

Population Ecology from Local to Global Scales: a case study using *Plantago lanceolata*

by

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Declaration

I declare that this thesis has not been submitted as an exercise for a degree at this or any other university and it is entirely my own work, except where contributions from co-authors and collaborators are explicitly mentioned within the authorship contributions statement starting this PhD. I agree to deposit this thesis in the University's open access institutional repository or allow the Library to do so on my behalf, subject to Irish Copyright Legislation and Trinity College Library conditions of use and acknowledgement.

Maude E. A. Baudraz

Summary

As biodiversity is showing a sharp decline globally, we are in need of applied conservation and management advice. Strategies are often developed by using population ecology, which studies populations of individuals of a species in one or more locations, for instance to infer on the mechanisms enabling population persistence. Most population studies are undertaken in very few locations of management interest, often only in a limited set of local conditions. To preserve our planet's biosphere, we need to study the mechanisms underlying population performance and persistence across multiple populations of the same species in multiple environmental and biotic contexts. As detailed population studies typically lack replication in space, we also need to use information to infer population performance from other, more readily available sources. Here we investigate approaches and methods to achieve this goal in the model organism *Plantago lanceolata*. This perennial herb is native to Eurasia, but its range is currently near-global due to repeated introductions. The demography of the species is monitored by the PlantPopNet collaborative science project in over 60 populations worldwide. We extended the PlantPopNet database by conducting demographic monitoring across 18 additional populations along a steep environmental gradient in the Alps, where *P. lanceolata*, a lowland species, is known to reach a niche limit.

In chapter one, we investigated whether the relationship between demographic performance and plant size remains the same across different parts of the range of *P. lanceolata*. In particular, we investigated whether different size metrics performed better in different parts of the range of the species. We established that simple size metrics such as leaf number captured patterns in vital rates similarly across populations, climatic gradients and both the native and invasive range of the species. We found that while demographic metrics in some populations were captured more or less well, there was no consistent effect of the choice of size metric in specific areas, in either geographic or climatic space. The most powerful and flexible modelling techniques to date describe changes in fitness among individuals within several populations based on the relationship between plant size and demographic outputs. Therefore, that the choice of size metric was of little impact greatly facilitates demographic modelling across multiple populations.

In chapters 2, 3 and 4, we made use of species distribution models to summarize multi-driver environmental gradients into one metric, the predicted probability of occurrence of the species. This metric also pulls information from readily available species occurrence information and offers a common environmental currency comparable across populations, locations and species. In chapter 2 we found a faster life cycle in areas with higher SDM-predicted probability of occurrence in our regional study in the Alps. The generation length and reproductive life expectancy were shorter, but the yearly reproductive rate was higher and populations relied less on retrogression in high suitability areas. These life history changes were shown to be mostly caused by a lower probability of survival in high suitability areas. Abundance decreased as predicted suitability increased. Population growth rates were found to be constantly close to 1 (stable population size), due to a density dependent recruitment regime. In chapter 4, we found a similar patterns of an increased pace in the life cycle of *P. lanceolata* in high probability of occurrence areas across the Eurasian native range of the species. This paves the way for the use of Species Distribution Models to infer local life history strategies of populations. In the discussion of this thesis, we discuss how these patterns could potentially extend to different species.

In chapter 3, we investigated the use of functional traits to predict the demographic performance of individuals along the steep elevation gradient. Functional traits are expected to capture changes in the fitness of individuals. They are easier to measure than the vital rates of growth, fecundity and survival. Nonetheless, studies investigating the relationship between functional traits and demographic performance typically find weak correlations. Inferring demographic functionality based on functional traits alone is therefore difficult. We found that functional traits measured in replicate populations corresponded with the shift in life history strategy observed in chapter 2. Plants produced thinner and broader leaves in high suitability areas, and many more seeds, with an uncertain trend towards a lower seed mass. We tested for the ability of functional traits to explain survival, the principal driver of changes in life history strategies along the studied gradient. We found that SLA and Leaf Area were correlated with survival in strong interaction with the climate; a higher Leaf Area was correlated with a lower probability of survival in low suitability areas, but a higher probability of survival in high-suitability areas. This strengthens the findings that climatic context is important to infer demographic performance based on functional traits.

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12.11.1975 - 13.12.2021.*

*Aoibheann, your energy, kindness and passion have been an
inspiration throughout this journey. It was deadly. You will be missed,
on the shores of the Irish Sea and on those of the Geneva lake.*

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Authorships contributions

The present thesis has been conceived, analysed and written by Maude E. A. Baudraz, under the supervision of Prof. Yvonne M. Buckley (Trinity College Dublin) and Prof. Antoine Guisan (Université de Lausanne). The nature of the work involved is collaborative, and we therefore provide a list of collaborators and their contributions for all chapters. None of the presented chapters have been published yet, and some data contributors may not yet have been invited to comment on the manuscripts of the present chapters, though they will be invited to do so before publication of the presented works. When submitted for publication all chapters will have Maude E.A. Baudraz as 1st author. Throughout the thesis “we” is used to reflect the collaborative nature of the research.

For all chapters (see following section), the notation “PlantPopNet Steering Committee” describes past and present members of the PlantPopNet Steering Committee as per the development of the demographic monitoring methods used in this thesis. The PlantPopNet Steering Committee following this definition is composed of; Yvonne Buckley (network coordinator), Johan Ehrlén, Elizabeth Crone, Glenda M. Wardle, Roberto Salguero-Gómez, Simone Blomberg, Jan van Groenendael, Anna-Liisa Laine, Maria Begonia Garcia, Debbie Roach, Anna Mária Csergő, Sergi Muune-Bosch, Alain Finn, Jesus Vilellas, Dylan Childs and Bret Elderd.

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Chapter 1:

The PlantPopNet (www.plantpopnet.com) consortium gathered the data and made it available. The PlantPopNet steering committee designed the demographic monitoring protocol and method used by the PlantPopNet consortium. Maude E.A. Baudraz conceived the research idea with Yvonne M. Buckley. Maude E.A. Baudraz performed the analysis with contributions from Yvonne M. Buckley. Annabel Smith provided a first cleaned version of the PlantPopNet data used at the start of the study. Jesus Vilellas provided the regression biomass equations. Ruth Kelly and Caroline McKeon provided intellectual input. Maude E.A. Baudraz wrote the first draft with contributions from Yvonne M. Buckley. Jesus Vilellas commented on a first draft of the manuscript. All co-authors edited the MS. Aldo

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Maude E.A. Baudraz conceived the research idea, with Yvonne M. Buckley and Antoine Guisan. Maude E. A. Baudraz gathered the data based on a sampling strategy developed with Antoine Guisan and using the demographic monitoring protocol and methods developed by the PlantPopNet steering committee. Maude E.A. Baudraz created the Species Distribution Model under the supervision of Antoine Guisan and Anna-Maria Csergő. Maude E.A. Baudraz performed the demographic analyses under the supervision of Yvonne M. Buckley and Dylan Z. Childs. Dylan Z. Childs provided the expertise for the implementation of density dependence in the population models. Maude E.A. Baudraz wrote the first draft of this chapter. Yvonne M. Buckley, Antoine Guisan and Dylan Z. Childs provided comments on the manuscript. Ruth Kelly, Anna-Maria Csergő, Caroline McKeon, Javier Puy and Pascal Vittoz provided intellectual inputs at different steps of the project. T. Panchard, A. Finn, B. Favre, C. Boujon, S. Gardzielewski, R. Kelly, M. Faugère, M. Gallot-Lavallée, J-A. Baudraz, O. Broennimann, D. Biancolini and Y.M. Buckley provided help in the gathering of demographic data on the field.

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Additional work

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Contribution in Hodgetts, Nick, et al. (2019) *A miniature world in decline European Red List of Mosses, Liverworts and Hornworts*. IUCN, 2019. Assessment of 37 species, in particular three European endemics now included in the IUCN red list :

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Introduction

As biodiversity faces a major crisis (Waters et al. 2016; Williams et al. 2015), and species and populations show an alarmingly fast rate of decline (IPBES 2019; Purvis et al. 2019; WWF 2020), we urgently need conservation and management advice. Conservation and management strategies are often developed by using population ecology, a field of ecology that studies the individuals of a species in a location (*i.e.* a local population) to infer on the mechanisms that determine local persistence (or extinction) (Crouse, Crowder, and Caswell 1987; Harper 1977; Morris and Doak 2002). Population ecology has been instrumental for the development of extinction risk quantification methods such as red listing methods (Faber-langendoen et al. 2012; Mace et al. 2008; Pearson et al. 2014). It is the basis of much of our understanding of the processes that drive the persistence and distribution of species (Holt 2009; Hutchinson 1957; Pulliam 2000).

Most population ecology studies are performed on very few populations, usually of conservation or management interest (Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Quedstedt, and Wardle 2010; Coutts et al. 2016; Salguero-Gómez et al. 2015). In 2015, over 50% of studies in the biggest database of plant population models in existence included less than 3 populations (Salguero-Gómez et al. 2015). As a consequence, studies often take place in one set of local conditions only, which remain often unquantified (Abeli et al. 2014; Pironon et al. 2017). This is problematic, as there is ample evidence that the processes underlying population persistence and performance are context dependent (Buckley and Kingsolver 2012; Catford et al. 2021; Kunstler et al. 2021; Paynter et al. 2016; Shea et al. 2005). Population persistence ultimately relies on the ability of individuals to complete their full life cycle (*i.e.* to survive, grow and reproduce) in a timing appropriate to local environmental pressures (Crouse et al. 1987; Reed et al. 2013). Processes within the life cycle, also called vital rates, can be affected by different environmental drivers (Maguire, 1973; Römer et al. 2021), leading them to potentially have opposing effects on population performance and persistence along geographic environmental gradients (Villellas et al. 2015). Components of a species' life cycle can also be affected by the density of con-specific individuals (Buckley et al. 2001; Holt 2009; Sletvold 2005) or individuals of other species (Adler, Ellner, and Levine 2010; Paynter et al. 2016). To better preserve our planet's

biosphere, we need to study the mechanisms underlying population performance and persistence across multiple populations of the same species in multiple contexts (Buckley and Puy 2021; Gurevitch et al. 2016).

Since the second decade of the 21st century, environmentally and spatially extensive demographic monitoring programs have begun to accumulate (Doak and Morris 2010; Eckhart et al. 2011; Römer et al. 2021; Smith et al. 2020; Treurnicht et al. 2016). Such projects aim to disentangle the drivers of population performance and persistence in a few intensively studied species across their entire range, or large portions thereof. They have provided numerous precious insights. For instance, Smith et al. (2020) found that the relationships between demography, environmental drivers and genetic diversity changed between the native and invasive range of the perennial herb *Plantago lanceolata*. Römer, Christiansen, de Buhr, et al., (2021) found that different components of population performance were driven by different environmental predictors, and with different relationships. For instance, in their study of the understory herb *Actaea spicata* L., the probability of survival increased with the proportion of neighbouring coniferous species, but the same variable had a quadratic effect on the number of fruits produced, with an optimum at intermediate values. The size of *Actaea spicata* individuals was impacted by soil depth, which did not affect survival or fruit production. Such results highlight the complexity of the processes underlying population performance across large scales.

The concept of scale was also shown to play a major role in our understanding of processes underlying population performance. A major part of the spatially replicated population information gathered to date stems from populations located close to each other (Clark et al. 1999; Coutts et al. 2016; Gurevitch et al. 2016), and in a restricted number of biomes or ecoregions (Adler et al. 2014; Kelly et al. 2021; Salguero-Gómez et al. 2015). Drivers of population performance and persistence at the level of the microhabitat (Blonder et al. 2018) might not be the same as at the regional (Treurnicht et al. 2016), continental (Villellas, Ehrlén, et al. 2013) or global scale (Smith et al. 2020). By sampling only a few points, from one single part of the distribution of the processes underlying population persistence and performance, we are unlikely to gain an overview of the full breadth of mechanisms (Gurevitch et al. 2016). Projects studying the drivers of population performance and

persistence at varying geographical scales are of high importance, though they will remain very rare until large scale demographic monitoring programs become more common.

Demography is the field of population ecology that focuses on the statistical study of the vital rates of survival, growth and fecundity of the individuals within a population (Harper 1977). Where we used the general terms of “components “of the life cycle of the species earlier in this text, we in fact meant vital rates. Vital rates are the basic rates that underly the life cycle of all species on earth, a sort of common currency. Reptiles may not germinate, plants may not moult, but all individuals of all organisms must ultimately grow, survive and reproduce, or at least attempt to, for their genes to remain in the evolutionary race (Darwin 1889; Dawkins 2016). Based on the study of vital rates of individuals within populations, demographers can infer population extinction risks (Mace et al. 2008; Morris and Doak 2002), population resilience (Capdevila et al. 2020; Reed et al. 2013; Stott et al. 2010) or population growth (Dauer and Jongejans 2013). This is typically achieved by the construction of structured population models, which attempt to predict the population size and structure in the future, based on observations of the fate of individuals over several years (Morris and Doak 2002). Individuals are often classified by age, size or life stages (Caswell 2001; Ellner, Childs, and Rees 2016). This classification is important, as demographic outputs tend to differ greatly throughout the life of individuals (Caswell 2001), and vary depending on individual size (Silvertown et al. 1993).

Structured population models can be used to infer future extinction risk (Morris and Doak 2002), or to describe populations’ evolutionary strategies (Cole 1954; Stearns 1992). Different combinations of survival, growth and fecundity of individuals may enable species to maintain viable populations via different evolutionary strategies, called Life History Strategies (Cole 1954; Grime 1977; Stearns 1992). A beech tree *Fagus sylvatica* relies on a long life span and the production of many fruits late in its life, whereas the annual plant *Anagallis arvensis* needs to grow fast enough to reach a reproductive state within one year (Stearns 1992). Likewise, populations of the same species can vary in their life history strategies, for instance along climatic or geographic gradients, but this phenomenon is much less studied. Understanding how individual and population level strategies change along environmental gradients is central to understanding the local adaptation and geographic distribution of species (Abeli et al. 2014; Pironon et al. 2017). For instance, a higher yearly

reproductive rate can compensate for a shorter life span to enable population persistence, but lead to very different consequences for the genetic diversity of the species and ultimately its conservation (Smith et al. 2020; Villellas et al. 2015; Willi and Van Buskirk 2019).

In the above paragraph, we drew information from interspecific comparisons to illustrate the importance of changes in life history strategies. This sliding from within to between species level comparisons illustrates one of the tension points in contemporary demography. Demography studies the balance of vital rates at the within species level (Caswell 2001; Ellner et al. 2016; Harper 1977). This is often performed within a single population, or through a comparison of one or two populations (Van Groenendael 1986; Shea et al. 2005). However, this is simply not enough to tackle the challenges facing our biosphere and the scale of the threats to biodiversity (Waters et al. 2016). We need to provide management and conservation advice for multiple populations, and indeed species, for which we currently do not have detailed information (Buckley and Puy 2021). Population macroecology (Buckley and Puy 2021) or landscape demography (Gurevitch et al. 2016) both describe the study of population ecology across multiple populations of the same species, across varying scales, environmental gradients, invasive and native ranges. In addition to the varying scales encompassed by landscape approaches, Buckley and Puy (2021) propose approaches for making use of between species comparisons. It is in this context that the present work is situated.

To achieve much needed inference on population performance across varying geographical scales and environmental conditions, three things at least are needed. First, more information on multiple populations of the same species needs to be gathered. Specifically, individual level measurements of vital rates, though resource intensive (Blonder et al. 2018; Gurevitch et al. 2016), need to be gathered in multiple populations of the same species across large spatial scales, as has already started (Doak and Morris 2010; Eckhart et al. 2011; Merow, Latimer, et al. 2014; Römer et al. 2021; Schurr et al. 2012; Smith et al. 2020; Treurnicht et al. 2016). Second, as broad geographic coverage is not a guarantee of extensive environmental coverage (Guisan, Thuiller, and Zimmermann 2017; Hirzel and Guisan 2002), demographic information along steep environmental gradients is also necessary. There is a bias in demography for populations to be monitored in areas of highly suitable

environmental conditions, driven by the need for replicated individual measurements (Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Quested, and Wardle 2010). This causes less suitable areas such as ecological or geographic range limits to be underrepresented (Abeli et al. 2014; Csergő et al. 2017; Pironon et al. 2017). Hence, there is a need for sampling of detailed population information along challenging environmental gradients. Third, we must judiciously exploit existing demographic data. Acquiring more, extremely detailed information on millions of species is impossible, and would take until long after the currently ongoing mass extinction event made inference on population performance pointless (Ceballos et al. 2015; Ceballos, Ehrlich, and Dirzo 2017). Therefore, we need to develop new approaches to make use of the currently existing, poorly replicated demographic information (Buckley and Puy 2021; Coutts et al. 2016; Csergő et al. 2017; Kelly et al. 2021).

Some such new approaches are of a technical nature. Thanks to the emergence of Integral Projection Models as a type of structured population model (Easterling, Ellner, and Dixon 2000; Ellner et al. 2016), the use of continuous models of vital rates to build structured population models has increased (Easterling et al. 2000; Merow, Bois, Allen, Xie, Silander Jr., et al. 2017; Merow, Dahlgren, et al. 2014). Previously, population models were typically parametrized by dividing populations into categories of individuals (seedlings, adults, fledglings, territorial male, female, post reproductive adult, etc.). What was statistically estimated was the probability of transition from category to category, including stasis (Caswell 2001). This approach is highly flexible in terms of the fate of individuals, but requires multiple observations per category (Doak et al. 2021). In contrast, classifying individuals by continuous variables such as age or size (the latter most easily estimable in the case of plants (Silvertown et al. 1993)) enables the estimation of vital rates as continuous processes (Easterling et al. 2000; Ellner et al. 2016). This approach is much more powerful: it takes only two parameters to describe a regression line, which can describe the growth of trees from seedlings into giants. The use of continuous models enabled the building of hierarchical or “mixed effects”, models of vital rates (Bolker et al. 2009; Buckley et al. 2003; Gelman and Hill 2007; Zuur et al. 2013). This enabled scientists to study vital rates across several populations of the same species in one model, pooling power from observations in each population. Again, this improved statistical power. Fewer observations per sites are hence needed, allowing for the sampling of more populations or geographic locations, without

compromising statistical power and inference capacity. Sufficient spatial replication can more easily be reached, so that models can incorporate environmental predictors varying between populations, interrogating the environmental drivers of population performance across space (Merow, Dahlgren, et al. 2014; Römer et al. 2021). Developing structured population models across large spatial scales or environmental gradients implies that the relationship between the structuring variable (usually size) and demographic output does not vary in different parts of the range of the focal species. There is little investigation of this assumption across large spatial scales, though there is evidence that changes in environmental drivers can affect demographic outputs via changes in size and vegetative growth (Töpper et al. 2018).

We also need to draw information on population performance from other sources, more readily available than detailed vital rates information (Buckley and Puy 2021). Many approaches have been attempted, including inferring vital rates and population performance information from closely related species (Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Quested, and Wardle 2010; Coutts et al. 2016; Salguero-Gómez et al. 2015), from functional trait measurements (Adler et al. 2014; Violle et al. 2007) or distribution and occupancy information (Csergő et al. 2017; Pearson et al. 2014). The two latter approaches are of particular importance in the context of the present work, and will be expanded further.

Functional traits are characteristics of species hypothesized to impact their fitness, that is, the ability of individuals to pass on their genes (Violle et al. 2007). Fitness is ultimately mediated by the vital rates of growth, survival and fecundity: if an individual dies young, fewer offspring can be produced and fitness decreases. If fecundity increases, more offspring per year can be produced, and fitness increases. Functional traits are hypothesized to be able to capture changes in survival, fecundity or growth of species or individuals (Moles 2018; Violle et al. 2007). As they are much faster and less resource intensive to measure than direct measurements of vital rates, they offer an opportunity to predict population performance (Adler et al. 2014; Kattge et al. 2020; Salguero-Gómez et al. 2018). Nonetheless, the endeavour of predicting population performance and life history strategies based on functional trait measurements presents difficulties, with most studies exhibiting very weak relationships (McGill et al. 2006; Moles 2018; Wright et al. 2010). Similarly to

demography, functional traits have been shown to vary in space, as does their relationship to vital rates and ultimately their connection to individual fitness (Adler et al. 2014; Kelly et al. 2021; Kuppler et al. 2020; Moles 2018). A lot of this variance can take place at extremely small scale, that of the within-site or microhabitat level (Blonder et al. 2018; Kuppler et al. 2020; Moles 2018). Yet due to a lack of data availability, most studies to date make use of species-average values to study the relationship between functional traits and demography (Adler et al. 2014; Kelly et al. 2021; McGill et al. 2006). To *“deliver[] the promises of functional trait ecology to the needs of demography and vice-versa”* (Salguero-Gómez et al. 2018), more studies of the predictive ability of functional traits on vital rates across multiple individuals or populations of the same species, in interaction with ecological gradients are needed (Kelly et al. 2021; McGill et al. 2006; Vilellas et al. 2021).

Occurrence information is readily available for many thousands of species (GBIF.org 2021). Some information on the impacts of environmental drivers on the ecology of species is contained within the patterns of occurrence of species (Guisan and Thuiller 2005) and their changes through time (Maiorano et al. 2013). There are several ways occurrence data could be used to inform macroecological population studies (Buckley and Puy 2021; Gurevitch et al. 2016).

