEG) 49 (PVEP + PVEG) 19 (PVEP + PVEG)	- - -	- - -	Tree height DBH Mortality Budburst Fruit ripening Leaf senescence	(Gárate Escamilla <i>et al.</i> 2019) (Gárate Escamilla <i>et al.</i> 2019)) (Gritti <i>et al.</i> , 2013)	(Pearman Peter B. <i>et al.</i> , 2008; Gritti <i>et al.</i> , 2013; Stojnic <i>et al.</i> , 2018)	Differences in the distribution depend on the trait used (Δ TraitSDM). Overall, predictions from Δ TraitSDM show larger potential distribution ranges than those predicted by SDM.
<i>Picea mariana</i>	37	28	9	Tree growth	(Yang <i>et al.</i> , 2015)	-	-
<i>Pinus pinaster</i>	43.1 (PVEP + PVEG)	-	-	Tree height Survival	(Benito Garzón <i>et al.</i> , 2011)	-	Reduction in suitable area estimated with SDM by 2080 = 60 %; reduction in suitable area estimated with Δ TraitSDM by 2050 = - 30%
<i>Pinus ponderosa</i>	-	-	-	Tree height	(Rehfeldt <i>et al.</i> , 2014)	(Rehfeldt <i>et al.</i> , 2014)	Large differences in tree growth and habitat suitability. No direct

							comparison of the two models.
<i>Pinus strobus</i>	32	29	3	Tree growth	(Yang <i>et al.</i> , 2015)	-	-
<i>Pinus sylvestris</i>	82.4 (PVEP + PVEG) 52.85 (PVEP + PVEG) 33 (PVEP + PVEG)	- - -	- - -	Survival Budburst Survival & radial growth Leaf unfolding	(Benito Garzón <i>et al.</i> , 2011; Valladares <i>et al.</i> , 2014) (Gritti <i>et al.</i> , 2013; Valladares <i>et al.</i> , 2014) (Duputié <i>et al.</i> , 2015) (Duputié <i>et al.</i> , 2015)	(Benito Garzón <i>et al.</i> , 2008) (Gritti <i>et al.</i> , 2013)	Reduction in area estimated with SDM by 2080 = 98%; reduction in suitable area estimated with Δ TraitSDM by 2050 = 1 %
<i>Pseudotsuga menziesii</i>	-	-	-	Tree height	(Chakraborty <i>et al.</i> , 2018)	(Chakraborty <i>et al.</i> , 2018)	Δ TraitSDM based on growth and SDM show very similar predictions under current climate.
<i>Quercus petraea</i>	60.8 58.1 71 (PVEP + PVEG) 7 (PVEP + PVEG) 24 (PVEP + PVEG)	59.4 56.6 - - -	1.4 1.5 - - -	Tree height Survival Budburst Fruit ripening Leaf senescence	(Sáenz-Romero <i>et al.</i> , 2016; Fréjaville <i>et al.</i> , 2019) (Duputié <i>et al.</i> , 2015)	-	-
<i>Quercus robur</i>	-	-	-	Phenology	(Gritti <i>et al.</i> , 2013) ¹	(Gritti <i>et al.</i> , 2013)	-
<i>Andropogon gerardii</i>	-	-	-	Biomass Height	(Smith <i>et al.</i> , 2017)	-	-