In fields where data are typically scarce and poorly replicated in space, we need to explore ways to break down the dimensionality of complex, potentially non-linear and interactive, environmental gradients (Buckley and Puy 2021; Pironon et al. 2017; Pistón et al. 2019; Römer et al. 2021). One can measure the changes in environmental predictors along a geographic gradient (Römer et al. 2021) or summarize them by use of PCA axes when data is too scarce (Kelly et al. 2021). Another option is to study not only the variance in the environment but also how far the experienced conditions are from the ecological requirements of a species (Broennimann et al. 2021). One powerful tool to quantify the ecological requirements of a species are correlative Species Distribution Models (SDM) (Elith et al. 2006; Guisan and Zimmermann 2000). Species Distribution Models aim to describe the niche of a species by correlating occurrence data with environmental predictors to explain their probability of occurrence (Hutchinson 1957; Soberón, Osorio-Olvera, and Peterson 2017). This probability of occurrence can be projected into geographic space to generate maps of predicted distribution as a function of local climate, understood as a map of

suitability of the environment for the species (Guisan and Thuiller 2005; Guisan et al. 2017). Species Distribution Models draw their strength from the immense quantity of occurrence data that has accumulated in recent decades, through atlases, museums, national floras and inventories, or online repositories (e.g., GBIF.org 2021; Ivanova and Shashkov 2016; Lauber, Wagner, and Gygax 2018; Meusel and Jäger 2011).

Species Distribution Models therefore represent a promising source of information for macroecological population studies, as they break down complex environmental gradients into a single metric, which is more meaningful for the ecology of the species than PCA axes of environmental variables (Buckley and Puy 2021; Gurevitch et al. 2016). Occurrence entails some demographic information: in the absence of migration or rescue effects, populations can only persist where the balance of vital rates enables a stable population (Hutchinson 1957; Maguire, 1973; Pironon et al. 2018). In addition, where absolutely *no* vital rate can take place (not even the survival of adult individuals), no occurrence is possible, even that of a sink population or vagrant individual (Broennimann et al. 2021; Lieury et al. 2016). Species Distribution Models draw power from the immense amount of occurrence data (GBIF.org 2021) and spatial climatic predictors available online and via remote sensing (Fick and Hijmans 2017). They can be created for multiples (orders of magnitude) more species and taxa than those for which we have detailed demographic information (Buckley and Puy 2021; Salguero-Gómez et al. 2015). Hence, they have been highlighted by several authors as an important candidate variable to complement demographic information for interpolation across landscapes (Buckley and Puy 2021; Gurevitch et al. 2016).

A main use of Species Distribution Models has been to predict species range shifts under climate change (Capdevila et al. 2020; Guisan and Thuiller 2005; Scherrer, Massy, et al. 2017). As a consequence, and given the urgency of the matter (Pearson et al. 2014; Williams et al. 2015), a large part of the literature integrating the use of Species Distribution Models and demographic approaches has focused on refining predictions of range shifts under climate change scenarios (Fordham et al. 2012, 2018; Keith et al. 2008; Swab et al. 2012, 2015 and many more). In short, although Species Distribution Models remain an important tool to predict the consequences of climate change on species (Araújo and Peterson 2012; Bakkenes et al. 2002; Guisan et al. 2017; Guisan and Zimmermann 2000; Thomas et al. 2004), they have limits. They assume equilibrium in environmental conditions, ignore dispersal

limits and biotic interactions, such as inter-specific competition or intraspecific density dependent feedbacks (Ehrlén and Morris 2015; Guisan et al. 2017; Holt 2009; Soberón and Nakamura 2009). Since Species Distribution Models are based on occupancy information alone, they do not include information about the mechanisms driving species range shifts, including demographic mechanisms. They were shown to be biased in their ability to predict species range shifts due to climate change as compared to when demographic information was available (Schurr et al. 2012; Swab et al. 2012): a bias that can be corrected by adding demographic and dispersion information (Fordham et al., 2018; Schurr et al., 2012; Swab et al., 2015 and several others). Species Distribution Models were also shown to not predict experimental demography (Bayly and Angert 2019; Greiser et al. 2020), though both approaches are informative to capture the mechanisms that could cause shifts in species ranges.

Given the large focus on predicting and mitigating the impacts of climate change, few studies to date have attempted to capture the relationship between probability of occupancy and population performance or life history strategies in the current, realized niche of species (Csergő et al. 2017; Pironon et al. 2017, 2018; Thuiller et al. 2014). In a study of 108 tree species across several study areas, Thuiller et al. (2014) found a counterintuitive negative to flat regional relationship between probability of occurrence and population growth rates (a common metric of population performance, (Caswell 2001; Greiser et al. 2020; Holden et al. 2021; Hutchinson 1957; Morris and Doak 2002), likely due to intraspecific density dependent feedbacks. Similarly, (Csergő et al. 2017) found no consistent relationship between population performance (measured as the population growth rate, the temporal variation thereof and extinction risk) and probability of occurrence in a study of 93 populations of 34 plant species. Nonetheless, Csergő et al. (2017) did find evidence for the effect of suitability on demographic pathways of extinction risk. For instance, they found that in areas of lower probability of occurrence, populations rely more on retrogression, and have a narrower range of transient population growth rates. There may therefore be general rules predicting the type of life history strategies used by species in areas of low- or high-probability of occurrence (as predicted by Species Distribution Models). These rules could in turn provide information on the best way to manage populations of the same species in varying contexts (Buckley and Puy 2021; Shea et al. 2005).

We have highlighted several pathways to scale up from demography (Caswell 2001; Ellner et al. 2016) to landscape demography (Gurevitch 2016) and population macroecology (Buckley and Puy 2021) and to provide much needed applied population management advice in a fast changing world: the spatially explicit modelling of multiple populations of the same species, the use of functional traits as proxies for vital rates and demography, and Species Distribution Models as proxies for demographic pathways to population performance. These approaches need in-depth exploration in extensively known systems before they can be applied across multiple organisms, scales and gradients. One potential approach is to use known study organisms for which extensive knowledge of different processes has been gathered (Penczykowski and Sieg 2021), including large scale demographic monitoring (Doak and Morris 2010; Eckhart et al. 2011; Römer et al. 2021; Smith et al. 2020; Treurnicht et al. 2016). One emerging demographic study organism is the perennial herb *Plantago lanceolata* L. (Penczykowski and Sieg 2021; Sagar and Harper 1964; Smith et al. 2020; Villellas et al. 2021). Native to Europe, it is now present on five continents due to repeated introduction events (Meusel and Jäger 2011; Smith et al. 2020). Hence, it is an excellent candidate for demographic studies at large scale. It does not seem to disrupt the ecosystems to which it is introduced to outside its native range, and can therefore be used for in-situ studies across continents (CABI 2019). Finally, it is extremely common, and has been extensively studied across several fields of ecology and evolution (Kuiper and Bos 1992), making it a prime candidate study organism (Penczykowski and Sieg 2021). The demography of *P. lanceolata* is being monitored in over 60 populations across its range by the PlantPopNet collaborative science project (www.plantpopnet.com).

In the present thesis, we will explore the different approaches for the study of population macroecology of *Plantago lanceolata*. Chapters 1 and 4 will make use of the global demographic information collected by PlantPopNet, and chapters 2 and 3 are based on demographic data collected along a steep environmental gradient specifically for the present project.

In chapter 1, we explore the relationship between size and vital rates across 55 populations of *P. lanceolata* on three continents, covering most of its global range. In particular, we interrogate whether the same measurements of size perform equally well at capturing changes in demographic outputs across all populations and four vital rates. We will explore

whether the best performing size measurements differ between parts of the range (native, invasive) or in certain parts of climatic gradients.

In chapter 2, we explore changes in demography and life history strategy of 18 populations of the same herb, monitored along a steep environmental gradient in the Swiss Alps. *Plantago lanceolata* is a lowland species, and the studied gradient leads to one of its known realized niche limits. The environmental gradient was summarized using a Species Distribution Model. This research was performed in a 700 km² research area, and individuals were monitored for three years

In chapter 3, using the same system, we explore the ability of functional traits to capture the changes in life history strategies and vital rates observed along the environmental gradient.

In chapter 4, we explore the ability of the probability of occurrence, as predicted by a Species Distribution Model, to capture changes in life history strategies across the whole native range of the species. In particular, we interrogate whether a lower probability of occurrence is indicative of a slower life cycle (Csergő et al. 2017; Harper 1977).

By exploring these different approaches, across multiple scales and gradients on a known study organism, we hope to provide stepping stones for the establishment of proxies to interpolate demography and life history strategies across multiple species. The even partially successful establishment of such proxies could be precious to population ecologists, currently limited in the ability to infer management advice for new locations and contexts (Paynter et al. 2016; Shea et al. 2005). Ultimately, it is our hope that such proxies could help management and conservation advise to rise to the challenges of the large scale threats faced by today's biosphere (Waters et al. 2016; Williams et al. 2015).

Chapter 1. What is size? size variable selection for demographic studies of multiple populations at a global scale

Maude E. A. Baudraz, PlantPopNet Steering Committee, PlantPopNet Consortium, Yvonne M. Buckley (see authors contribution section at the start of this thesis)

1.1 Abstract:

1. The size of individuals is critical for their demographic output. Bigger individuals typically have higher survival or reproductive output; however, size can be measured in several different ways (height, biomass, length, etc) and there is no consensus on the best size metric for modelling demographic rates. As demographic datasets increase in geographic coverage, we will face choices about how to capture size for the same organism in many different environmental contexts.

2. Here, we assess the performance of six different size metrics across 55 populations of the perennial herb *Plantago lanceolata* on three continents making use of the PlantPopNet dataset. We built a series of generalized linear mixed models explaining growth, survival, flowering probability and reproductive effort. We compared the performance of each candidate size metric between demographic transitions and between populations, as well as across environmental gradients, by means of the generalized R^2_c and within population error.

3. All candidate metrics performed well (R^2_c 0.54 to 0.72), and similarly across all populations. We found that simple metrics such as the number of leaves or the total leaf length performed best. This offers encouraging insights for our ability to consistently model species range-wide demography at a very large geographic scale.

Synthesis Size of individuals is an important determinant of reproductive output and survival. Different aspects of size can be more important under different selective pressures. As demographic datasets increase in scale, differences between populations in our ability to capture demographic processes could emerge. Using a dataset of unprecedented scale we find that a) we are capable of building consistent models of growth, survival and reproduction at a global scale, and that b) the tested size metrics perform similarly well. This is encouraging for work increases the scale of demographic studies and for comparative projects which use different size metrics across populations and/or species.

1.2 Introduction:

The size of individuals is critical for forecasting individual vital rates, such as fecundity, growth and survival, particularly in plants (Caswell 2001; Easterling et al. 2000; Morris and Doak 2002; Roff 1986; Stearns 1992). Bigger individuals of the same age are often interpreted as having more resources available to them, and a higher expected output in terms of survival and reproduction (Stearns, 1992). Bigger is not always necessarily better, as size can also increase apparency to herbivores, susceptibility to disturbances such as mowing and lead to architectural instability (Díaz et al. 2007). The influence of stochasticity on the fate of individuals is not to be understated (Snyder and Ellner 2018), but size linked demographic rates are ubiquitous (see Roff, 1982, 1986; van Benthem et al., 2017 for examples).

Yet “size” is not simple to measure. It is frequent to see several size measurements, adapted to different organisms and different research questions, such as snout-vent length for snakes (Meik, Michelle Lawing, and Pires-daSilva 2010), body mass for rodents (Michaux et al. 2002), various length measurements for birds (Illera et al. 2014) or even craniometric measurements (Vega et al. 2016). Plants present their own difficulties, as they do not have a deterministic growth form (Eichhorn, Evert, and Raven 2000), and a substantial part of the biomass is underground (Wallen 1986). Many size metrics are used, such as trunk diameter in trees (Meunier, Sirois, and Bégin 2007), diameter on the ground (Ellner and Rees 2006), number of leaves (Oldfather 2018a, 2018b), and many more. The abundance of size metrics makes it difficult to determine the optimal metric for capturing the concept of size as a determinant of demographic fate among different statistical models.

Size is a fundamental predictor in many demographic approaches, especially in plants, where age is considerably harder to access than size. Yet the selection of an appropriate size variable is typically only briefly mentioned in publications (Ellner et al. 2016; Oldfather 2018b). There is some advice about how to select the best stage variable for demographic studies, which mostly focuses on comparing different stage or variables candidates and compare them in terms of AIC (Caswell 2001; Morris and Doak 2002). The aforementioned advice is mostly aimed at demographic studies where a population model is developed for one or a few populations, which are generally located within close proximity and similar

environments (Coutts et al. 2016). Indeed, in the biggest online repository of plant demographic models existing to date, the Compadre database, the median number of populations per study is around three (Salguero-Gómez et al. 2015). As demographic data is collected at larger spatial and environmental scales through harmonized protocols, such as PlantPopNet (Buckley et al. 2019) and other spatially distributed demographic studies (Colautti et al. 2014; Doak and Morris 2010; Jongejans et al. 2011; Merow, Bois, Allen, Xie, and Silander 2017; Smith et al. 2020; Vilellas et al. 2021), new challenges will undoubtedly emerge. Particularly, the same size variable might not be optimal for all populations if those populations are in different niche conditions, with potentially distinct evolutionary pressures and histories. For instance, the number of leaves per rosette in a rosette forming plant might be more important in an alpine location to avoid damage by winter frost, but plant height may be of more importance in a mesic temperate meadow (Falster and Westoby 2003; Halbritter et al. 2018).

It may also be necessary to adapt the way we assess performance of a size metric if using multiple populations. In the case of a mixed effects model, the overall performance of the model could be high, but the studied process much better explained in some populations than others. The existing approaches to size variable selection do not, to our knowledge, account for geographical or environmentally driven variation in the performance of stage variables. As the most commonly cited limitations in demographic studies are the limited geographical range (Coutts et al. 2016; Salguero-Gomez et al. 2012; Tredennick et al. 2018) and the lack of replication (Csergő et al. 2017; Salguero-Gomez et al. 2012; Salguero-Gómez et al. 2015), these considerations are of rapidly growing importance.

Since the second decade of the 21st century, several large scale demographic projects have emerged (Colautti et al. 2014; Doak and Morris 2010; Jongejans et al. 2011; Merow, Bois, Allen, Xie, and Silander 2017; Smith et al. 2020; Vilellas et al. 2021). Among them is PlantPopNet, a spatially distributed model system for population ecology (www.plantpopnet.com) monitoring >60 populations of the perennial plant *Plantago lanceolata* on three continents including both native and introduced ranges. Populations are continually monitored for growth, survival and fecundity of all individuals by a network of local collaborators using a standardized protocol (Buckley et al. 2019). *Plantago lanceolata* is a rosette forming herb that is native to Europe but has also been widely and repeatedly

introduced throughout the globe resulting in a cosmopolitan distribution (Sagar and Harper 1964; Smith et al. 2020). The PlantPopNet network includes populations across a wide range of environmental conditions, from six different biomes (**Figure 1.1**). Given the broad range of climates faced by the studied populations, the PlantPopNet data is a prime example of a dataset in which one does not only want a stage variable to produce the best overall model, but also to perform consistently across geographic and climatic space, across populations and across vital rates. Here we develop a framework to select the best performing and most consistent metric across populations and vital rates as a critical first step in developing a spatially distributed population model.

This framework is not only necessary for enabling the development of powerful vital rates models at a global scale, but also has important consequences for the field of demography. Much current comparative demographic work uses collated demographic models across multiple species (Kelly et al. 2021; Salguero-Gómez et al. 2015). If the choice of size variable is mainly locally influenced, it would caution against the comparison of demographic models interpreted at the species level yet developed on different local populations in very different places. Conversely, if different size variables perform equally well across populations the comparison of populations modelled using different size variables may be robust to this methodological difference.

1.3 Methods

Overview:

We used the globally distributed demographic dataset from PlantPopNet to compare the performance of different size variables as predictors in demographic models of growth, survival and reproduction across 55 populations of *Plantago lanceolata* worldwide (**Fig. 1.1**). We computed a series of candidate size variables and developed generalized linear mixed effects models of growth, survival, probability of flowering and reproductive effort using the candidate size variables to explain these demographic transitions. We then determined the optimal size variable by comparing the performance of the models across demographic transitions, populations and regions of the world. Models were compared using R^2 , the Mean Absolute Error (MAE) per population and the variance in slopes of the vital rate models.

The species

Plantago lanceolata L. is a short-lived, perennial, rosette forming herb (Kuiper and Bos 1992; Sagar and Harper 1964). Each individual (genet) is composed of one to several rosettes (ramets). Small flowers (4 mm diameter) are arranged in linear inflorescences which vary in length and are arranged on a variable number of flowering stems per rosette and per individual plant (Sagar and Harper 1964). Each flower produces up to two seeds (Lauber et al. 2018). Native to Eurasia, *P. lanceolata* is now widespread throughout the globe and present on all continents except for mainland Antarctica as an introduced species (CABI 2019). The plant is variable in size and shape, with leaves ranging from 2 to 45 cm in length (Sagar and Harper 1964).

Dataset

The PlantPopNet network (www.plantpopnet.com; Figure 1.1) gathers demographic information on 64 populations of *P. lanceolata* across three continents. The present study included 55 populations that had at least two consecutive yearly censuses. Each population consists of an initial minimum of 100 individuals permanently marked within plots and revisited yearly at the peak of the flowering season. New recruits are recorded and followed in subsequent years. Several measurements of each individual are recorded each year: number of rosettes, number of leaves per rosette, length of the longest leaf and width of the longest leaf for each rosette, flowering status (flowered, not flowered), as well as survival or death of each plant. The reproductive effort is estimated via the number of scapes (i.e., flowering stems), and inflorescence length for the longest scape. In the present study, we focused on one (first) yearly transition of version 2 of the PlantPopNet database (November 2020 and March 2021, Supplement S1.1.1). As only the individual (genet) identity and not the individual rosette (ramet) identities were recorded at all sites, this study was performed at genet level. For additional information on the PlantPopNet protocol, see (Buckley et al. (2019).

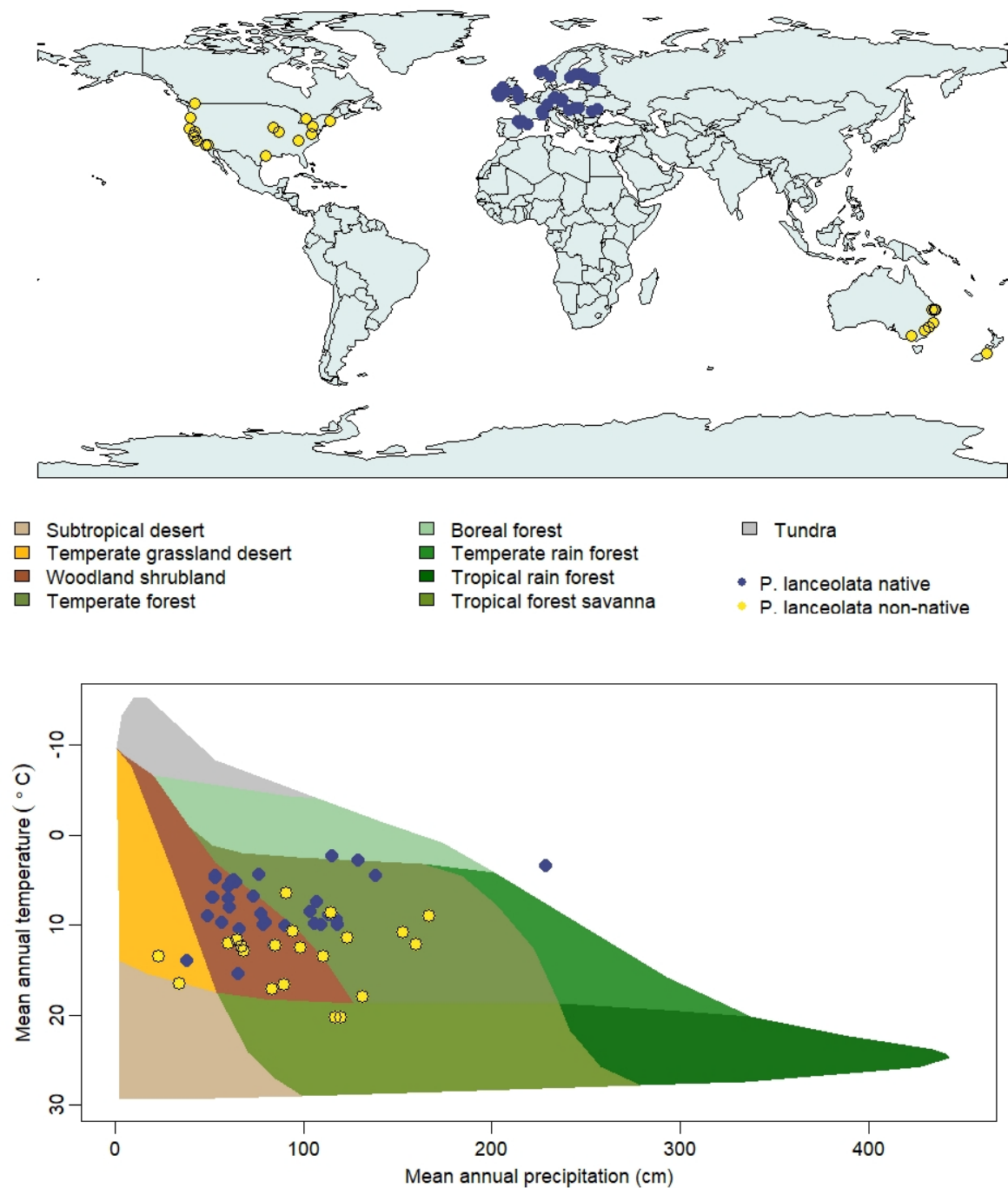


Figure 1.1 The distribution of the 52 populations of *Plantago lanceolata* included in this study in geographical space (A) and in environmental space (B). Panel A shows which biomes of the world *P. lanceolata* occurs in (Whittaker 1970). The biomes are classified by their mean annual precipitation values and mean annual temperature. Plots were developed with the BiomePlot (Kunstler 2014) and rworldmap packages (South 2011).

Demographic transitions

From these data we computed the following demographic transitions: survival, growth (size at time $t+1$ as a function of size at time t) and fecundity, modelled in two parts: probability of flowering and reproductive effort. As a proxy for the number of seeds produced when flowering occurs, we computed reproductive effort as the length of the longest inflorescence per the number of stems produced at a flowering event.

Choice of candidate size variables

Several size metrics have been used to characterize growth, survival and reproduction for *P. lanceolata*. Most authors aimed to estimate biomass using a variety of different approaches (Antonovics and Primack 1982; Van Groenendael 1986; Van Groenendael and Slim 1988; Hamre, Rydgren, and Halvorsen 2010). We estimated size using six candidate size variables that were chosen based on their occurrence in the literature and the availability of measurements via PlantPopNet (Table 1.1). For the estimation of biomass, we used the equation developed by Villellas *et al.* (2021; supplement S1.1.2), using a greenhouse experiment including 396 individuals from 16 PlantPopNet populations to obtain dry aerial biomass (Table 1.1). Villellas *et al.* (2021) developed several regression equations to estimate biomass using destructive or non-destructive size metrics available from field populations. In the present study, we use the equation that only requires non-destructive predictors (supplement S1.1.2). The parameters for this estimated biomass equation are specific to our focal species, although the method can be generally applied to other organisms.

Development of the vital rates models

We built a series of generalized linear mixed models to explain the variation in each of the demographic transitions (growth, flowering probability, reproductive effort and survival probability). Six models were built for each vital rate, each testing one size variable as a candidate fixed effect. This led to a total of 24 models. The models included random slopes and random intercepts at the population level, and a random intercept at the plot level. To ensure comparability between the model outputs, we used the same dataset for each model; *i.e.*, no missing values for any size metric. Growth and survival at year $t+1$ were

predicted as a function of size at time t . The reproductive transitions were modelled as a function of the size of the plant in the same year. Binomial errors were used for the probability of flowering and survival, and Gaussian errors were used for growth and reproductive effort. All size metrics were used as log transformed, but for the number of leaves.

In general, the use of log transformed count data as a response variable should be avoided (O'Hara and Kotze 2010). In addition, in the building of size-structured population models, which often is an objective while building vital rates models, the choice between a continuous or discrete size metric can shift the population model from a continuous Integral Projection Model to a Matrix Population Model (Caswell 2001; Easterling et al. 2000). Therefore, we used the number of leaves as both continuous and log transformed. We modelled the number of leaves as count data through a generalized linear mixed model with negative binomial size distribution with square root link and constant variance (Hardin and Hilbe 2018), as it fitted the data best as compared to a Poisson or other negative binomial family distributions. This final model was fitted the `nbinom1` family in the `GlmmTMB` R package (Brooks et al. 2017). All models were built in R version 3.5.1, using the `nlme4` and the `glmmTMB` packages (Bates et al. 2015; Brooks et al. 2017; R Core Team 2020).

Evaluation of the models and best size variable selection

Our objective was to select size variables from models that a) met their statistical assumptions, b) had consistent performance across demographic transitions, c) had high explanatory power, and d) had consistent performance across populations.

For each criterion assessed for each model, the candidate size variables were ranked relative to each other. The highest ranked candidate variable averaged across all criteria was selected. Variables that did not meet the model assumptions were filtered out of the model ranking process. We used two different performance metrics; an R^2 adapted to generalized linear mixed models (Johnson 2014; Nakagawa, Johnson, and Schielzeth 2017; Nakagawa and Schielzeth 2013), and the Mean Absolute Error (MAE) (Chai and Draxler 2014; Willmott and Matsuura 2005). Nakagawa's R^2 is divided into conditional and marginal R^2 . Marginal R^2 (R^2_m) can be understood as the variance explained by the fixed effects in the model, while the conditional R^2 (R^2_c) is the variance explained by the entire model including the random structure. We used R^2 as an overall metric of model performance, and MAE as a way to

investigate further the error of the model in each separate population.

The Mean Absolute Error is computed as:

$$MAE = \frac{\sum_i^n |e_i|}{n} \quad \text{eqn 1}$$

Where e_i is the i -th model error of a model with n observations.

To obtain MAE values comparable between models calibrated on different responses, we mean centred and standardized the residuals of all models and calculated the MAE based on those standardized residuals. See Supplement S1.1.3 for more details about the performance metrics selection.

Criterion a) Assumptions check

We verified that each model met its respective assumptions. As many issues (such as zero inflation or non-homoscedasticity of the residuals) are hard to assess in generalized linear mixed models with non-gaussian error, we performed a standard check for all models using the DARHMa package (Hartig, 2018; see Supplement S1.1.4). The DARHMa package helps with diagnosis of overdispersion, zero inflation (or depletion) and model misspecification in case of non-gaussian response variables. It also can apply to Gaussian response variables. As the resulting plots are numerous (five to six diagnostic plots for each of our 24 models), we display examples of the results of the DARHMa model diagnostic procedure in **Supplement S1.2**. We also used the sjPlot package to display random effect normality (Lüdtke 2020).

Criterion b) Performance across vital rates

We used R^2 (Nakagawa and Schielzeth 2013) to assess the goodness of fit for each vital rate model. A model with higher R^2 was ranked higher. We investigated both the R^2_c and R^2_m for our models but used only the R^2_c for the final variable selection step.

Criterion c) Performance across populations

We determined how well the model performed within each population by computing the MAE for each population (Willmott and Matsuura, 2005, see above). MAE is obtained as the sum of the absolute values of the residuals from each population (a measure of the “total error” of the model in this population) divided by the number of individuals in the population. A low Mean Absolute Error means that the model performs well for that

population.

Criterion d) Consistency of performance between populations

We investigated which candidate size variable had the most consistent performance across populations by calculating the variance in MAE across all populations. The reasoning behind this is that even if a metric has the lowest MAE on average, it does not mean the spread of performance between populations will be narrow. We therefore checked for the variance in population MAE as a metric of the spread of performance (criterion d.1). In addition, we assessed whether the relationship between size and vital rates was constant over populations by plotting the random slopes and intercepts for all populations. Very distinct, or even opposite slopes, would indicate either an ecologically different relationship between size and any demographic transition in different populations (or regions of the world), or an inadequately modelled process. The variance in slopes of the population random effects was computed as a selection criterion to take this into account in the selection process (criterion d.2).

Although it was expected that the failure to correctly model part of any environmental gradient would be captured by criterion d.1, we checked whether the performance was consistent across environmental gradients. The environmental gradients used were Mean Temperature and Mean Annual Precipitation, sourced as bioclim layers (Fick and Hijmans 2017). We plotted the population MAE along those gradients and tested for any effect of the size metric, the climatic gradients, as well as the native versus non-native range on the population MAE. We built a linear mixed model explaining population MAE as a function of the temperature and precipitation values at each site, the part of the range (native versus invasive), the size metric candidate (categorical) and the population of origin as a random intercept. This model was built using the lme4 package in R (Bates et al. 2015).

Best size variable selection

Candidate variables were ranked according to each of the criteria. The best performing metric was ranked 1 (highest R^2_c , lowest population MAE, lowest variance in population MAE, lowest variance in slope), the worst performing metric was ranked 6. We filtered out the variables that did not meet the model assumptions. The candidate variable with the highest average ranking across the four criteria was selected

Metric	Calculated as	Rationale	References
Number of leaves	N° of leaves	Intuitive measure, easy to compute and measure on the field	(Antonovics & Primack, 1982; Shefferson & Roach, 2012)
Log transformed number of leaves	$\ln(\text{n° of leaves})$	Normalized number of leaves to respect assumptions of a gaussian distributed model	-
Photosynthetic area	Length of longest leaf * width of longest leaf * n° of leaves	Strong link to photosynthetic process.	-
Total Leaf Length	Length of longest leaf * n° of leaves	Common use in literature, strong link to photosynthetic process and ease of measurement on the field.	(Van Groenendael, 1986; Van Groenendael & Slim, 1988) (Noé & Blom, 1982)
Leaf length	Length of the longest leaf	Quickest to measure on the field, low level of expected causal links to photosynthesis.	-
Regressed biomass	$\exp(0.556 + 1.924 * \log(\text{n°leaves}) - 0.213 * \log(\text{n°leaves})^2 + 0.003 * \text{leaf length} + 0.833 * \log(\text{leaf width}))$	Integrated measure that estimates biomass using several non-destructive size measures. Requires destructive measurement in order to develop the parameterisation which is time consuming	Hamre et al. 2010, Vilellas et al. 2020

Table 1.1 Candidate size metrics considered in this study. The biomass regression equation is taken from (Vilellas et al. 2021) who grew and harvested plants from a subset of the PlantPopNet populations included in this study to calibrate their regression equation.

1.4 Results

Model diagnostics

None of the twenty-four models considered failed to meet their respective assumptions reasonably well (Supplement S1.2). The binary vital rates were well captured by all candidate size metrics. Leaf length and the non-log transformed number of leaves had difficulties capturing the continuous processes of growth and reproductive effort (non-normality of random effects and slight patterns in the residuals over predictors plots), but the imprecisions were qualitatively deemed acceptable. The two growth models using the number of leaves as a response (log and not log transformed) would expect more zeros (zero depletion, see discussion).

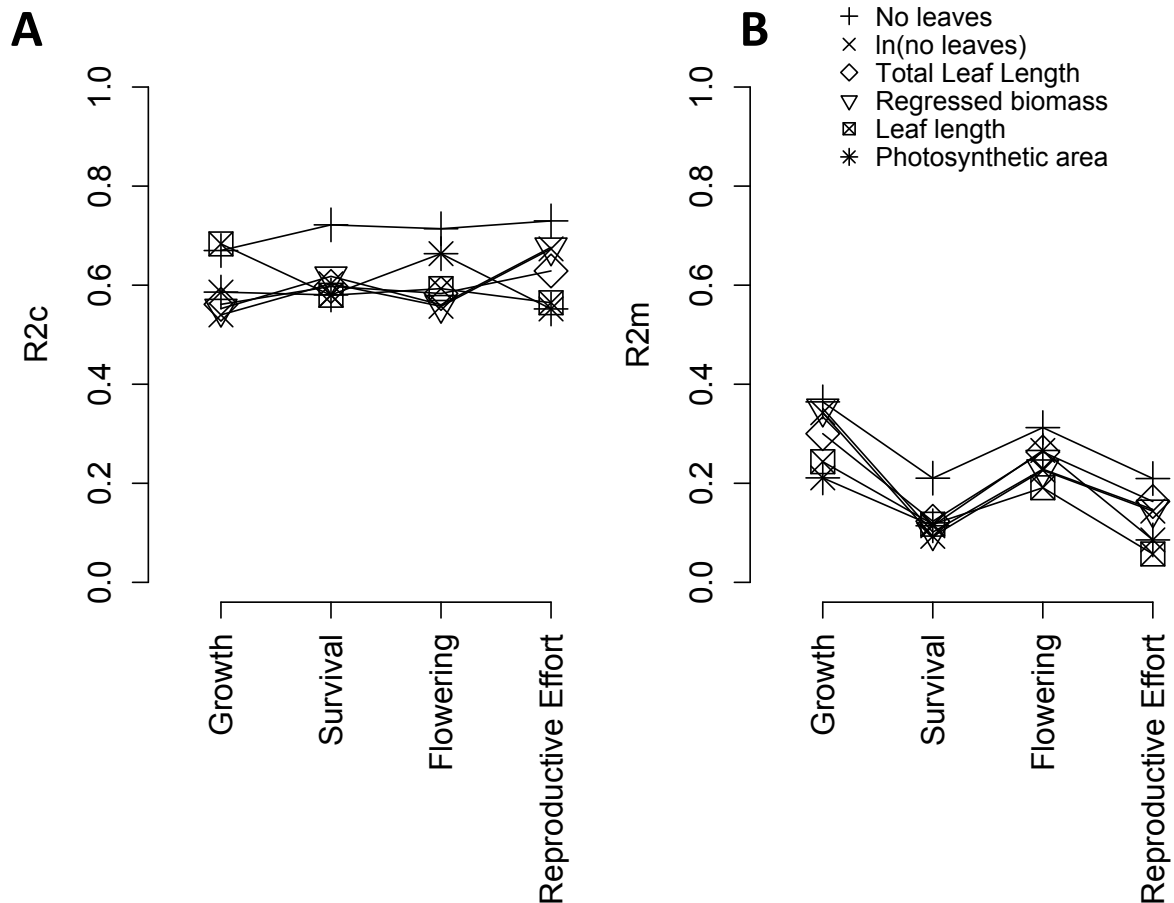


Figure 1.2: performance of the candidate size metrics across rates (growth, survival, flowering probability and reproductive effort, on the x-axes), expressed in terms of (A) conditional and (B) marginal R^2 (R^2_c and R^2_m respectively, on the y-axes). R^2_m is a measure of the variance explained by the fixed effects in the model, R^2_c of the variance explained by the fixed effect and the random effects taken together. Shapes represent different size metrics.

Performance across vital rates

For the performance across demographic transitions, all the size metrics performed relatively well, with conditional R^2_c ranging from 0.54 to 0.72. The number of leaves (not log-transformed) consistently emerged as the best variable (Figure 1.2). The rank of the size

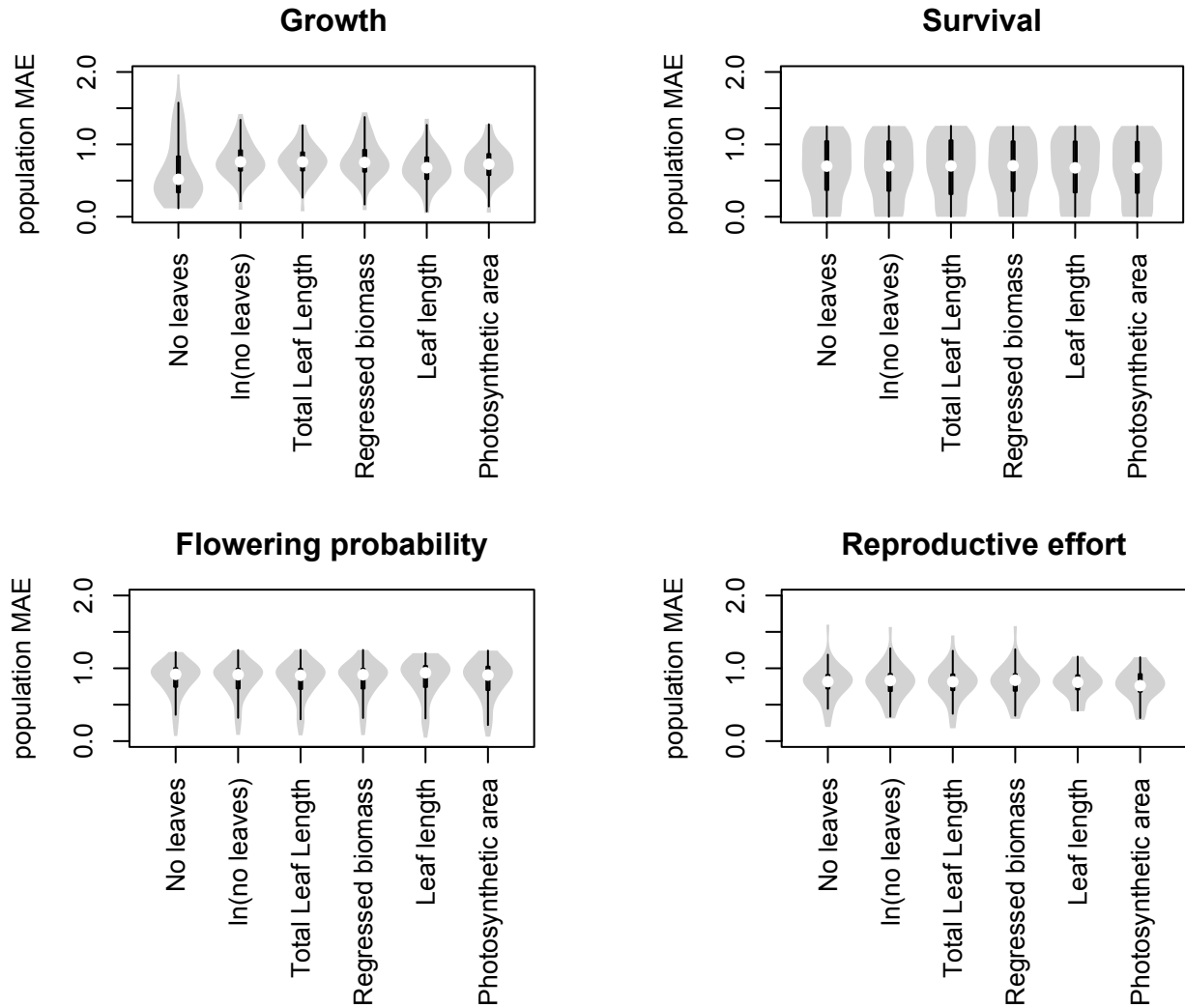


Figure 1.3 Performance of the different size metrics (x axis), illustrated by the density plot of the Mean Absolute Errors (y axis) for all 52 population. The width of the density plots illustrates the density of points at that MAE value. MAE is the sum of the absolute values of the residuals for each population, over the number of observations in that population. Residuals were standardized for all models and are on the logit scale for the binomial models. Longer density plots imply a broader spread of performance.

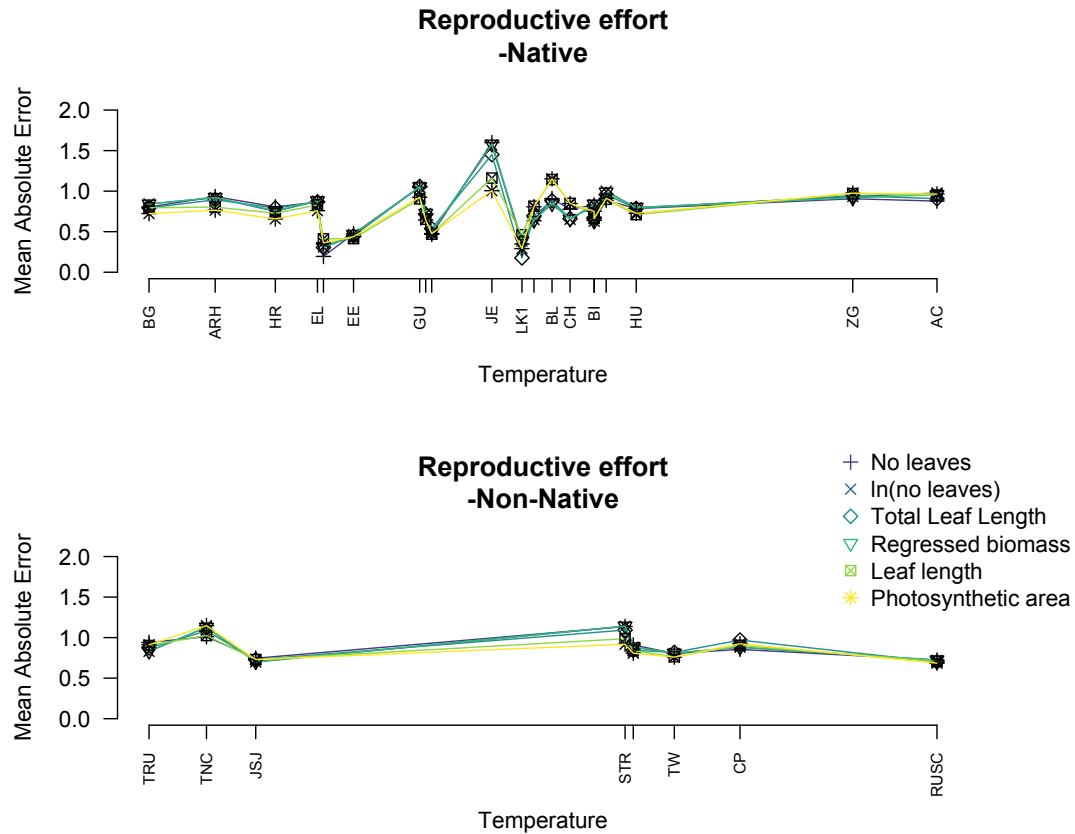


Figure 1.4 Performance of the different size metrics (lines and types of points) across the temperature gradient (*x* axis, each point value on the *x* axis is a different existing PlantPopNet population), measured in Mean Absolute Errors by population (*y* axis).

variables differed between rates, with for instance photosynthetic area being ranked 2 for probability of flowering in terms of R^2c , but ranked 6 for reproductive effort. The size metrics alone explained between $R^2_m = 0.6$ and $R^2_m = 0.36$ of the variance (Figure 1.2B).

Performance across populations and along climatic gradients

All size variables performed similarly across populations for the rates of survival, probability of flowering and reproductive effort (Figure 1.3). The analysis of performance along environmental gradients showed little difference between candidate metrics and vital rates. As the results were so similar, only one demographic transition is illustrated in this manuscript as an example (Figure 1.4), with details for other transitions and for the precipitation gradient available in Figure S1.3.1. Some populations were explained better

than others, but this was not significantly affected by the size metrics, nor the environmental gradients (Supplement S1.3.2.).

Consistency of the ecological relationship across populations

The ecological relationship between size and the vital rates of growth, survival and flowering likelihood was mostly consistent over all populations. Larger plants tended to be bigger at the time of the next census, and to be more likely to flower and more likely to survive, although the magnitude of the relationship differed between populations (Figure 1.5). For survival and flowering probability, the relationship to size was inverted in some few populations, with bigger plants being more likely to die the next year.

Variable selection

The ranking through our variable selection framework yielded different results for each criterion (Table 1.3). Overall, the number of leaves (both log and not log transformed) were the best performing metrics, followed by the Total Leaf Length and regressed biomass (Table 1.3).

Variable	Model assumptions met (a)	Best accross rate (b)	Best accross populations (c)	Most consistent accross performance across populations (d)	Most consistent slope across populations (d)	Overall
Photosynthetic area	ok	5	2	6	5	5
Number of leaves	suboptimal	1	1	1	1	1
Ln(number of leaves)	ok	6	5	2	5	2
Total leaf length	ok	4	4	3	3	3
Leaf length	suboptimal	3	3	5	6	4
Regressed biomass	ok	2	6	4	2	3

Table 1.3: Final selection of the best candidate variable. Candidate variables were examined over three criteria; performance across rates, performance across populations and consistency of the performance across populations. Candidate variables were excluded if model assumptions were not met. The remaining variables were ranked with the best performing metric at each criterion 1, and the worst performing metric 6. Rankings were then summed and ranked (Overall). Characters between parentheses relate to the Methods section and the description of the criteria.