				Leaf width Chlorophyll content			
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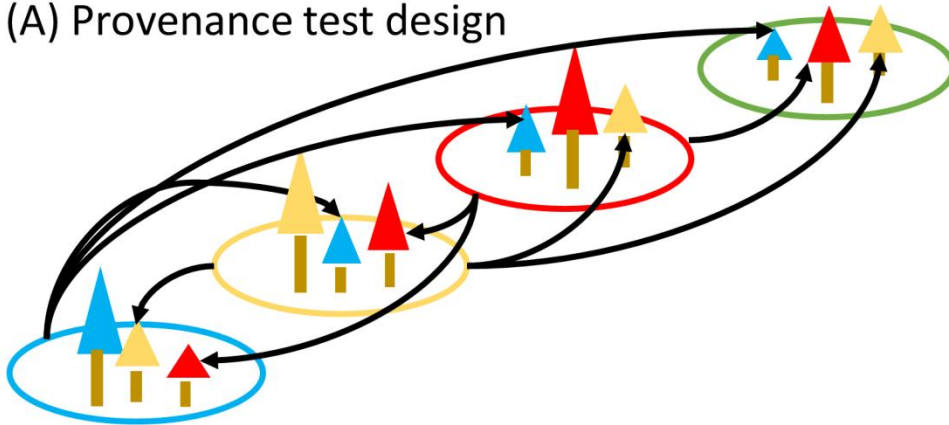
¹ Reaction norms accounting for plasticity are estimated only at the core of the species distribution.

TPVE: Total percentage of the variance explained by the model; PVEP: Percentage of the variance explained by plasticity; PVEG: Percentage of the variance explained by local adaptation; Traits: phenotypic traits used by the model; References: references from which the data for the Δ TraitSDM and SDM have been extracted to compare the two modelling approaches. DBH: diameter at breast height.

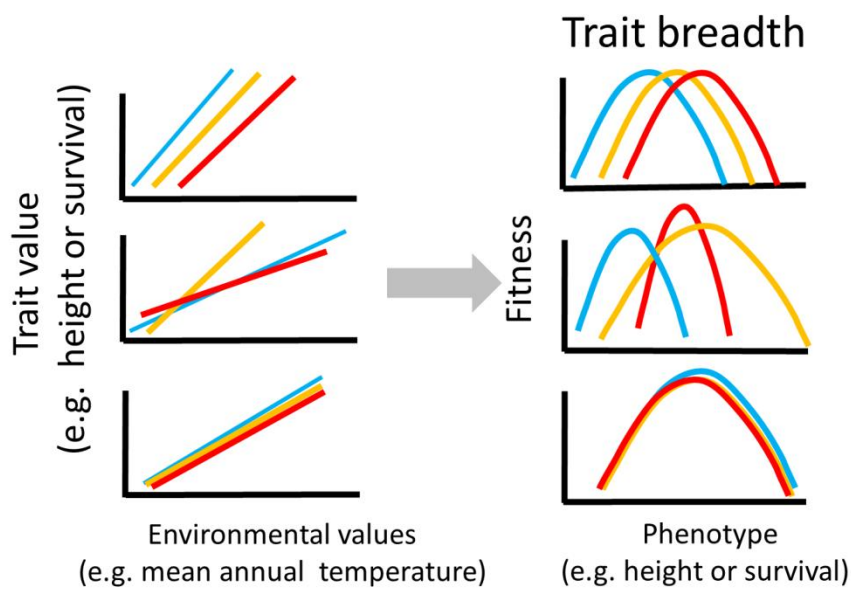
Table 2. Comparison between predictions of habitat suitability (SDM) and probability of young tree survival (Δ TraitSDM) shown in Fig. 2 (see Fig. 2 caption for details).

	SDM – Δ TraitSDM comparison for <i>Fagus sylvatica</i>	SDM – habitat suitability (%)	Δ TraitSDM survival (%)
PRESENT	current occupied range predicted to have high suitability/survival (blue in Fig. 2)	93.56	52.65
	current occupied range predicted to have low suitability/survival (green in Fig. 2)	6.27	47.34
	current un-occupied range predicted to have high suitability/survival (orange in Fig. 2)	30.90	113.30
2070 RCP 8.5	current occupied range predicted to have high suitability/survival – range persistence (blue in Fig. 2)	48.22	49.64
	current occupied range predicted to have low suitability/survival – range retreat (green in Fig. 2)	49.98	50.36
	current un-occupied range predicted to have high suitability/survival (orange in Fig. 2)	88.72	100.45

(A) Provenance test design



(B) Reaction norms



(C) Trait spatial distribution