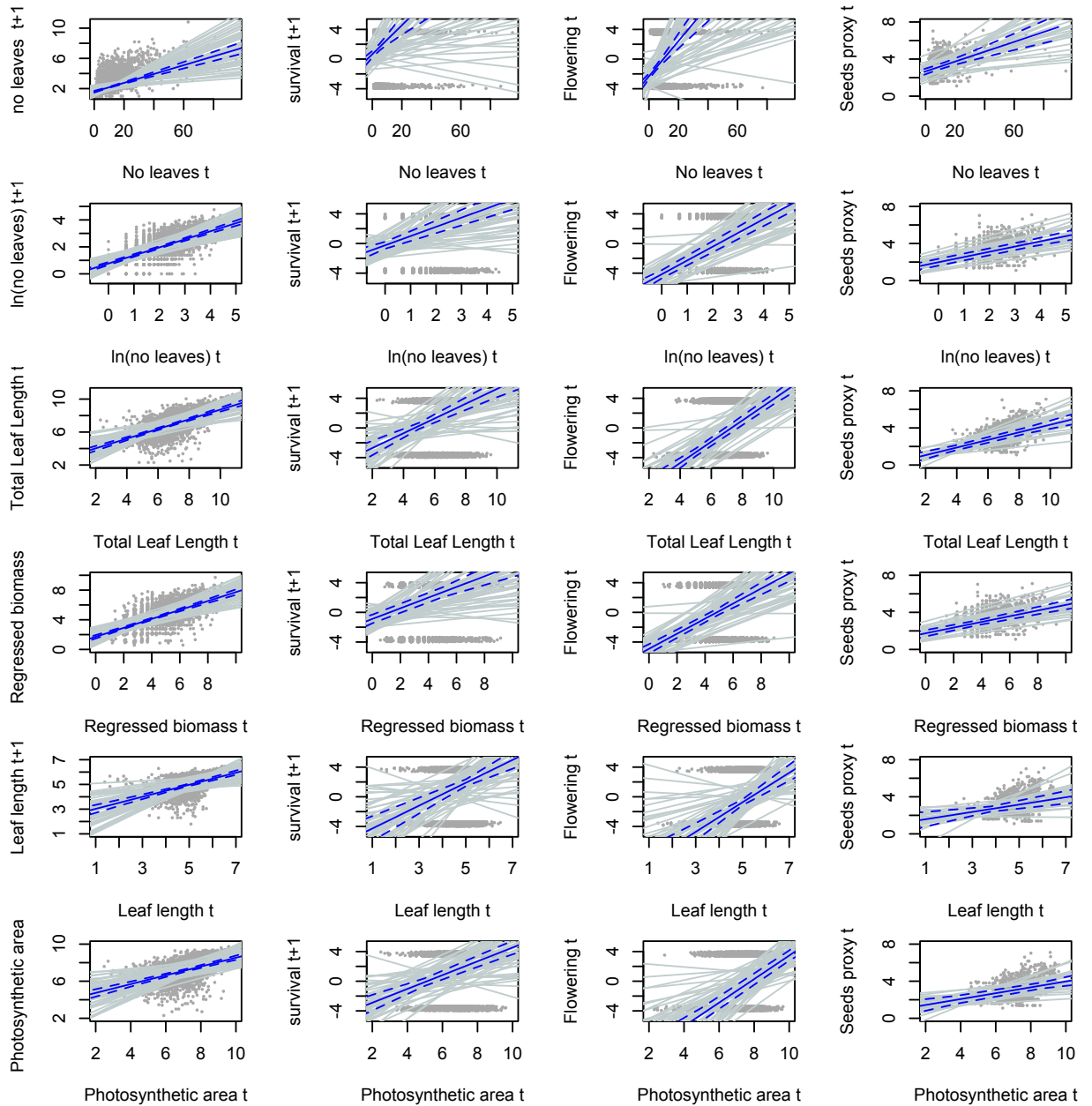


Figure 1.5 Consistency of the relationship between the vital rates and candidate size metrics. Blue lines show the fixed effect of the model. Grey lines show the random effects for each population. Grey dots in the background show original observations, in the link scale (logit scale for binomial models, log scale for negative binomial) to facilitate plotting of the model predictions as straight lines. Observations in the binomial distribution are plotted as their logit values, 3.66 and - 3.66 respectively, with some jitter around points to allow to visualize observation density.

1.5 Discussion and conclusion

We found that the different size metrics commonly used in the literature for local studies performed comparably well in their ability to predict vital rates at a global scale for the common herbaceous perennial *Plantago lanceolata*. The percentage of explained variance in vital rates ranged between 53 and 72% (R^2 ; Nakagawa and Schielzeth, 2013), with slight differences in the best performing candidate size variable across vital rates. The ability of our model to explain the variance in vital rates varied between populations, but no size metric was systematically better and there were no trends along studied environmental gradients. The ecological relationships (slopes) illustrated between size and demographic transitions is consistent between size variables, although some populations have contrasting behaviour; in most cases bigger plants are likelier to both survive and flower, whereas in a few populations, smaller plants have a higher probability to survive, as well as to flower. Overall, all metrics performed well and comparably.

The PlantPopNet network is the first attempt to monitor the demography of a species at a global scale (Buckley et al. 2019, Smith et al. 2020). The most commonly cited limitations in demographic studies are the limited geographical range (Coutts et al. 2016; Salguero-Gomez et al. 2012; Tredennick et al. 2018) and the lack of replication (Csörgő et al. 2017; Salguero-Gomez et al. 2012; Salguero-Gómez et al. 2015). In this context, this study advances our knowledge on how to capture size-structured changes in demography at a global scale. A first important result is that we *can* model vital rates at global scale using a single size metric and do so with a high percentage of explained variance (53 to 72%). These results were achieved while using only the size of the individuals and the population and plot of origin as predictors. The inclusion of additional appropriate biotic and abiotic explanatory variables may further increase the explanatory power. Another powerful finding is that all tested size metrics performed well at a global scale.

In our final ranking (Table 1.3), the number of leaves was the best performing metric across all four criteria, followed by the metric we call “Total Leaf Length” (number of leaves in a genet times the length of the longest leaf of the genet). Both of these variables are fairly straightforward to measure in the field. The number of leaves only requires the counting of the number of leaves per individual, with the addition of the length of the longest leaf in the

genet in the case of Total Leaf Length. This is much easier than to collect entire specimens to obtain a regressed biomass equation such as that used by (Villellas et al. 2021), which ranked third together with Total Leaf Length. The number of leaves is widely used in many study organisms (Jongejans et al. 2010; Oldfather 2018b), including *P. lanceolata* (Antonovics and Primack 1982; Shefferson and Roach 2012).

The identification by this study of such simple metrics that are useful across many different populations is of great significance for collaborative projects such as PlantPopNet. Indeed, simplified protocols seem to have the greatest practical longevity (Pocock et al. 2014). Another strong limitation in existing demographic datasets is the lack of long-lasting time series (Crone et al. 2011; Reed et al. 2003; Zeigler, Che-Castaldo, and Neel 2013), as temporal variation in demographic processes has been shown to be high (Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Quested, and Wardle 2010; Jongejans and De Kroon 2005). Our results provide important insights into optimal procedures for maintaining longer time series, and highlight the potential to do so through a simplified protocol. In our study, the growth models using the number of leaves (log transformed or not) as a predictor and response variable were zero depleted. This is inevitable as size zero is confounded with death in our system as we use only one yearly demographic transition. Similarly, the log transformed size predictors cannot handle plants of size zero and dormancy. With time, re-emerging plants in the dataset will become apparent, and the ability to handle zero-leaf sizes and plant dormancy will become a further advantage of the number of leaves as compared to the other metrics tested here.

One of the strengths of the PlantPopNet dataset is that it is not limited by a lack of spatial replication, which is often highlighted as a major hindrance in the field of demography (Ehrlén et al. 2016). Hence, although the scope of this publication is to select a good size metric prior to studying the effects of numerous potential environmental drivers of demographic processes (see for instance Römer et al., 2021), our results give some insights about the importance of environmental predictors to be added in demographic models later on. Our results show high quality vital rates models, with no strong increase in Mean Absolute Error at either temperature or precipitation extremes. This tends to confirm that broad scale variation in environmental predictors can be efficiently captured by the grouping in populations of origin alone. In our study, the population of origin is a coarse proxy for

large scale variation in climatic, anthropogenic and genetic factors between populations (Smith et al. 2020; Villellas et al. 2021). Yet this coarse proxy of environmental processes does not shed light on what mechanisms are shaping the variance in demographic processes. It is interesting to note that depending on the rate, the belonging to a certain population of origin is more or less explanatory (R^2_c versus R^2_m comparison). This probably indicates different mechanisms creating the variance in demographic processes depending on the studied rates. Finally, some populations were shown to have poor performance for all metrics, and these are not correlated with extremes in any of the environmental gradients studied in the present work. This highlights the need for further exploration of environmental drivers of demographic processes (Ehrlén et al. 2016; Merow, Dahlgren, et al. 2014; Merow, Latimer, et al. 2014; Römer et al. 2021).

In conclusion, we find in a globally distributed demographic dataset for a single species that a simple metric such as the number of leaves or the number of leaves times the length of the longest leaf in the genet, can perform very well in size structured demographic studies. Despite the wide geographic and climatic range included here, the same variables performed well in all 55 populations stemming from 3 different continents and six different biomes. This offers further support for works in the field of demography seeking generalization through compilation of models from different studies and populations. Our work suggests a method to perform a size variable selection in demographic studies in complex cases with numerous populations and several rates. This work provides important insights for size metric selection that can be applied to further studies.

Acknowledgements

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Chapter 2. Vital rates and life history strategies of *P. lanceolata* are correlated with SDM predicted suitability along a steep environmental gradient in the Swiss Alps

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2.1 Abstract

Demography and life history are key determinants of population performance, known to vary in space and within species' environmental niches. Suitability gradients along niche dimensions can be quantified using Species Distribution Models (SDM), which model the probability of occurrence as a function of environmental drivers. Whether readily available measures of "suitability" from SDM are associated with variation in species demography and life history strategy remains unclear.

Here, we investigated whether SDM-suitability was correlated with demographic processes using the perennial herb *Plantago lanceolata*. We first used SDM-suitability to sample 18 populations along a steep suitability gradient in the Swiss Alps, monitoring all individuals for three years. We assessed the ability of SDM-suitability to explain vital rates using generalized linear mixed models. We built density dependent Matrix Population Models and explored the ability of SDM-suitability to capture overall population performance (abundance, population growth rate, carrying capacity) and life history strategies. We performed an LTRE to explore which changes in vital rates impacted performance and life history strategies.

We found a faster life cycle in areas with higher SDM-suitability. The generation length and reproductive life expectancy were shorter, but the yearly reproductive rate was higher and populations relied less on retrogression in the case of this perennial herb. These changes were shown to be mostly caused by a lower probability of survival in high suitability areas. Population size was stable due to density dependent recruitment, and abundance decreased with SDM-suitability. Overall, SDM-suitability was a meaningful predictor for demographic processes at a fine scale, but not integrated population performance.

2.2 Introduction

Predicting and mitigating the impact of climate change on biodiversity is one of the most pressing issues for ecologists and conservationists of this century (Pearson et al. 2014; Williams et al. 2015). Correlative species distribution models (SDM), which aim to capture the niche of species by correlating occurrence data with environmental predictors, are commonly used to determine potential changes in species distribution (Fordham et al. 2018; Guisan et al. 2017; Thurman et al. 2020). Integrating demographic information into correlative SDM has been suggested as a powerful way to improve these predictions (Fordham et al. 2018; Keith et al. 2008; Schurr et al. 2012; Swab et al. 2012, 2015). Compared to correlative models alone, such approaches were shown to produce less biased (Schurr et al. 2012) or different (Swab et al. 2015) results, or to provide a more complete picture of the ecological drivers of observed changes (Swab et al. 2012). However, demographic data are often limiting (Coutts et al. 2016; Salguero-Gómez et al. 2015).

Very few studies investigate the relationship between demography and SDM-predictions in current climatic conditions (Csörgő et al. 2017; Thuiller et al. 2014), and even fewer do so in the current realized niche of the species (Holt 2009; Hutchinson 1957; Soberón et al. 2017), i.e. including biotic interactions (Bayly and Angert 2019; Greiser et al. 2020). Demography focuses on the study of the vital rates of survival, growth and fecundity of individuals within populations (Caswell 2001; Harper 1977). Collecting detailed demographic information often takes years of monitoring the survival, growth and reproduction of hundreds of individuals for a single population (Caswell 2001; Ellner et al. 2016; Morris and Doak 2002). As a result, we lack replicated demographic datasets (Salguero-Gómez et al. 2015). Data availability is particularly limited along quantified environmental gradients (Abeli et al. 2014; Pironon et al. 2017) and from challenging environmental conditions (Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Quested, Wardle, et al. 2010; Csörgő et al. 2017). Consequently, little is known about the changes in demographic strategies along probability of occurrence gradients, despite the interest of incorporating demographic information into SDMs and *vice versa* (Buckley and Puy 2021; Gurevitch et al. 2016).

Vital rates are the fundamental processes underlying population persistence and performance (Holt 2009; Hutchinson 1957). Life history strategies are the population level

consequence of changes in individual's vital rates and can be understood as the evolutionary response of a species to local conditions (Cole 1954; Grime 1977; Stearns 1992). There are many metrics for population performance, such as abundance (Ehrlén and Morris 2015; Vanderwal et al. 2009), carrying capacity (the maximal abundance of a species a site could support; Vanderwal et al. (2009), population growth (Caswell 2001; Csergő et al. 2017; Thuiller et al. 2014), increase in multiple raw vital rates (Bohner and Diez 2020) or fitness (Coutts et al. 2021; Moles 2018). The implicit assumption of many applied uses of SDMs is species will “perform better” in high occurrence probability areas, also called “high suitability” (Alagador, Cerdeira, and Araújo 2014; Araújo and Williams 2000; Guisan and Thuiller 2005). For instance, several SDM-demographic predictive models assume a higher carrying capacity in higher probability of occupancy areas (Keith et al. 2008; Swab et al. 2012, 2015), and the selection of areas of high SDM-suitability for conservation implies the expectation of a higher abundance or population stability of the focal species (Araújo and Williams 2000; Ehrlén and Morris 2015; Vanderwal et al. 2009). Yet the relationship between occupancy and population performance is increasingly shown to be complex (Bohner and Diez 2020; Csergő et al. 2017; Ehrlén and Morris 2015; Pironon et al. 2017; Thuiller et al. 2014). Probability of occupancy was shown not to correlate with population growth rates (Bohner and Diez 2020; Csergő et al. 2017; Thuiller et al. 2014), and there is evidence that it does not overlap with the optima of single vital rates (Bohner and Diez 2020; Pironon et al. 2017). Furthermore, SDM predictions have consistently failed to predict experimental demography (Bayly and Angert 2019; Greiser et al. 2020). There is some support for a positive relationship between population abundance and probability of occupancy, but both very high and very low abundances can occur in high-suitability areas (Vanderwal et al. 2009; Weber et al. 2017). Thuiller et al. (2014) found a generally positive relationship between population density and SDM predictions in a study of 108 tree species, and a weaker, usually positive, relationship with carrying capacity. Thuiller et al. (2014) interpret their results as meaning that intraspecific competition is lower in high SDM-suitability areas. Generally, there seem to be mismatches between SDM predictions and population performance.

Even if population performance may not be correlated with SDM-suitability, suitability could still have a relationship with the underlying demography (Buckley and Puy 2021; Csergő et al. 2017; Gurevitch et al. 2016). Different vital rates can have variable relationships with

environmental drivers (Maguire, 1973; Pironon et al. 2017, 2018). Opposing responses of vital rates to drivers can lead to demographic compensation, stabilizing population growth along environmental gradients, through alternative strategies (Bohner and Diez 2020; Villellas et al. 2015). Different combinations of survival, growth and fecundity can result in a multitude of life history strategies (Cole 1954; Grime 1977; Stearns 1992). Species life histories can be described using a pace of life axis, with long-lived slow growing species producing few sexual recruits vs. short-lived fast growing species producing many sexual recruits, and a second axis impacted by clonality and the timing of reproduction within the life span (Salguero-Gómez et al., 2016). Similarly at the intraspecific level, populations can vary in their life history strategies, though the phenomenon is much less studied (Cole 1954; Grime 1977; Moles 2018; Stearns 1992).

Population performance is also known to be driven by historical processes (Bohner and Diez 2020; Ehrlén and Morris 2015; Holt 2009). In freshly colonized or disturbed sites, population density is likely to be low. In such cases, competition is relaxed and the presence of conspecific individuals can even lead to positive density dependent feedback (Courchamp, Berec, and Gascoigne 2008). In long established populations, density is likely to be high for the focal species and other members of the community. In such cases, density dependent feedback likely to be negative (Courchamp et al. 2008; Holt 2009). An extreme case of density dependence occurs where recruitment is limited by microsite availability (Ellner et al. 2016). In such cases, the population density and growth will be limited by the number of available microsites and a “seed lottery” will determine which adult individuals get to succeed in their reproductive effort. Microsite availability might be driven by many factors, such as the density of conspecific individuals, interspecific interactions or disturbance.

Consequently, SDM-suitability could be more strongly linked to the mechanisms underlying population performance, rather than performance directly. In a study of 93 populations of 34 species, (Csörgő et al. 2017) found that SDM-suitability was a predictor of pathways of population performance: populations in low suitability climates had higher retrogression associated with resistance to extinction and higher variability in some demographic rates associated with vulnerability to extinction. Some species delay reproduction and shift to slower life history strategies in harsher conditions (Harper 1977). Csörgő et al. (2017) were limited in their conclusions by data availability especially in low SDM-suitability areas.

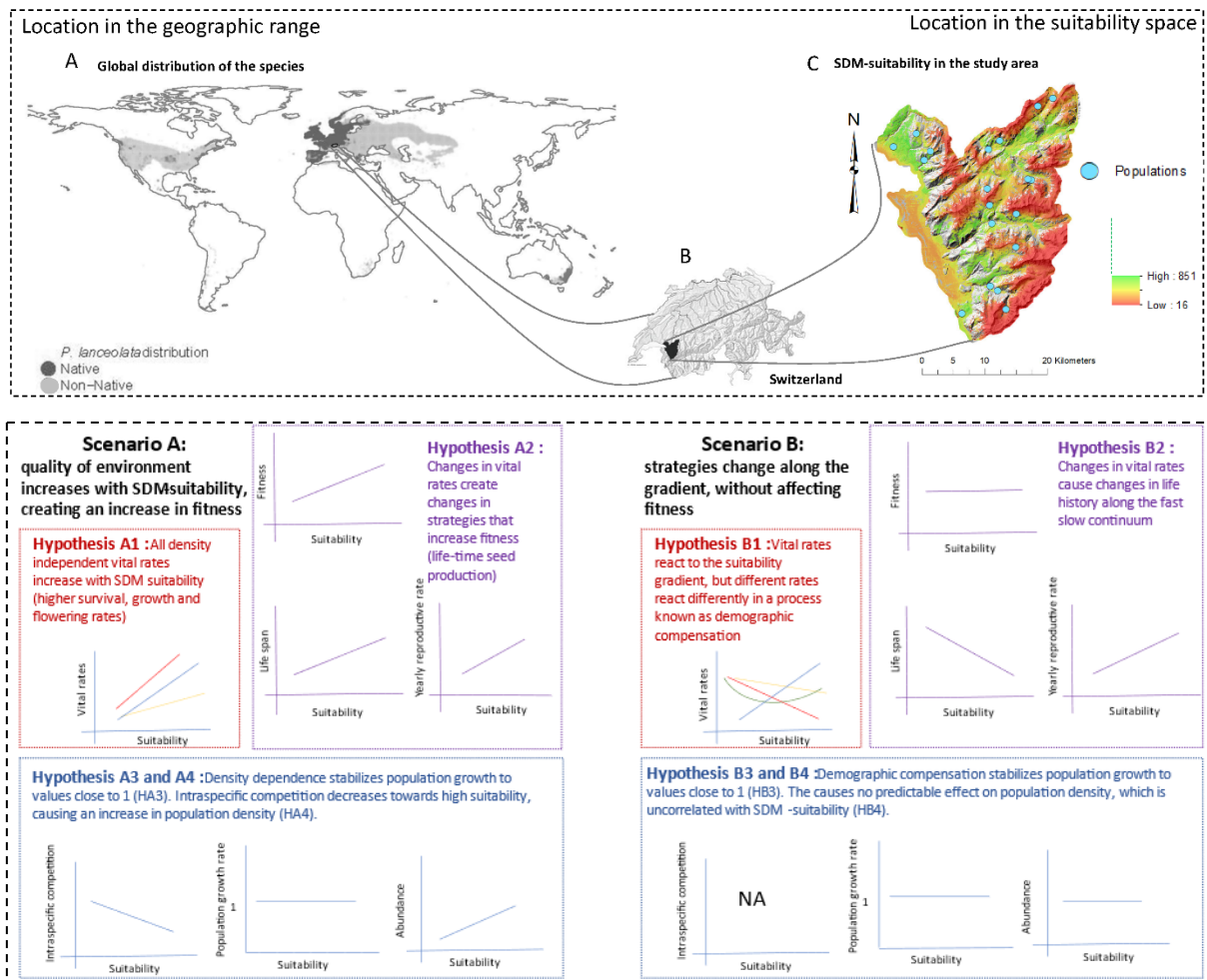


Figure 2.1 Overview of our study. Upper panel: Location of the study in a) the world b) Switzerland c) the western Swiss Alps. We sampled 18 populations of the species *Plantago lanceolata* at a climatic niche edge, central to the geographic range, and studied the changes in the species' demography along this suitability gradient. Environmental suitability (ϖ , in shades of red (low) to green (high)) was quantified via an SDM. Our gradient may be truncated and not show the most optimal conditions for the species, this is represented by the dashed line at the high end. Blue dots = sampling points of the populations described in this study. Lower panel: graphical overview of our hypotheses.

We used Species Distribution Models (SDMs) to quantify the suitability gradient at a known climatic niche limit of the perennial herb *Plantago lanceolata* L. in the Swiss Alps (Figure 2.1). *P. lanceolata* L. is a lowland species, long established in the area and likely to have reached some form of equilibrium with its environment. We monitored the vital rates of the species in 18 populations sampled regularly along the SDM-suitability gradient. We built environmentally explicit population models by including SDM-suitability as a predictor of the vital rates of the species. We incorporated density dependence at the level of the recruitment. We assessed whether SDM suitability could explain variance in a) the vital rates of individuals (growth, survival and fecundity), b) life history (generation length,

reproductive life expectancy, yearly reproductive rates and reliance on retrogressive and progressive growth) and c) population performance (population growth rate, population density and average fitness of individuals).

We proposed two alternative scenarios of demographic response to the gradient (Figure 2.1). In scenario A (Figure 2.1) we assumed an increase in environmental quality with SDM-suitability with correlated increases in population performance leading to the following expectations: HA1) all density-independent vital rates increase with suitability, HA2) life history metrics positively associated with fitness, such as reproductive life span and life time seed production, increase with suitability, HA3) as we study established populations, at equilibrium with their environment, population growth rate will be close to one (Courchamp et al. 2008; Holt 2009; Hutchinson 1957), due to negative density dependent feedbacks on recruitment (one plant can be replaced, in average, by only one recruit over its life time), HA4) given that intraspecific competition has been shown to decrease at higher SDM-suitability (Thuiller et al. 2014), population density increases with SDM-suitability (each plant will have a higher density of neighbours).

In scenario B (Figure 2.1), we expect changes in *strategies* to lead to similar population performance and fitness along the gradient, assuming demographic compensation (Vilellas et al. 2015) leading to the following expectations: HB1) some vital rates increase while others decrease with SDM-suitability, HB2) a shift in life history strategies with metrics related to slower pace of life – longer generation time and life span, higher retrogression – associated with low suitability (Buckley and Puy 2021; Csergő et al. 2017), HB3) demographic compensation leads to no consistent SDM-suitability correlation with population growth rate, HB4) no consistent SDM-suitability correlation with density.

We note that demographic compensation does not exclude the existence of density dependence and *vice versa*.

2.3 Methods

Overview

We used a Species Distribution Model (SDM) to characterise environmental suitability for

the study species, *Plantago lanceolata* L., in a 700 km² area in the Swiss Alps and used randomized stratified selection of 18 demographic survey sites across this suitability gradient. A matrix population projection model was parameterized for each site using vital rates (such as flowering, survival, growth and recruitment) modelled as a function of suitability and density when appropriate. The parameterised Matrix Population Model therefore varied as a function of environmental suitability. We used this Matrix Population Model to calculate Life History Strategy metrics for each population to test how life history strategy varied along the suitability gradient.

Species

Plantago lanceolata L. is a perennial, short-lived, rosette forming herb (Kuiper and Bos 1992; Sagar and Harper 1964), increasingly used as an ecological model organism (Penczykowski and Sieg 2021). Native to Eurasia, it is now widespread throughout the globe (CABI 2019). Each individual (genet) is composed of one to several rosettes (ramets). Small flowers are arranged in linear inflorescences which vary in length and are arranged on a variable number of flowering stems per rosette and per individual plant (Sagar and Harper 1964). Each flower produces up to two seeds (Lauber et al., 2018). The plant is variable in size and shape, with leaves ranging from 2 to 45 cm in length (Sagar and Harper 1964). In the Swiss Alps, *P. lanceolata* is known to be commonly present in the lowland, being replaced by the congeneric species *P. atrata* and *P. alpina* at higher elevations (Lauber et al., 2018).

Study area

The study area covers 700 km² in the western Swiss Alps with an elevation ranging from 375 to 3210 m (Figure 2.1), and is a priority region for interdisciplinary research; <https://rechalp.unil.ch> (Von Däniken, Guisan, and Lane 2014). The vegetation reflects the typical elevational gradient of Central Europe, with broadleaf deciduous forests at the lowest elevations (colline belt), followed by mixed deciduous-coniferous (montane belt), then coniferous forests (subalpine belt) and open habitats (e.g. grasslands) above the treeline (alpine and nival belts; see Dubuis, Rossier, et al. (2013) or more information). Open areas just above and below the treeline usually correspond to anthropogenic habitats, most of which are used for agriculture, with pastures in the lowlands to the upper-subalpine and lower-alpine zones, and meadows primarily in the colline and montane belts (Randin et al., 2009).

Niche and distribution models

The environmental niche of the species in the study area was characterized through fitting species distribution models (SDMs; Guisan et al. 2017). We used pre-existing presence-absence data for the species collected through several research projects in the research area (see Baudraz et al., 2018; Dubuis et al., 2011; Pellissier et al., 2013; Scherrer, Massy, Meier, Vittoz and Guisan, 2017 for the original datasets) . This led to a total of 1476 visited sites outside forested areas, including 353 presences for *P. lanceolata*. The environmental predictors used in the SDM are detailed in Table 2.1. Their choice was based on prior knowledge on the ecology of the species (Kuiper and Bos 1992; Villellas et al. 2021) as detailed in Supplement S2.1.1.

We used Biomod2 to fit the individual SDMs and derive the final prediction of habitat suitability (Thuiller et al. 2016). Three modelling techniques were included in the ensemble: boosted regression trees (Elith, Leathwick, and Hastie 2008), random forest (Prasad, Iverson, and Liaw 2006) and generalized linear model (Guisan, Edwards, and Hastie 2002). The models and final predictions were evaluated through repeated split sampling using AUC, max-Kappa and max-TSS (Guisan et al. 2017). A final, average ensemble model of probability of occupancy using all of the data was then projected over the study area and used as an environmental suitability metric (Guisan et al. 2017).

Site selection for population monitoring

Sites were selected following a random stratified sampling strategy (Guisan et al. 2017). The suitability range (from min to max log odds value) was divided into five strata each covering interval classes of 20% of all possible suitability values. Known *P. lanceolata* occurrences were randomly selected and visited. If the occurrence of *P. lanceolata* was confirmed and the site deemed suitable for the PlantPopNet protocol (Buckley et al. 2019), a population monitoring site was set up. A total of 18 populations were used, four in each suitability stratum except for the lowest and middle suitability (supplement S2.1.2) where three were used.

Table 2.1 Predictors included in the Species Distribution Model. All raster layers had a grid cell size of 25 x 25 m.

Variable	Definition	Unit	Source
Moisture index	Mean difference between precipitation and potential evapotranspiration over the 1/10 growing season (water potentially available in soil)	mm	Dubuis, Giovanettina, et al. (2013); Zimmermann and Kienast (1999)
Slope	Slope of the grasslands	°	Swisstopo.ch; Zimmermann and Kienast (1999)
Topographic position	Index where positive values = ridges and tops, negative values = valleys and sinks	unit-less	Dubuis, Giovanettina, et al. (2013; Zimmermann et al. (2007)
Mean temperature	Mean temperature over the growing season	°C	meteosuisse.ch; Zimmermann and Kienast (1999)
Meadow Height	Predicted vegetative height of meadow communities (community weighted mean)	m	Baudraz et al. (2018)

Fieldwork and gathering of demographic data

Once a site was selected, the original marking of the populations and subsequent demographic census at that site were performed following the PlantPopNet protocol (Buckley et al. 2019). In Summer (June-August) 2017, 100 individuals per site were mapped in small quadrats of 50 by 50 cm along 10 m transects. Each individual was marked with a small linoleum square. As many quadrats and transects were established as necessary to gather 100 individuals. Size (number of leaves and length/width of the longest leaf) and reproductive effort (number of stems and inflorescence length of longest flowering stem) of each rosette from every individual were recorded during the summer for three years (2017-2019). As an addition to the general protocol, when new individual rosettes were produced, they were also tagged and measured, and given an individual identifier, either within the

genet they belonged to or as separate, new recruits. Seedlings were counted, but not marked until their second year, to avoid tagging related mortality.

Population model

We built a size-structured population model, based on the number of leaves per individual (Chapter 1). As the size structuring variable was discrete, Matrix Population Models were parameterised. However, the methods for parameterisation and projection were taken from Integral Projection Modelling (IPM; Easterling et al. (2000); Ellner et al. (2016). Recruitment was allowed to be density dependent, whereas other vital rates were considered density independent. Bold, capital letters refer to matrices and matrix components. Small, italicized letters refer to vital rate models and the functions used to parametrize said matrices.

Species life cycle

Plantago lanceolata's lifecycle is described in Figure S2.2.1, with variables and parameters detailed in Table 2.2. Overall, adult individuals of size z at time t contribute to the pool of individuals in the next year if they survived (s) and grew (g) (or shrank) to a size z at time $t+1$. All individuals have a probability of flowering (h). We measured reproductive effort as a proxy for number of seeds (o), which is the number of flowering stems multiplied by the length of the longest inflorescence in mm (see supplement S2.3). Each unit of reproductive effort has a probability of contributing to the pool of recruits (b) entering the population the next year with a size given by the recruit size density function (c). Although the entry of recruits through a size distribution function allows for the production of some large recruits, this life-cycle assumes that all recruits are produced sexually, ignoring clonal reproduction (Kuiper and Bos 1992). This model also ignores recruitment from soil seed bank (see discussion).

Density independent vital rates

The vital rates models were built using a series of generalized linear mixed models, each corresponding to a vital rate (Figure S2.2.1). Growth (g) was modelled as size z_{t+1} with size z_t as an explanatory variable. Survival (s) and flowering (h) were modelled as probability of flowering or surviving over one year using a binomial error distribution and logit link function. Reproductive effort (o) (Supplement S2.3), was modelled with a Gaussian error distribution. In the PlantPopNet protocol, recruits are only tagged and tracked once they

reach the minimal size of 2 leaved-individuals, to minimize the impacts of tagging on seedlings and cotyledon-staged individuals. Hence the size of the recruits model (c) was limited to a 2-leaved minimal size. The size of recruits (c) was modelled as a truncated negative binomial with log link on the number of leaves z_{t+1} of observed recruits.

Table 2.2 definition of notations used

Symbol	Name	Definition
z_t	Size of individuals (number of leaves) at time t	Measured in number of leaves, with $\min(z) = 2$ as the smallest individuals entering the matrix have 2 leaves and $\max(z) = 69$.
T	transition	Yearly transition. 2017-2018 = T_1 2018-2019 = T_2 .
ϖ	suitability	Suitability value from the Species Distribution Model
w	site	Locations of the populations
u	Plot identity	Identity of any given 50 cm x 50 cm plot used to map and monitor <i>P. lanceolata</i> L. individuals within sites
t	time	t = the time point at the start of a transition, $t+1$ = the time point at the end of a transition. In this case, time intervals are yearly intervals.
a	area	The number of 0.25 m ² plots covered by the population.
r	number of recruits	Measured at the site level
Matrix Population Model components		
S	Survival	A diagonal matrix of size $n \times n$ matrix, where n = observed size range, and $s_{i,i}$ is the probability of survival for a plant of size class i and all other values are set to 0.
G	Growth	An $n \times n$ matrix, where n = observed size range, and $g_{i,j}$ is the probability of transitioning from size class i to size class j , conditional on survival to $t+1$.
P	Survival and growth component of the matrix model	A matrix of size $n \times n$ matrix, where n = observed size range, and $p_{i,j}$ the probability of survival and transitioning to size class j . For size class z_i , $s_{i,i}$ $g_{i,j}$ is the probability of transitioning from size class i to size class j .
F	Fecundity component of the matrix model	A matrix of size $n \times n$ matrix, where n = observed size range, and $f_{i,j}$ is the contribution of any individual of size class i to recruits of size class j the following year. F is populated through equation 2.
H	Flowering	A diagonal matrix of size $n \times n$ matrix, where n = observed size range, and $h_{i,i}$ is the probability of flowering for an individual of size class i .

O	Reproductive effort	A diagonal matrix of size $n \times n$ matrix, where n = observed size range, and $o_{i,i}$ is the estimated reproductive effort (measured in mm of inflorescence, as a proxy for number of seeds) predicted for an individual of size class i , conditional on flowering.
C	Size distribution of recruits	A $n \times 1$ dimension matrix, where n = observed size range and $c_{i,1}$ is the probability for a recruit to be in size class i .
η	Contribution to the pool of recruits	The contribution of any one unit of reproductive effort (mm of inflorescence, as a proxy for number of seeds) to the pool of recruits entering the population, obtained by eq 3.
\mathbf{n}_t	State vector at time t	Vector of the number of individuals in each size class in the population at time t .

Vital rates models and functions used to parametrize the matrices

Vital rate	Function	Name	Definition
s	$s(z_t, w, \varpi, T)$	Probability of survival	$s(^{\circ})$ predicts the probability of survival of an individual of size z_t for site w , suitability ϖ and transition T .
g	$g(z_{t+1}, z_t, w, \varpi, T)$	Growth or stasis	$g(^{\circ})$ predicts the probability for an individual of size z_t to transition to a size z_{t+1} , conditional on survival.
h	$h(z_t, w, \varpi, T)$	Probability of flowering	$h(^{\circ})$ predicts the probability of flowering of an individual of size z_t for site w , suitability ϖ and transition T .
o	$o(z_t, w, \varpi, T)$	Reproductive effort	$o(^{\circ})$ predicts the reproductive effort (mm of reproductive material) of an individual of size z_t conditional on flowering.
c	$c(z_{t+1}, w, T)$	Size distribution of recruits	$c(^{\circ})$ Predicts the probability of a recruit to be of size z_{t+1} upon entering the population (at size w in transition T).
b	$b(\varpi)$	Recruitment	$b(^{\circ})$ predicts number of new recruits expected to enter a population, as a function of suitability ϖ .

Vital rates models are described in Table S2.2. The predictions are site and transition specific, and depend on suitability when indicated. Note the functions predict for an average plot \hat{u} . The functions were applied on the range of sizes z_t (1 to 70) and z_{t+1} (1 to 70) to populate the matrices. As a result, the j -th column of the matrix corresponds to size z_t and the i -th row of the matrix corresponds to a size z_{t+1} .

Fixed effects were selected through a multi-model inference technique (MMI; Burnham and Anderson (2002)). Plausible candidate models were compared using AICc (MuMIn package,

Bartoń, 2018; Burnham and Anderson, 2002). For the vital rates of adult plants (g, s, h, o), the candidate models included transition, size of individual plants at time t , and all combinations of: suitability, its quadratic term and the interaction between suitability and size. Five candidate models were produced, including one model where suitability was not included at all (Table S.4.1A-E).

Suitability was always standardized (mean centred and divided by standard deviation). The linearity of the relationship between vital rates and individual size was assessed visually through an exploratory gamm (generalized additive mixed model, Wood and Scheipl (2020). In the case of flowering, evidence of a non-linear relationship with size was found (see Figure 2.2) and the quadratic term of size was also included in the candidate models. For size of recruits (c) candidate models included either suitability, suitability and its quadratic term, or no suitability (Table S2.4.1E).

For models g, s, h, o and c , the site (w), and plot (u), nested within sites, were used as random effects. A random structure with a random slope and intercept for both site and plot levels was kept constant in our models, matching the sampling design. The random effects structure

was simplified only where it enabled models to converge. Transition was treated as a fixed effect as we only had two levels. Transition was included in all models but the recruitment model b , where the sample size was limited to a single transition (see below).

Details of the resulting models are provided in Table S2.4.2. Models were built in R version 3.6.3, using the lme4 and the glmmTMB packages (Bates et al. 2015; Brooks et al. 2017; R Core Team 2020). The variance explained by all models was assessed through the generalized R^2 adapted to mixed effects models (Nakagawa et al. 2017; Nakagawa and Schielzeth 2013). The marginal R^2 (R^2_m) is a measure of the variance that can be explained by the fixed effect part of a mixed model, whereas the conditional R^2 (R^2_c), measures the variance explained by both the fixed and random effects of a mixed model.

Recruitment and density dependence

Several candidate recruitment models (b) were attempted, corresponding to different density dependence regimes: compensatory density dependence, density independence and constant recruitment models (supplement S2.5). The models were compared using AICc

(MuMIn package, Bartoń, 2018), and the best fit model was the constant recruitment model (Table S2.5.1). The final recruitment model was fitted by generalized least squares using the nlme package (Pinheiro et al., 2020). The response variable was square root transformed to normalize the residuals and yield a more homogeneous error distribution. The populations have different densities, with as many 50 cm x 50 cm plots as necessary to sample at least 100 individual genets in the first year. This site specific number of plots (“area”) is written a_w . We fitted our recruitment model on the number of recruits per plot (r_w/a_w) in any site w . The final best recruitment model was a constant recruitment model, where the density of recruits (r_w/a_w) varied only with suitability (see Table S2.5.1).

Matrix Components

Once the models were fitted, we extracted BLUPs (Best Linear Unbiased Predictors) of each vital rate statistical model for the site, transition and suitability values of the focal site to parametrize our functions $g(z_{t+1}, z_t)$, $s(z_t)$, $h(z_t)$, $o(z_t)$ and $b(w)$. Each function predicts the corresponding model, using the mean value of the normal distribution of plot random effects, \hat{u} . The vital rate functions were applied on the range of sizes z_t (1 to 70) and z_{t+1} (1 to 70) to populate the matrices detailed below. The j -th column of the matrix corresponds to size z_t and the i -th row of the matrix corresponds to a size z_{t+1} .

We built the Matrix Model described in equation 1 and following, where \mathbf{G}° , \mathbf{S}° and \mathbf{F}° are the growth, survival and fecundity components of the matrix. Size bins in the matrix were defined as one-leaf size increments. The resulting transition matrices are of dimension 70 x 70, ranging from individuals (genets) of a minimal size of 1 to 70 leaves. Overall, we built one matrix transition model for each site and transition combination, leading to a total of 38 transition matrices. Fixed effects are shown as superscripts, and the random effects as subscripts.

$$\mathbf{G}_{\hat{u},w}^{\varpi,T} \cdot \mathbf{S}_{\hat{u},w}^{\varpi,T} + \mathbf{F}_{\hat{u},w}^{\varpi,T} \quad \text{equation 1}$$

The fecundity component (\mathbf{F}°) (equation 2) is the product of the probability of flowering of an individual of size z_t , $h(z_t)$, multiplied by the reproductive effort $o(z_t)$. This gives the expected contribution of adult individuals to the pool of recruits. We calculated the expected contribution of a unit of reproductive effort to the pool of recruits the next year

(η , eqn. 3), as the ratio of all reproductive units (mm of inflorescence) at any given site w over the density of recruits the following year at the same site (r_w/a_w). This gives us the probability of a unit of reproductive effort contributing one recruit the following year (η). We multiply these recruits by the size distribution of recruits $c(z_{t+1})$ to obtain the probability of a new individual of size z_{t+1} being recruited.

$$\mathbf{F} = \mathbf{H}_{\hat{u},w}^{\varpi,T} \cdot \mathbf{O}_{\hat{u},w}^{\varpi,T} \cdot \eta \cdot \mathbf{C}_{\hat{u},w}^T \quad \text{equation 2}$$

Where η is the average contribution of a reproductive unit (mm of inflorescence) to the pool of recruits entering the site level population the following year;

$$\eta = \frac{\left(\frac{r_w}{a_w}\right)^{\varpi} \cdot a_w}{\mathbf{H}_{\hat{u},w}^{\varpi,T} \cdot \mathbf{O}_{\hat{u},w}^{\varpi,T} \cdot n_t} \quad \text{equation 3}$$

As PlantPopNet only records recruits once they left the seedling stage (over 2 leaved size), recruits can only enter the system with a minimal size of 2 leaves (Table S2.4.2B, S2.4.1) and the fecundity matrix will only have 0s for individuals of size $z_{t+1} < 2$.

Matrix simulations

We projected the MPM 500 times, using the same starting stage distribution for all populations and assuming the same number of plots per site (18, the median of our observations). The standard deviation over the last 10 yearly population growth rates was 0 or lower than 10^{-10} (Figure S2.2.4).

Population performance and fitness

We measured population performance using three different metrics: population growth rate, population density and fitness. For the population density and population growth rate, we used both data observed in the field and the output of our population models. For the observed population density, we took the observed number of individuals in each year of observation in our study (2017, 2018 and 2019) per unit area (i.e., the number of 0.25 m² plots in the monitoring set up in each location). The observed population growth rate was given as the ratio of the number of individuals in a population at time $t+1$ over the number of individuals at time t . Population growth rate at equilibrium is defined as the ratio of the population size (number of individuals) at iteration 500 over the population size (number of individuals) at iteration 499. The population density at equilibrium was defined as the

number of individuals per unit area (i.e., the 18 plots of 0.25 m² our matrices were projected on) after the 500th iteration of our population model.

We computed the fitness of an individual as its life time seed production (Caswell 2001; Coutts et al. 2021; Ellner et al. 2016; Moles 2018). We computed it as the sum of the yearly reproductive effort of an individual born with the average starting size of a recruit and living until a) the end of the maximal reproductive life expectancy at the site or b) living until the

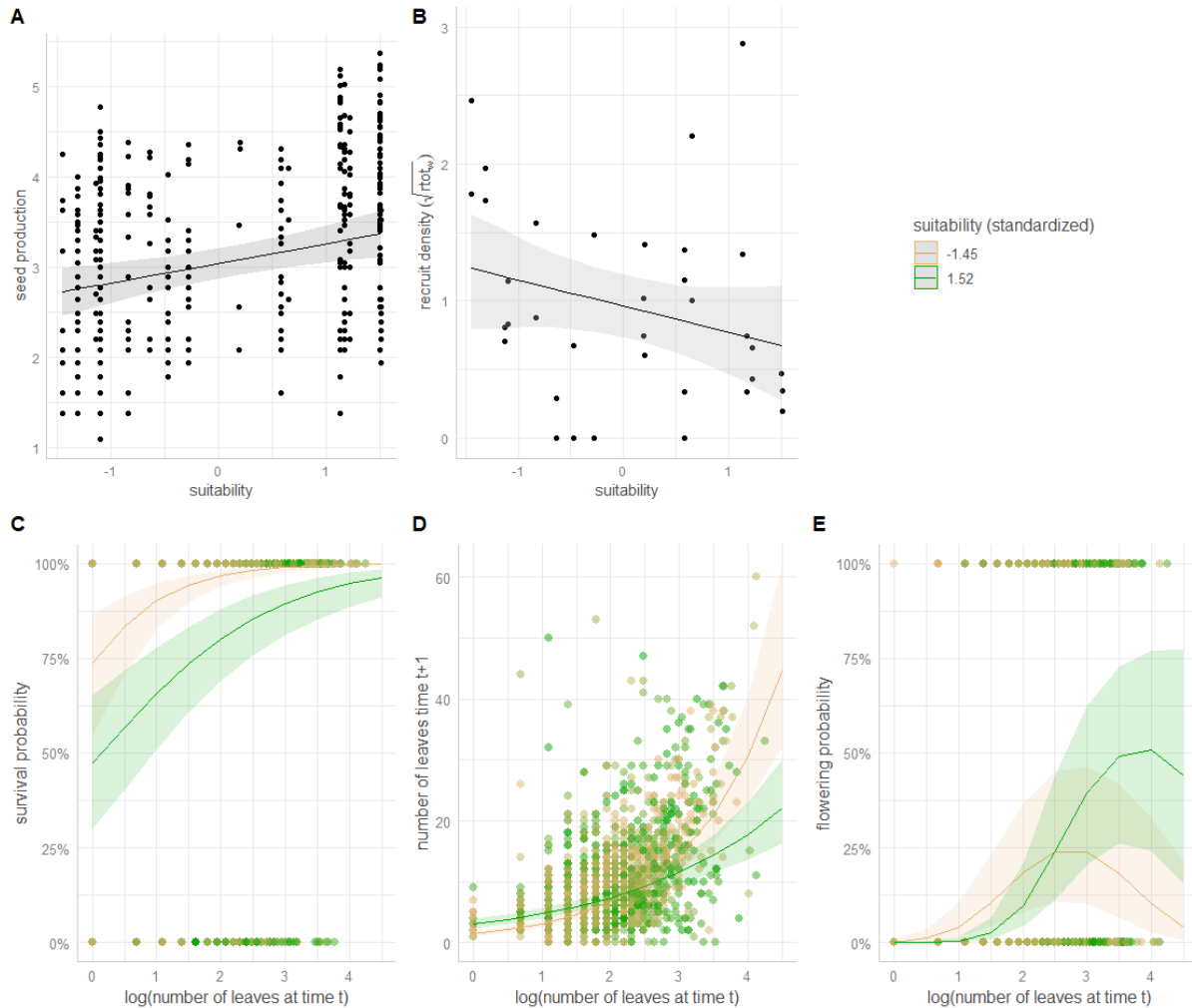


Figure 2.2 Relationship between the vital rates of individuals and SDM-predicted environmental suitability. Reproductive effort (A) and recruitment (B) react linearly to the suitability gradient, whereas survival (C), growth (D) and flowering probability (E) include an interaction between suitability (coloured lines) and size (x axis). The green lines represent the relationship between the vital rate and size at the highest suitability value observed in the study area, whereas the orange line represents what happens at the lowest suitability value observed in the study area. More information in Table S2.4.2 and Figure S2.3.

age at which 50% of individuals at the site die. Both the starting size and the reproductive life expectancy were population and year specific. Note that these metrics are simulations of the life of an average individual.

Life History strategies

We characterized the life history strategies of all population by computing the generation length (number of years it takes for a cohort to replace itself), reproductive life expectancy (number of years between first reproduction and the age at which 99.9% of individuals in the populations are dead), mean reproductive rate (average yearly reproductive output of adults), and rates of progressive and retrogressive growth (probability of an individual of transitioning to a bigger or smaller size class respectively) as in Kelly et al., (2021). Packages used to compute the life history strategy metrics are expm (Goulet et al. 2021), ineq (Zeileis 2014), MASS (Venables and Ripley 2002) and popbio (Stubben and Milligan 2007), with functions extracted from package Mage (now deprecated, see Rage: (Jones et al. 2021)), adapted by Kelly et al. (2021). We computed the generation length based on the survivorship table ($\text{Generation time} = \sum_{x=1}^{x=500} x l_x m_x / \sum_{x=1}^{x=500} l_x m_x$, where l_x is the survivorship until age x , m_x the mortality at time x) based on (Caswell 2001; Healy 2021).

To illustrate the tendency of each LHS along the environmental suitability gradient, we display the LHS values at MPM equilibrium together with trend lines. We built generalized linear mixed models explaining the LHS by environmental suitability (fixed effect) and the site of origin (random effect). The observed trends are inherent to change in underlying vital rates values. We hence display the trends between suitability and LHS together with the output of a Life Table Response Experiment (see next section). In addition, as suitability is a predictor of vital rates, we do not provide confidence intervals for the LHS models.

Life Table Response Experiment

We performed a Life Table Response Experiment (LTRE) analysis to decompose the changes in life history strategy metrics and lifetime seed production (fitness) due to suitability. We used the regression design as described in Caswell (2001), generalised for any life history strategy metric (LHS) calculated from the MPM. We used the parameters of each vital rate models as vital rate values (instead of matrix cell entries as is usual in Matrix Models) (Ellner et al. 2016; Maldonado-Chaparro et al. 2018; Rees and Ellner 2009).

We included all intercepts and interaction terms varying as a function of the suitability ω . The equation we used is

equation 4

$$LHS^{\omega_{max}} - LHS^{\omega_{min}} = \sum_{\rho=g,s,h,o,b} \left. \frac{\partial LHS}{\partial I_{\rho}} \right|_{\omega_{mid}} (I_{\rho}^{\omega_{max}} - I_{\rho}^{\omega_{min}}) + \sum_{\rho=g,s,h} \left. \frac{\partial LHS}{\partial \beta_{\rho}} \right|_{\omega_{mid}} (\beta_{\rho}^{\omega_{max}} - \beta_{\rho}^{\omega_{min}})$$

where ρ is each vital rate model that varies as a function of suitability (g,s,h,o,b), I_{ρ} denotes the realized intercept of each model and β_{ρ} the realized slope of the applicable models. By realized intercept, we mean the intercept of the model, plus effect of suitability at the site. By realized slope, we mean the parameter for z_t in the vital rate model, plus the parameter for ω multiplied by the appropriate ω value. The realized slope only applies to models g , s and h that had an interaction term between suitability and z_t . The contribution of the change in I_{ρ} and β_{ρ} was summed up to obtain the total contribution of any vital rate ρ . The superscript (ω_{min} , ω_{mid} or ω_{max}) corresponds to the minimal, mean or maximal observed suitability value. For each vital rate ρ , $\left. \frac{\partial LHS}{\partial I_{\rho}} \right|_{\omega_{mid}} (I_{\rho}^{\omega_{max}} - I_{\rho}^{\omega_{min}})$ is the contribution of a change in each intercept I_{ρ} to the observed change in LHS across the suitability spectrum, used in the LTRE, and likewise for β_{ρ} . For this analysis, we only used the fixed effects part of the vital rate models, predicting the vital rate functions on an average site and plot. The sensitivity of the LHS to a change in the intercept of each vital rate $\frac{\partial LHS}{\partial I_{\rho}}$ was estimated at the mid suitability value. The effect of the demographic transition T was set to the average year by setting the intercept of all models to the mid-value between both observed intercepts, in each vital rate model. We used the finite differences approach (Ellner et al. 2016) which states that

$$\frac{\partial LHS}{\partial I_{\rho}} \approx \frac{LHS(I_{\rho} + \Delta) - LHS(I_{\rho} - \Delta)}{2\Delta}$$

equation 5

where Δ is a small difference in parameter value I_{ρ} whose effect on the LHS value we want to assess. We set $\Delta = 2 * 10^{-10}$ as this was small enough that the results remained stable over 4 orders of magnitude. The same equation holds for β_{ρ} .

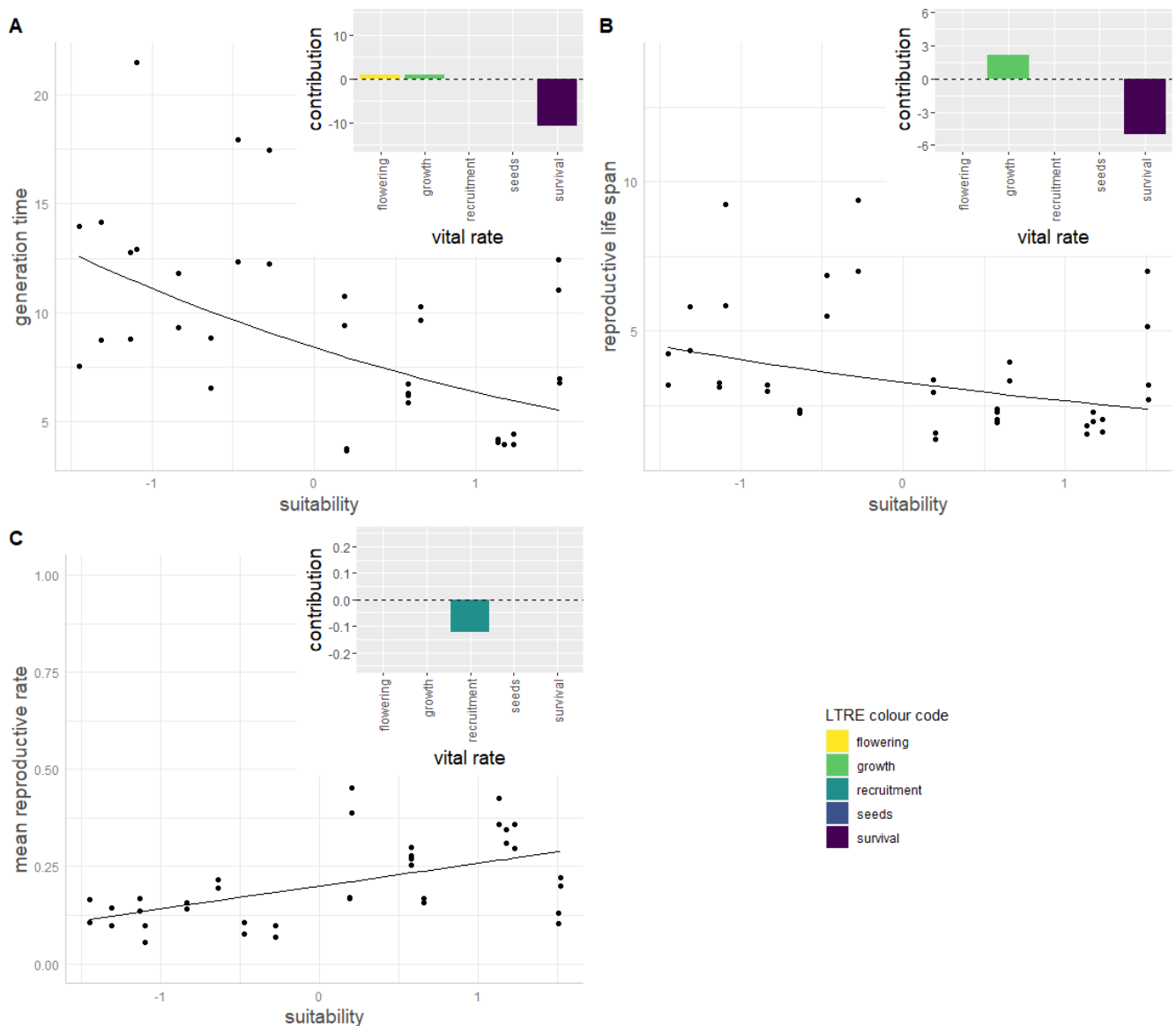


Figure 2.3 Display of the changes in Life History Strategies resulting from changes in vital rates along the suitability gradient. The contributions of changes in each vital rates to the observed population level patterns are illustrated by the results of the LTRE (insets). Generation length [years] (A), reproductive life expectancy [years](B), retrogressive growth [probability for individuals to survive and shrink in size] (E) decreased with suitability (x-axis), whereas mean yearly reproductive rate (C) increased and progressive growth [probability for individuals to grow] (D) was close to constant. Insets: results of the Life Table Response Experiment. Rectangle shows the contribution of a change in the parameters of one vital rate model to the observed changes in LHS between the extremes of observed suitability values. One observation = one population in one year. The black lines are predictions of a linear mixed model explaining fitness as a function of suitability, transition and the site of origin as random intercept

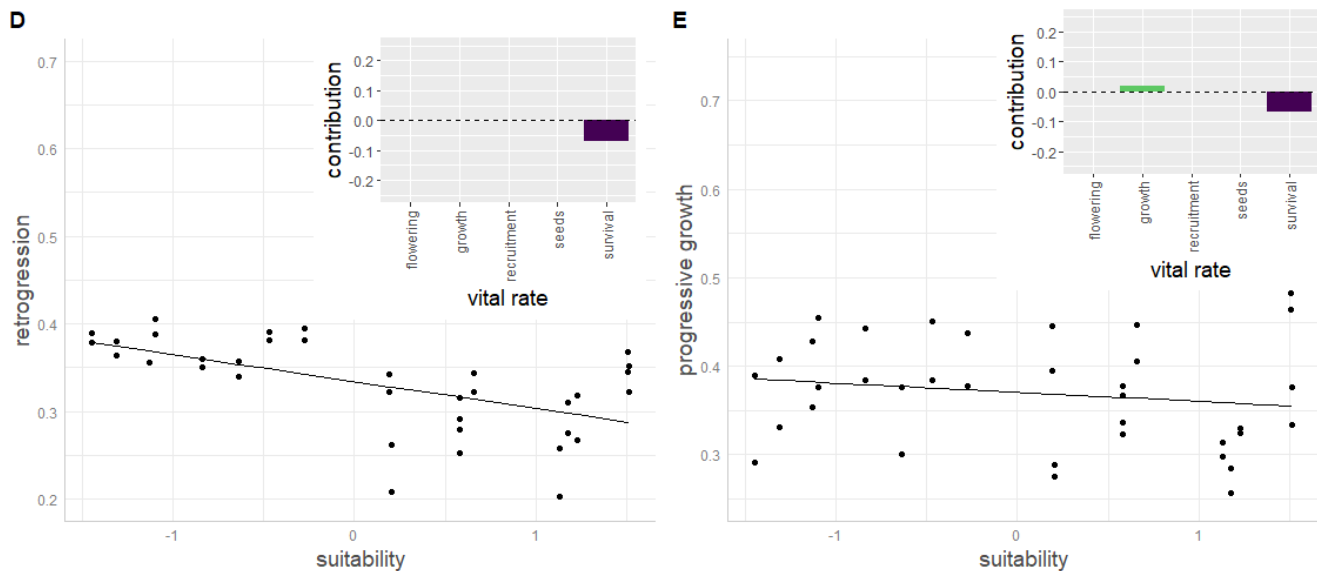


Figure 2.2 continues

2.4 Results

SDM

Our ensemble model predicted occurrence very well in the study area (AUC 0.949, max-TSS 0.735, max-Kappa 0.683). A map of the predicted suitability is provided in Figure 2.1 and Figure S2.2.2. Overall, the moisture index was the most important variable (weighted averaged variable importance = 0.37), followed by the slope (0.2), meadow height (0.15), topographic position (0.06) and mean summer temperature (0.04).

Vital rates models

Suitability affected vital rates in different shapes and directions (Figure 2.2). Survival and recruit density decreased with suitability, whereas the number of seeds produced increased (Figure 2.2, S2.2.3). Suitability was not retained as a predictor in the model describing the size distribution of the recruits. There were interactions between plant size and suitability explaining growth and probability of flowering (Figure 2.2). The marginal R^2 (R^2_m , Nakagawa and Schielzeth, 2013) ranged between 0.01 for the recruitment size model (that only contained transition as a fixed effect) and 0.35 for the growth model (Table S2.4.2). The conditional R^2 (R^2_c) ranged between 0.33 (reproductive effort and survival) and 0.51 (growth model).

Recruitment and density dependence

The constant recruitment model best matched our data, where the recruit density (r_w/a_w) varied only with suitability, and not with the number of seeds produced (see Table S2.5.1A). This corresponds to a scenario where a certain number of microsites are available every year, allowing for a fixed density of recruits (r_w/a_w) to join the population. Suitability had a negative effect on the density of recruits in our populations (Figure 2.2), but a model where recruitment did not vary as a function of suitability performed nearly equally well (Table S2.5.1, see also Figure S2.5.1).

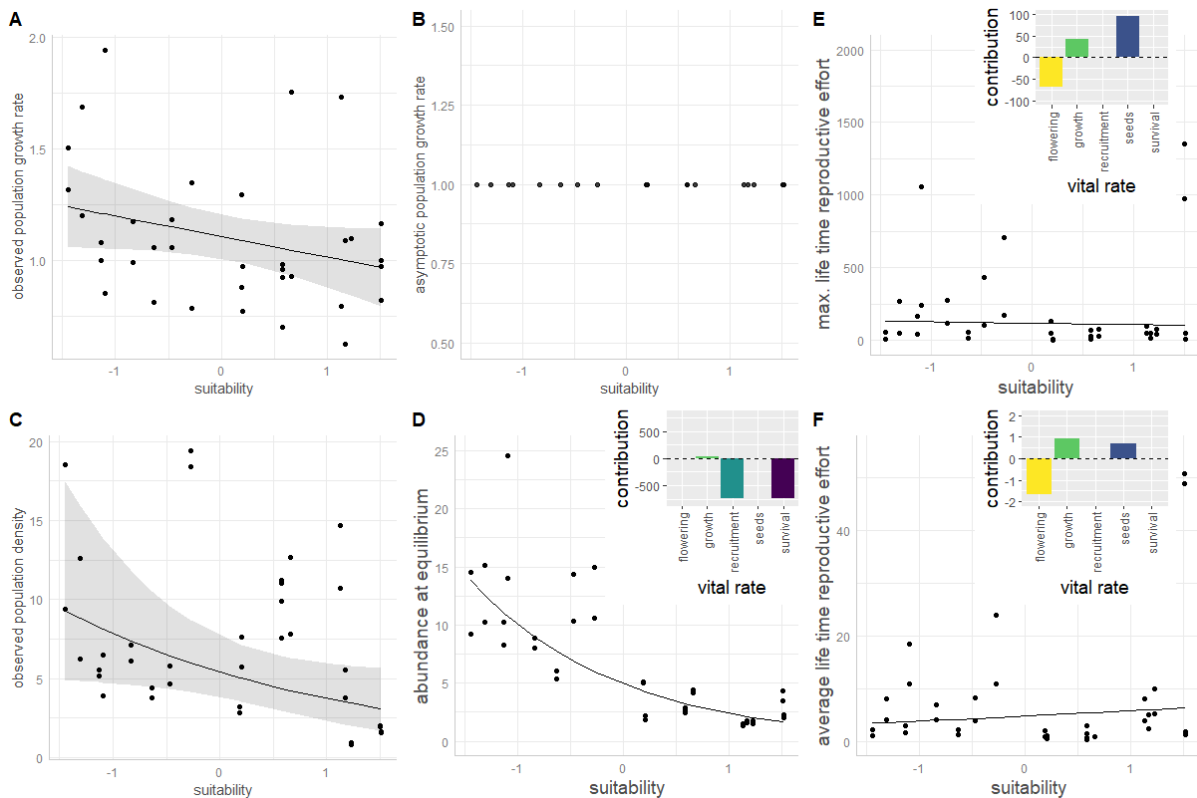


Figure 2.4 Population performance along the suitability gradient. A-B) Population growth rate C-D) population density E-F) population fitness, measured in lifetime seed production. First column = direct field observations (includes the effects of recent stochastic perturbations). Second column = outputs of the population model at stable stage (no stochastic perturbations). Third column = population fitness, measured in lifetime reproductive output (millimetres of inflorescence) with simulations running until E) maximal life span F) half life span. Insets show the LTRE contributions of the different vital rates (colour code, see Figure 2.3). Trend lines are the average predictions of a linear model explaining the observed values as a function of environmental suitability and transition, with a random effect for site of origin where possible (B,C,D,E), with 95% confidence interval where applicable. Confidence intervals for panels B,D,E,F were not provided as suitability is included as a predictor of the underlying vital rate models.

Life history strategies and Life Table Response Experiment

The effect of suitability on life history metrics is shown in Figure 2.3. Overall, the pace of life slows down in harsher conditions with longer generation time and reproductive lifespan in low suitability sites (Figure 2.3A&B). Mean reproductive rate responded in the opposite direction with lower values in low suitability sites (Figure 2.3C). Retrogression was higher in less suitable conditions, though the observed changes in progressive and retrogressive growth were small (Figure 2.3D-E). The effect of suitability on survival was the main cause of the observed changes in LHS (Figure 2.3, insets). The negative trends in generation time and reproductive life span were mostly due to changes in survival (Figure 2.3A-B), though this effect was partially compensated for by a positive effect of changes in growth in the case of reproductive life span. The increase in mean yearly reproductive rate of adult individuals was mostly due a change in recruit density (Figure 2.3C, and see Figure S2.2.5 for the raw data of the number of recruits and population area separately). Retrogression decreased as suitability increased (Figure 2.3D), mostly impacted by changes in individual survival. The contributions of the changes in vital rates on retrogression and progressive growth were very small (Figure 2.3D-E).

Population performance and fitness

Our population model described a constant population size at stable stage (population growth rate = 1, Figure 2.4B) and a decreasing population density towards higher suitability values (Figure 2.3D). These trends were supported by the raw observations of values in the field

(Figure 2.4A&C), though the observed population growth rates tended to be higher than one (=increase) in low suitability areas, and lower than one (=decrease) in high suitability areas. Note that given our strongly density dependent recruitment, the population density at stable stage is also the carrying capacity of those populations. Lifetime reproductive effort did not change with suitability (Figure 2.4E-F). The LTRE on lifetime seed production showed that the constant fitness along the suitability gradient was facilitated by a negative effect of suitability on flowering probability being compensated for by positive effects of reproductive effort (seed production) and growth. As we use a simulation of the fate of an average-sized individual over its life span (average, Figure 2.4F, or maximal, Figure 2.4E), survival could

only show an effect on the LTRE plots if a perturbation were causing an increase of one full time step.

2.5 Discussion

This study is the first detailed investigation of the changes in demography in populations sampled along an *a-priori* quantified gradient of probability of occurrence. We focused on naturally established populations, in their realized niche (including biotic interactions). Overall, we found substantial changes in life history strategies and underlying vital rates along the SDM-suitability gradient. Populations shifted towards a slower pace of life in less suitable conditions, with faster turnover due to higher mortality in high SDM-suitability areas. We found no evidence of higher population performance at high SDM-suitability; population growth rates were strictly equal to one along the gradient due to density dependence acting on recruitment and fitness remained constant across the gradient. Abundance decreased towards higher SDM-suitability.

Changes in vital rates and Life History Strategies

We proposed two scenarios in our study (Figure 2.1) and found evidence to support scenario B – that life history strategies change along the suitability gradient, stabilising fitness. Our results support hypothesis B1 (Figure 2.1) with demographic compensation occurring, with some vital rates increasing while others decrease (Villellas et al. 2015). We found that survival decreased with suitability, whereas reproductive effort tended to increase. Plants were larger at higher suitability, with an interactive effect of SDM-suitability explaining the growth rate. Opposite or differing reactions of vital rates to climatic gradients has been long theorized (Maguire, 1973) and found in several organisms (Greiser et al. 2020; Römer et al. 2021), including in another *Plantago* species (Pironon et al. 2018). Nonetheless, these works mostly considered single ecological driver axes. Our study is the first to acknowledge that conflicting responses of vital rates along climatic gradients could be modeled using probability of occurrence (SDM-suitability). Our models capture a substantial proportion of the variance in vital rates ($R^2_c = 0.33-0.51$ and $R^2_m = 0.16-0.35$ for models including SDM-suitability).

As a result of demographic compensation, we observe a tendency towards a slower pace of life in less suitable conditions (Figure 2.3), with a longer life span and generation length

(Figure 2.3A-B). We also found a lower reproductive rate (3C) and more reliance on retrogression (3D) in less suitable conditions. This shift in life history strategy is consistent with scenario B (hypothesis H2B). It also corroborates, at a population level, life history strategy shifts expected of temperate versus alpine species (Kelly et al. 2021; Körner 2003). At the intraspecific level, there is also evidence for populations of perennial plants delaying reproduction when facing adverse conditions (Harper 1977).

The relationship between probability of occupancy (captured by an SDM) and vital rates was indirectly predicted to be species and rate specific by (Pironon et al. 2017). Rather than uncorrelated rate specific patterns, what we find is a potential shift of vital rates to slower life history strategies in adverse conditions. Following our results, the relationship between probability of occupancy and vital rates or life history strategies might therefore be directional. One then needs to interrogate whether these patterns are specific to the studied species or gradient. The results of our Life Table Response Experiment (LTRE) show that the changes in LHS were mostly driven by changes in the probability of survival along the gradient (Figure 2.3). *Plantago lanceolata* is a species of disturbed land (Lauber et al. 2018; Sagar and Harper 1964). We would expect the species to mostly occur where disturbance is frequent, and life span possibly shortened as a consequence. Populations could only persist where a shorter life span can be compensated by a higher seed production, the latter probably requiring favorable climatic and soil conditions. These patterns are compatible with our results and would be specific to the ecology of the species. In addition, in the region, land use also is correlated with the elevation gradient (Randin et al. 2009). At high elevations, open landscapes like those in our study are mostly used for the free grazing of cows over the summer months. In low elevations, agricultural use can be more intensive. In some of our populations, an early or late grass cut for hay storage can take place. A disturbance gradient may therefore be correlated with the observed suitability gradient. On the other hand, in their study of the relationship between demographic pathways to performance along SDM-suitability gradients, in 93 populations of 34 species, (Csergő et al. 2017) also found that populations tended to rely more on retrogression in low-SDM suitability areas. Their study therefore offers some support for a similar relationship between at least retrogression, one marker of a slow life pace (Salguero-Gómez and Casper 2010), and SDM-suitability in other species. It would be necessary to conduct studies of

other species, looking specifically for shifts in the pace of life and retrogression along SDM-suitability gradients (Salguero-Gómez et al. 2016), to generalize further. Likewise, it would be interesting to perform studies along probability of occupancy gradients that are not linked to elevation.

Population performance

Overall, the results of our “population performance” metrics (population growth rate, abundance and fitness) supported a mix of our two alternative scenarios (Figure 2.1). Asymptotic population growth rates were strictly equal to one in all our populations due to microsite limited density dependent recruitment (Figure 2.4B). This is in agreement with scenario A and hypothesis HA3. However, lifetime seed production did not increase with the gradient, which supports scenario B. Finally, density of populations decreased with suitability, which is not in agreement with either of our scenarios (HB4 and HA4) and may be related to biotic interactions such as inter-specific competition and herbivory.

In our population model, the constant population growth rate is a product of density dependent recruitment. The recruitment regime best supported by our data was a strongly density dependent, microsite limited one, where only a certain density of recruits can be produced each year (Kachi, 1983, as reported in Ellner et al., 2016). The density of recruits decreased with suitability (Figure 2.2B). This goes against the suggestion of lower intraspecific competition at high environmental suitability (hypothesis H3, (Thuiller et al. 2014)). However, there are several caveats in our recruitment modes. First, the decrease in recruit density can be due to the broader areas covered by populations rather or a decrease in number of recruits (Figure 2.3C, S2.2.5), whereas other vital rates are not related to density in our population model. This explains why the population yearly reproductive rate increased as recruit density decreased (Figure 2.3C). In addition, a model where recruit density did not decrease with suitability performed nearly as well in our AICc selection process (Table S2.5.1). Our data were limited to two observations per site for recruitment pattern. While we know the recruitment to be density dependent (the number of seeds produced each year does not correlate directly with the number of recruits the following year), more information, from longer time series, could bring valuable insights. We did consider a compensatory recruitment regime in this study (Beverton and Holt 1957), which

concluded that most populations were close to carrying capacity. In such a case, correctly modelling the few populations that are not fully at carrying capacity would require several more years of information, but could bring valuable insights. We have no seed bank or clonality information in the present study. Nguyen, Buckley, Salguero-Gómez and Wardle (2019) state that the non-inclusion of cryptic life stages in demographic studies has relatively little influence on the ability to capture population dynamics, especially on stable populations ($\lambda_1 \approx 1$) with high post-seedling survival. This happens to be our case. In addition, Van Groenendael and Slim (1988) found in the same species that the seed bank had little importance, and clonality mostly contributed to vegetative growth, with the growth of side rosettes providing more seeds rather than new adult clone individuals. For those reasons, we are confident these omissions do not strongly affect our results. Nonetheless, the inclusion of more information on recruitment pathways might provide valuable insights.

Recruitment was also a driver of the decrease in population density we observed along the SDM-suitability gradient (Figure 2.4C-D). The caveats of the recruitment models hence also apply to this finding. However, a decrease in population density along the suitability gradient was also observed in the sites (Figure 2.4C), and the decrease in survival also contributed to the changes predicted by our population model (Figure 2.4D, LTRE inset). A decrease in population density not consistent with either of our scenarios (Figure 2.1). Consequently, neither a decrease in the strength of intraspecific competition at high SDM-suitability (HA4), or a compensatory effect of vital rates on abundance and population growth rates (HB4) are enough to explain the patterns we observe in population density. We can see two potential causes for the decrease in density at high SDM-suitability. First, an increase in interspecific competition has been shown to make populations deviate from their expected maximal local abundances (Braz et al. 2020; Ehrlén and Morris 2015). Biotic interactions are often omitted in the building of SDMs (Soberón and Nakamura 2009), although we attempted to counter this here by including vegetation height information in our model (Baudraz et al. 2018). In the Alps, climatic harshness is expected to drive plant performance and distribution at high elevations, whereas biotic interactions take over at lower elevations (Louthan, Doak, and Angert 2015; Normand et al. 2009). This causes a hump shaped pattern in the species richness along the elevation gradient (Dubuis et al. 2011; Körner 2003). The suitability map

for *P. lanceolata* (Figure 2.1) shows that the species is present only in the second half of this hump, where species richness decreases towards the lowest elevations due to biotic competition and exclusion (Lauber et al. 2018). Species richness indeed was negatively correlated with suitability in our study systems (Figure S2.2.5F). In addition, *P. lanceolata* was shown to suffer more damage from herbivores, mainly insects, at low rather than high elevations in the same study area (Pellissier et al. 2014). Together, these elements could be interpreted as signs that biotic interactions and interspecific competition become more important at higher SDM-suitability (which is correlated with low elevation in our study area). A second potential explanatory factor of the observed decrease in the confounding effect of human land use in the study area as described earlier (Randin et al. 2009). Both an increase in land use intensity and disturbance, and an increase in interspecific competition could modulate the number of microsites available for recruitment (Adler et al. 2010). We do not know for certain how land use affects the demography of *P. lanceolata* in this system. In a study of 46 populations of *P. lanceolata* across its entire global range, Villellas et al. (2021) found that increased vegetation cover from neighbouring plants decreased the probability of flowering in *P. lanceolata* via competition for light. On the other hand, mowing increased the biomass and probability of flowering of *P. lanceolata*. Therefore, an increase in agricultural use intensity, particularly through the addition of mowing, could be beneficial for the ecology of the species. Yet there is no indication of the impact of mowing on population abundance or density in Villellas et al. (2021). Therefore, though there are indications that interspecific competition might disadvantage *P. lanceolata* and create the decrease in abundance we observed along our gradient, interspecific competition remains confounded with a change in agricultural activity, and we cannot infer with certainty on the cause of the decrease in abundance. More experiments, for instance via exclosures and interruption of land use, or investigations of the effects of neighbouring communities on recruitment (Alexander, Diez, and Levine 2015), would be necessary to definitely infer on the cause of the decrease in population density we observe.

Whether due to an increase in competition via interaction with non-human species, or an effect of land use or disturbance on recruitment, the decrease in density is captured by our population model, which only includes SDM-suitability as an environmental predictor. Deviations from the overarching trend of increased abundance at higher probability of

occupancy are common and reported for some regions and/or species by nearly all studies focusing on the question (Thuiller et al. 2014; Weber et al. 2017). They are usually interpreted to be mostly caused by factors that are not included in the SDM model (Thuiller et al. 2014; Vanderwal et al. 2009). This is not exactly the case here. In our study, when included as a predictor of demography, SDM-suitability could adequately capture a decrease in abundance. Therefore, the appropriate elements seem to be included in or captured by our SDM, though the overall trend differs from the usual expectation (Thuiller et al. 2014; Weber et al. 2017). As the regime of density dependence best supported by our data is very strong, our long established, naturally occurring populations can be considered at carrying capacity. In our system, the assumption of a higher carrying capacity at high SDM-suitability does therefore not seem to hold (Keith et al., 2008; Swab et al., 2012, 2015, but see the limitations on inference on recruitment in our study).

Perspectives and implications

Our study offers several useful perspectives on the interconnections between demography and SDMs. First, we provide a case study of *how* demographic compensation, density dependent feedbacks and biotic interactions are at play (Beverton and Holt 1957; Courchamp et al. 2008; Holt 2009; Kelly et al. 2021; Villellas et al. 2015), stabilizing population along an SDM-suitability gradient in the realized niche of the species (Hutchinson 1957; Soberón and Nakamura 2009). The “realized niche of a species” is opposed to the fundamental niche, the latter incorporating areas and climates the species could in theory live in, but could not reach yet, or is excluded from because of biotic interactions (Soberón et al. 2017). SDMs are calibrated on observed occurrence data, and hence can only capture the realized niche of species (Holt 2009; Hutchinson 1957; Soberón and Nakamura 2009). What we find is that a) the assumption that “it only gets better” at high SDM-suitability does not hold and b) carrying capacity was not higher in high SDM-suitability areas. Hybrid SDM-demographic models, often assumed a higher carrying capacity with increasing SDM-suitability (Fordham et al. 2012; Swab et al. 2012, 2015). Yet this assumption finds no support in our work. We also find that the presence of the naturally occurring community and land use makes demography potentially predictable by SDM-suitability, which differs from results obtained when individuals were transferred outside their native range and without their original community (Bayly and Angert 2019; Greiser et al. 2020). As

communities will likely change under climate change (Alexander et al. 2015; Scherrer, Massy, et al. 2017), the relationship between SDM and demography is likely to do so as well. Nonetheless, in our work, life history changes along SDM-suitability gradients were potentially directional (shift from fast to slow pace of life), paving the way for future, more specific hypotheses for how SDM-suitability can be used to inform on demography and life history strategy in plants.

Second, we find that SDM-suitability was a useful predictor to explain variance in vital rates and a shift from slow to fast life history strategies along an environmental gradient. There have been repeated calls to use SDM-suitability to summarize complex environmental gradients in demographic studies attempting to compare multiple populations of the same species (Gurevitch et al. 2016), or even across several species (Buckley and Puy 2021). Our study offers some support for these suggestions. There are hundreds of species for which only few populations have been studied in detail (Salguero-Gómez et al. 2015). In those cases, the number of environmental drivers one can study is severely limited (Buckley and Puy 2021; Römer et al. 2021; Shea et al. 2005). Using SDM-suitability as a summary-predictor could enable researchers to harvest the power of poorly replicated intraspecific demographic datasets, to advance our ability to predict demography in new locations (Buckley and Puy 2021; Gurevitch et al. 2016). This is a pressing issue for population management (Buckley and Puy 2021; Shea et al. 2005). For instance a link between SDM-suitability and the fast-slow axis of life histories could have direct implications for our ability assess extinction risks of species (IUCN 2001; Pearson et al. 2014). The temporal frame for a threat to affect a population following the IUCN red listing methodologies is “*Ten years or three generation lengths*” (IUCN 2001; IUCN Standards and Petitions Committee 2019; Mace et al. 2008). In the case of *P. lanceolata*, we observe a change from a generation length of <5years to >20 years. The time frame for IUCN criteria application would therefore vary from 15 to 60 years, were we to use population-specific generation length estimates. Such breadth in generation time could change the red list assessment of species for which declines were known, but stopped in recent past (e.g., Baudraz et al., 2019).

2.6 Conclusions

We monitored the demography of multiple established populations along an *a priori* quantified SDM-suitability gradient leading to a niche limit. We found that SDM-suitability is a predictor of slower life history strategies and quantify the demographic pathways, including demographic compensation, through which suitability influences life history. We found no increase in population performance or individual fitness at higher SDM-suitability. Contrary to our expectations, population density decreased with SDM-suitability. These findings pave a way for the use of SDM-suitability maps to infer local demographic strategies of species (Buckley and Puy 2021; Gurevitch et al. 2016). Furthermore, we provide hypotheses on the relationship between demography and SDM-suitability that can be tested on other species and demonstrate the potential for the integration of demographic and SDM approaches.

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Chapter 3. Intraspecific variation in functional traits and their demographic consequences along an environmental suitability gradient for a perennial herb

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3.1 Abstract

Despite the fundamental assumption that functional traits influence fitness, observed relationships between functional traits and demographic performance (survival, growth and fecundity) are generally weak. While most studies use species-averages as trait values, evidence is growing that intra-specific variance in functional traits (ISVT) is high, which may explain the weak empirical functional traits – fitness relationship. There is a need to investigate the drivers of ISVT, and the resultant impacts on the functional traits – fitness relationship.

We analysed four functional traits in 18 populations of the perennial herb *Plantago lanceolata* L. along an elevation gradient. We assessed (a) how to capture ISVT along the gradient, and whether ISVT can capture changes in (b) evolutionary strategies and (c) survival.

Elevation, temperature and environmental suitability derived from a Species Distribution Model (SDM) all performed well to explain variation in most functional traits. Using SDM-suitability to summarize the gradient, we found that functional traits reflect a shift from a slower to faster leaf economics, coupled with higher yearly seed production, with increasing habitat suitability. We found that Specific Leaf Area and Leaf Area explained the probability of survival of individuals in interaction with climate. Higher Leaf Area and Specific Leaf Area were correlated with a lower probability of survival in harsher conditions (\cong higher elevation), but with a higher probability of survival in more mesic conditions (\cong low elevations). Our results strengthen the calls to take local climatic context into account when attempting to infer functionality from functional trait measurements.

3.2 Introduction

Functional traits are characteristics of an individual expected to be linked to its fitness (Violle et al. 2007). They are extensively used to describe the functionality, evolution and ecology of species. For instance, functional traits have been used to predict community assembly and the functioning of ecosystems (Díaz et al. 2004; Guisan et al. 2019; McGill et al. 2006; Shipley, Vile, and Garnier 2006). The use of functional traits for the study of evolutionary and ecological processes relies on their hypothesized link to fitness. This link between functional traits and fitness is in turn exerted through the demographic rates of survival, fecundity and growth of individuals (Adler et al. 2014; Caswell 2001; Harper 1977; Moles 2018). Yet mostly weak trends are observed between functional traits and demography, particularly in long lived species (Moles 2018; Wright et al. 2010).

The study of functional traits, including their relationship with demographic rates, typically focuses on average values at the species level (Adler et al. 2014; Díaz et al. 2016; McGill et al. 2006), although exceptions exist (Blonder et al. 2018; Kuppler et al. 2020). As a consequence, much less is known about the patterns, magnitudes and drivers of intraspecific variance in functional traits. Typically, the climatic and biotic context in which measurements of a given species were taken is ignored (McGill et al. 2006; Moles 2018). However, there is strong evidence that functional traits within a species vary along environmental gradients (Knops and Reinhart 2015; Kuppler et al. 2020; Siefert et al. 2015). In particular, mean trait values in local populations are expected to be driven by climatic gradients (Moles 2018), whereas between individuals variance within populations (repeatedly shown to be of high importance; Albert et al. (2010); Kuppler et al. (2020) is expected to be driven by plasticity, microhabitats and genetic factors (Blonder et al. 2018; Moles 2018). In addition, the fitness consequences of functional traits might vary depending on the life stage of individuals (McGill et al. 2006). The use of species-averaged values and the overlooking of the climatic- and life-history context in which the traits were measured is hypothesized to be responsible for the weakness of functional traits to demography relationships (McGill et al. 2006; Yang, Cao, and Swenson 2018). The question of whether functional traits can adequately capture variation in demography, and, through it, changes in fitness of individuals therefore remains open (Adler et al. 2014; McGill et al. 2006).

Over the last few decades, millions of (average) trait measurements have accumulated in databases, which, for the most part, are freely accessible (Enquist et al. 2016; Kattge et al. 2020; Royal Botanic Gardens Kew 2014). This far outstrips the amount of data available on the survival, fecundity and growth of individuals (Salguero-Gómez et al. 2015). Opportunities for studying the causal links or relationships between functional traits and fitness components are therefore rare, though several examples exist. Adler et al. (2013) found that functional traits can explain patterns in life history strategies using an interspecific comparison of 222 species. They found that functional traits were significantly correlated with the elasticities (i.e., the “impact”) of vital rates on population fitness, and that trait gradients captured shifts along the fast-slow continuum of life history strategies. Specifically, Adler et al. (2013) found that species with large seeds or long-lived leaves had slow life histories, and their fitness was more strongly influenced by survival than by growth or fecundity. Leaf Area (LA) and Specific Leaf Area (SLA, the area of a leaf over its dry mass) expected to capture changes in leaf longevity and the investment strategy of plants (Moles 2018; Pérez-Harguindeguy et al. 2013; Wright et al. 2004). This ranges from “cheap” thin leaves that capture a lot of light in a short amount of time (high LA; Moles (2018) to smaller or denser leaves, expected to represent higher energy investment but a longer, steadier energy income and leaf longevity with better protection against wear and tear and herbivory (low SLA; Moles (2018); Wright et al. (2004). An increase in LA also represents a higher vulnerability to herbivory (Moles 2018), whereas the trade-off between area and mass inherent to SLA can encompass the investment in defensive strategies (Moles 2018; Pellissier et al. 2014). A trade-off between the production of few, big seeds, versus many small seeds, which imply a lesser cost of production per seed is commonly reported in interspecific comparisons (Díaz et al. 2016; Leishman et al. 2000). It was long believed to be due to a trade-off between the higher cost of production of bigger seeds, and an increase in offspring survival (Leishman et al. 2000). However, offspring survival advantage alone was shown not to be sufficient to outcompete the fitness advantages of producing many more seeds, each with one small probability of producing a full offspring (Moles and Westoby 2004). The trade-off between seed mass and number was shown to make sense in the light of plant longevity: longer lived plants can afford to produce fewer, bigger seeds, as they will reproduce more often over their life span (Moles 2018). The production of many seeds of

low mass therefore aligns with a fast life history strategy, whereas the production of few seeds of high mass aligns with slower life history (Moles 2018; Moles and Westoby 2004).

Kelly et al. (2021) found that functional traits predict life history strategies in interaction with climate in a study of 80 species. In colder climates, for instance, smaller species lived longer than in warmer climates. Similarly, Adler et al. (2013) found that climatic context was often necessary to reveal relationships between functional traits and life history strategies, though their resolution level was extremely coarse on that aspect (biome of origin). In both these studies, the availability of demographic data was limiting. Average values per species were used both for trait and demographic information, and variance reduction techniques (PCA axes, use of broad climatic categories as “biomes”) had to be implemented. The complexity of environmental gradients is a critical issue for the relationship between functional traits and demographic rates, particularly for the general transferability of the conclusions (Buckley and Puy 2021; Catford et al. 2021; Kelly et al. 2021; Kuppler et al. 2020; Römer et al. 2021). Many environmental factors (climatic, biotic, historic, etc (Holt 2009) are at play, and exert their pressures differently on different traits and species (Kuppler et al. 2020; Louthan et al. 2015; Moles 2018; Römer et al. 2021; Treurnicht et al. 2016). It is often impossible, given the size of existing datasets, to study every possible driver (Römer et al. 2021). The consequences of omitting important explanatory variables and their interactions limit our ability to transfer results (Catford et al. 2021; Mod et al. 2016). We are therefore in need of tools to decompose complex environmental gradients and transform them into common currencies (Buckley and Puy 2021) that would be transferable across different gradients and scales (e.g., Petitpierre, Broennimann, Kueffer, Daehler and Guisan, 2017).

One powerful tool to quantify the ecological requirements of a species are correlative Species Distribution Models (SDM: (Elith et al. 2006; Guisan and Zimmermann 2000). SDM describe the niche of a species by correlating occurrence data with environmental predictors. The predicted probability of occurrence can be projected into geographic space to generate maps of the distribution of a species as a function of climate, understood as a map of suitability of the environment for the species (Guisan and Thuiller 2005; Guisan et al. 2017). SDM-suitability, the probability of occurrence predicted by an SDM, is likely to be more meaningful, and comparable across species, than other techniques such as dimensionality reduction techniques (e.g. PCA; Blonder et al., 2018). For this reason, they

are often suggested by population ecologists as interesting candidate explanatory variables (Buckley and Puy 2021; Gurevitch et al. 2016), though this remains rarely tested (but see Bohner and Diez, 2020; Csergő et al., 2017; Thuiller et al., 2014). However, SDMs were shown to predict functional traits in some species, but not all in multiple species studies (Thuiller et al. 2010). Therefore, while SDM gradients are potentially useful there is a need to proceed with caution (Buckley and Puy 2021; Gurevitch et al. 2016). SDMs often make use of generic sets of environmental variables as predictors, to predict the distribution of multiple plant species (Mod et al. 2016; Thuiller et al. 2010, 2014). The need to tailor SDMs more tightly to the ecology of target species, especially for uses other than the description of current or future distribution, is widely acknowledged (Austin 2002; Guisan et al. 2006; Mod et al. 2016). This need is likely to apply to the inference on functionality based on SDM predictions (Thuiller et al. 2014).

In this study, we make use of detailed multi-year monitoring of 18 populations of the perennial herb *Plantago lanceolata* L. along a climatic gradient in the Swiss Alps, where it reaches an edge of its climatic niche. The populations were sampled along an *a priori* modelled SDM-suitability gradient (Baudraz et al., chapter 2). The SDM was built specifically to describe the ecology of the focal species. Individuals within populations were monitored for their demography of for three years, and functional traits for individuals were gathered at each site at one time point. The demography of the species along this environmental gradient was studied by Baudraz et al. (Chapter 2). They found a shift from slower to faster life cycles with increasing environmental suitability (as captured by the SDM). Survival was shown to be the main driver of changes in life history strategies along the gradient (Chapter 2). A changing relationship between functional traits and survival along the gradient would therefore have the strongest consequences for the fitness of individuals and populations (Blonder et al. 2018; Salguero-Gómez et al. 2018).

In the present study, we addressed:

- Whether probability of occurrence as predicted by an SDM (SDM-suitability) explains the variance in functional traits observed along the gradient.

- Whether changes in functional traits across populations describe a shift from fast to slow life history strategies, as was found by Baudraz et al. (Chapter 2) in the same study system using direct demographic measurements
- Whether functional traits can predict direct demographic measurements along this steep environmental gradient. Particularly, we will focus on the ability of functional traits to predict survival, as survival was shown to be the main driver of intraspecific shifts in life history strategies (Chapter 2).

We expected that SDM-suitability would be a good predictor of changes in functional traits along the gradient, but not as good as raw environmental predictors (land use, temperature, elevation and combinations of those factors). Nonetheless, we expect the best predictor for each functional trait to differ, while SDM-suitability would be a good overall predictor. We expect that functional traits will capture a shift along the fast-slow axis of plant life history strategies (Wright et al. 2004), similar to what (Adler et al. 2014) found at the interspecific level. We expect functional traits to explain demography (survival) at the intraspecific level in interaction with climate (Adler et al. 2014; Kelly et al. 2021), though we might be limited in our ability to capture this by our sample size at the population level.

3.3 Methods:

Overview

We collected functional trait measurements (Specific Leaf Area (SLA), Leaf Area (LA), Seed Mass and Seed Number) from individuals of *Plantago lanceolata* L. stemming from 18 populations along a suitability gradient in the Swiss Alps, adjacent to existing demographic monitoring sites. The populations were selected in regular strata along an environmental suitability gradient quantified by a species distribution model (Chapter 2). We first assessed whether environmental suitability is a good predictor of variance in functional traits between these populations, by comparing it with other predictors in a multimodel inference framework. We then investigate the changes in functional traits along the gradient, and their implications for life history strategies. Finally, we test whether population average measures of LA and SLA can adequately capture changes in individual survival, and whether interaction

with climatic predictor is necessary to explain the relationship between functional trait and individual survival.

Research area

The study area covers 700km² in the western Swiss Alps with an elevation ranging from 375-3210 m (Von Däniken et al. 2014). The vegetation reflects the typical elevation gradient of Central Europe, with broadleaf deciduous forests at the lowest elevations (colline belt), coniferous forests (subalpine) and alpine grasslands above the tree line (see Dubuis, Rossier, et al. (2013) for more information). Outside of the forests, most of the area is used for cattle grazing, with pastures in the lowlands to the lower alpine zones and some meadows primarily in the colline and montane belts (Randin et al. 2009).

Table 3.2 Predictors included in the Species Distribution Model. All raster layers had a grid cell size of 25 x 25 m.

Variable	Definition	Unit	Source
Moisture index	Mean difference between precipitation and potential evapotranspiration over the growing season (water potentially available in soil)	1/10 mm	Dubuis, Giovanettina, et al. (2013); Zimmermann and Kienast (1999)
Slope	Slope of the grasslands	°	Swisstopo.ch; Zimmermann and Kienast, (1999)
Topographic position	Index where positive values = ridges and tops, negative values = valleys and sinks	unit-less	Dubuis, Giovanettina, et al. (2013); Zimmermann et al., (2007)
Mean temperature	Mean temperature over the growing season	°C	meteosuisse.ch; Zimmermann and Kienast (1999)
Meadows Height	Predicted vegetative height of meadow communities (community weighted mean)	m	Baudraz et al., (2018)

Niche and distribution models

The environmental niche of the species in the study area was characterized using species distribution models (SDMs; Guisan et al. 2017). An ensemble SDM was fitted and projected over the whole study area, and the probability of occurrence was interpreted as the suitability of the environment for *P. lanceolata* (Chapter 2, Supplement S2.1.1). We used pre-existing presence-absence data for the species collected through several research projects in the RechAlp area (see Baudraz et al. (2018); Dubuis et al. (2011); Pellissier et al. (2013); Scherrer, Massy, Meier, Vittoz, and Guisan (2017) for the original datasets). 1476 sites were visited outside forested areas, and included 353 presences for *P. lanceolata*. The environmental predictors used in the SDM were based on prior knowledge of the ecology of the species (Kuiper and Bos 1992; Villellas et al. 2021) and availability of the information in a georeferenced format for the study area at high (25 m x 25 m) resolution. The layers used are detailed in Table 3.1 and Supplement 2.1.1. All variables were cropped to exclude forested areas. We used Biomod2 to fit SDMs and derive the prediction of habitat suitability (Thuiller et al. 2016). The three following modelling techniques were included in the ensemble: boosted regression trees (BRT; Elith et al. (2008), random forest (RF; Prasad, Iverson, and Liaw (2006) and generalized linear model (GLM; Guisan, Edwards, and Hastie (2002). The models and the ensemble prediction were evaluated through repeated split sampling (models calibrated on 70% of the data, and evaluated on 30%) using AUC, max-Kappa and max-TSS (Guisan et al. 2017). A max-TSS- weighted ensemble model using all of the data was projected over the study area and used as an environmental suitability metric in the rest this study (Guisan et al. 2017).

Demographic and functional trait site selection

The SDM was projected onto the study area, and the suitability range was divided into five strata each covering 20% of all possible suitability values. Seven known *P. lanceolata* occurrences in each stratum were randomly selected as candidate sites. In 2017, candidate sites were visited and demographic monitoring was established following the PlantPopNet protocol (Buckley et al. 2019). Sites with foreseeable land use change were avoided and three sites were moved a couple of hundred meters (carefully aiming to remain in the same suitability values) due to safety concerns. In total, 19 populations were set up, four in each

suitability stratum, except for the lowest suitability where only three populations were established due to very low density of *P. lanceolata*. Information about the land use of the parcel was gathered by observations and discussions with farmers. Therefore, we classified the land use into two broad categories based on information gathered on-site; whether the site is a pasture (used solely for cattle grazing), or a mix of land uses (used for cattle grazing with one or two hay cuts at the start or beginning of the season).

Trait measurement and demographic monitoring

In 2017, leaves and seeds were collected from individuals directly adjacent to the demographic census plots for destructive functional trait analyses. First, the full size of each individual (number of leaves on all rosettes (Chapter 1, 2) was measured. Ten leaves were collected from different individuals at each site, for a total of 190 leaves. The leaves were maintained in cool conditions until scanned on a clear background with a ruler for scale. Once scanned, the leaves were air dried and stored for mass measurements. Trait measurements were performed following Pérez-Harguindeguy et al. (2013). For SLA, the surface area of each leaf was calculated (in mm²) using ImageJ software from scans of fresh leaves (Abramoff, Magalhães, and Ram 2004). Leaves were oven-dried at 60°C for 24 hours and weighed using a micro-scale. Up to 15 inflorescences with mature seeds were collected per site, based on availability and phenology, leading to a total of 152 collected inflorescences (out of 14 sites, with a sample size of 2-15 inflorescences per site). All mature, normally-developed seeds in an inflorescence were weighed, and an average seed weight per inflorescence was calculated (i.e. total seed mass/seed number per inflorescence). An additional 97 inflorescences were collected just before full maturity in 2019 from 12 sites, so that no seed had dispersed yet. These 2019 inflorescences were used to count the number of seeds produced by one inflorescence. All seeds on the inflorescence were included (i.e., inclusive of not fully developed seeds). We did not measure seed mass on the 2019 inflorescences, as their seeds were harvested before full maturity.

For demographic monitoring, 100 individuals per site were mapped and tagged following the PlantPopNet protocol (Buckley et al. 2019). The size (number of leaves, length and width of the longest leaf) and reproductive effort (number of stems and inflorescence length of the longest flowering stem) of each rosette were recorded once a year in each site at peak

flowering for three years (2017-2019). In one population, the tagging failed and the site was omitted from further demographic analysis. When new rosettes were produced, they were also tagged and measured, and given an individual identifier, either as a new recruit or a new ramet within an existing genet if linkage to an existing genet was apparent. As per the PlantPopNet protocol, seedlings were counted, but not marked until their second year, to avoid tagging-related mortality. Vital rates (survival, probability of flowering, annual growth

	Scenario name	Model predictors	Underlying hypothesis
A	Suitability only	Suitability + (1 site_code)	Suitability explains variance in functional traits, due to correlation with underlying environmental gradients or their combination.
B	Land use only	Landuse + (1 site_code)	Land use explains variance in functional traits
C	Temperature only	summer temperature + (1 site_code)	Temperature over the growing season explains variance in functional traits
D	Land use and temperature	summer temperature * landuse + (1 site_code)	Land-use, temperature over the growing season and their interaction explain variance in functional traits
E	Suitability and land use	Suitability * landuse + (1 site_code)	Suitability, land-use and their interaction explain variance in functional traits
F	elevation	Elevation + (1 site_code)	Unmodelled environmental factors covarying with elevation explain variance in functional traits.
G	Null	1 + (1 site_code)	Null model

Table 3.3 Explanatory variables for a set of small models and their underlying hypotheses to analyse variance in each functional trait. This set of models was created for each functional trait as a response variable, i.e. LA, SLA, seed mass and seed number.

or shrinkage) were determined from repeated annual censuses of each individual in the population. A size-structured population model was developed and is described elsewhere (Chapter 2).

Statistical analysis

Comparison of candidate environmental predictors

We used a multi-model inference framework (Burnham and Anderson 2002) to compare the ability of SDM-predicted suitability to capture changes in functional traits with that of other candidate predictors. We built a series of competing models, each representing a plausible hypothesis of the main drivers of changes in functional traits (Vicente et al. 2010). The multi-model inference approach enabled assessment of support for each hypothesis. Given the limited number of sites over which the environment can vary we used a set of small, plausible models. The models are presented in Table 2. Each model corresponds to one scenario of potential environmental drivers in the study area. Models A to E correspond to scenarios where suitability, land use, temperature or combinations thereof are the most important drivers of functional traits along the gradient. In model G, the null model, only the random structure is maintained and no fixed effects are included in the model. It is the “empty control”. In model F, elevation is used as fixed effect, with the random structure maintained. Elevation itself (number of meters above sea level) is not expected to be the mechanism driving the variance in functional traits in *P. lanceolata*; rather, we use it as a proxy for multiple environmental drivers (temperature, change in biotic interactions, growing season length, Körner (2003). Suitability and elevation are both compound summary metrics of the multi-dimensional environmental space; however suitability is traceable and optimized for *P. lanceolata* occurrence whereas elevation is independent of the ecology of this species. Plots of the correlations between drivers are available in supplement S3.1.

The models were built as generalized linear mixed models with site as a random effect using the lme4 package in R (Bates et al. 2015; R Core Team 2020). Models for seed mass and SLA were built assuming a Gaussian error distribution. Seed mass was mean centred and standardized, and SLA was log transformed. The seed number model was an over-dispersed Poisson model, with the over-dispersion accounted for by adding a random intercept per

individual (Zuur et al. 2013). We weighted our models based on their AICc following the multimodel inference approach described by Burnham and Anderson (2002). This technique provides a weight for each model (how informative it is as compared to all candidate models) and a delta-AICc (how much worse than the best model each candidate model is performing). Models with delta-AICc (ΔAICc) >2 were not deemed informative enough to be maintained. We performed this using the MuMIn package (Bartoń 2018).

We used the predictions of Model A (Table 3.2) built using each functional trait as a response variable (in turn) to investigate the relationship between functional traits and SDM-suitability along the environmental gradient.

Do functional traits explain the survival of individuals?

We used average functional trait values per site per site for this analysis, as trait information was only available from individuals directly adjacent to the demographic plot, and not the individuals whose demography was monitored. This was necessary to avoid biasing measures of growth, survival and recruitment by collecting leaves and seeds from the demographically monitored individuals. To test whether between sites variance in functional traits predicted survival, we built linear mixed effects model explaining individual survival as a function of the site-averaged trait value, SDM-suitability and the interaction between SDM-suitability and the site-averaged trait value. The site of origin was treated as a random effect, and the demographic transition as a fixed effect as we only had two levels (Y1-2, Y2-3). We built two separate models for Leaf Area and Specific Leaf Area. All explanatory variables were standardized and mean centered. Models were built in lme4 (Bates et al. 2015). Performance of the models was assessed via the generalized R^2 expanded to mixed models (Johnson 2014; Nakagawa and Schielzeth 2013). The conditional R^2 (R^2_c) is a measure of how much variance is explained by both the random and fixed terms in the model, whereas the marginal R^2 (R^2_m) measures the variance explained specifically by the fixed effects of the model.

	Scenario name	SLA				LA			
		Ranking	AICc	delta	weight	Ranking	AICc	delta	weight
A	Suitability	2	-3.9	0.91	0.234	3	297.4	1.29	0.233
B	Land use only	7	5.6	10.35	0.002	7	308.4	12.3	0.001
C	Temperature only	4	-2.8	1.97	0.138	2	297.2	1.15	0.251
D	Land use and environmental predictors	1	-4.8	0	0.368	4	301	4.89	0.039
E	Suitability and land use, in interaction	5	-2.4	2.43	0.109	5	301.5	5.4	0.03
F	Elevation	3	-2.9	1.87	0.145	1	296.1	0	0.445
G	Control 1	6	3.6	8.41	0.005	6	308.2	12.1	0.001

	Scenario name	Seed Mass				Seed Number			
		Ranking	AICc	delta	weight	Ranking	AICc	delta	weight
A	Suitability	3	357	2.95	0.086	1	719.8	0	0.507
B	Land use only	6	358.6	4.58	0.038	7	731.7	11.9	0.001
C	Temperature only	1	354.1	0	0.378	3	722	2.24	0.165
D	Land use and environmental predictors	5	357.6	3.58	0.063	4	723.2	3.45	0.091
E	Suitability and land use, in interaction	7	361.3	7.21	0.01	5	724.2	4.46	0.055
F	Elevation	2	354.2	0.19	0.344	2	721.9	2.11	0.177
G	Control 1	4	357.2	3.11	0.08	6	729.5	9.72	0.004

Table 3.4 Support for each scenario, obtained through multi model inference. Each scenario (ie., candidate model) is presented as a row, with functional traits as columns. See Table 3.3. for details of the scenarios. The ranking (in bold) summarizes which scenarios were best at explaining the variance in each functional trait. Scenarios can reach a similar level of support in this type of analysis. Scenarios whose delta AICc is lower than 2, the usual threshold to select one best model, are highlighted in grey. The rows with blue hashed borders show the control scenario (the empty model). Multi-model inference was performed through the MuMIn package (Bartoń 2018) following the process described by (Burnham and Anderson 2002).

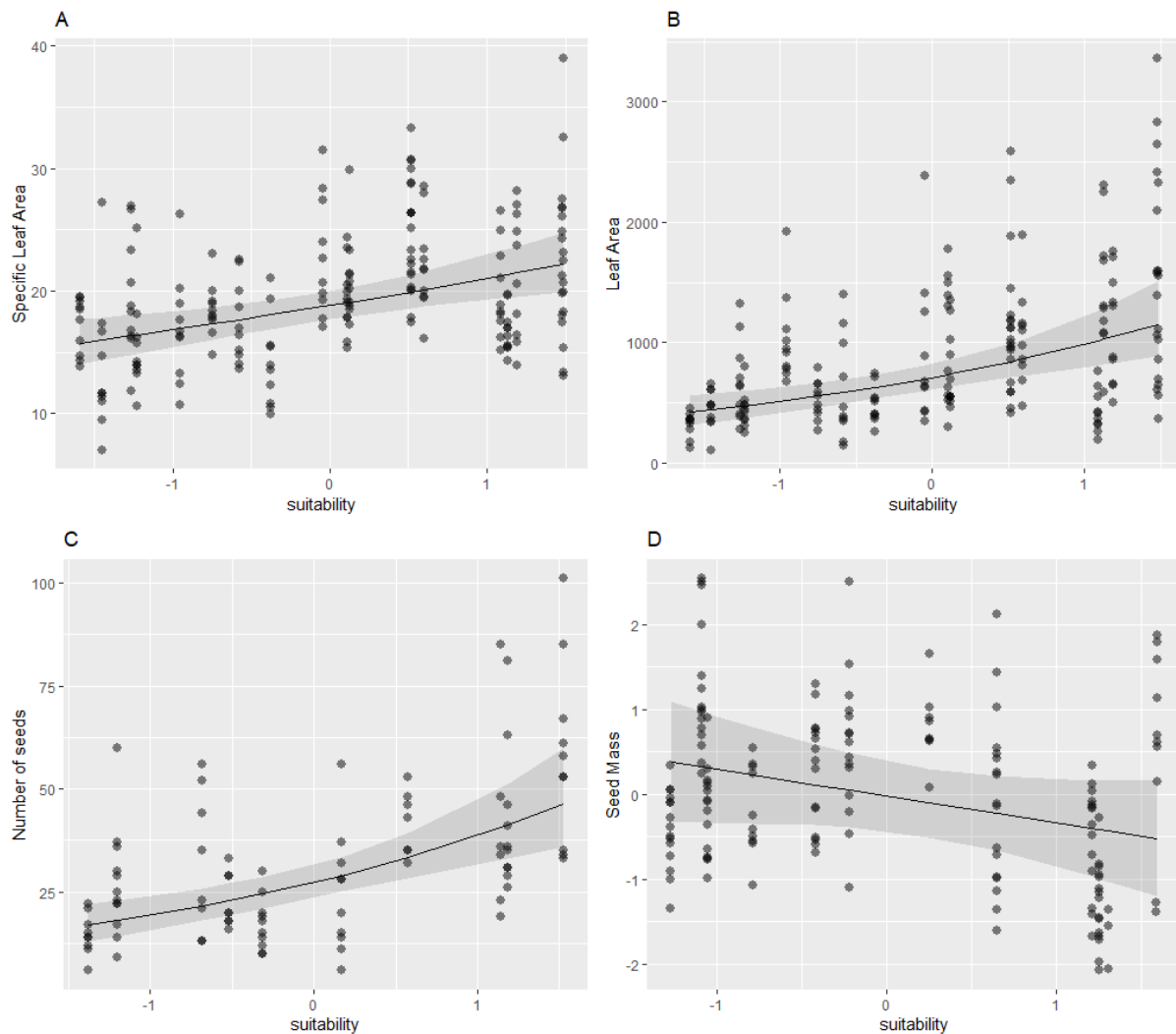


Figure 3.1 Relationship between SDM-predicted suitability and functional traits: A) SLA, B) LA, C) Number of seeds per inflorescence D) seed mass. The prediction line and 95% confidence intervals stem from a linear mixed model with suitability as a fixed effect and site as a random effect. Suitability is the mean standardized output of the Species Distribution Model.

3.4 Results

Best predictors of variance in traits in the study area

The results of the multimodel inference are shown in Table 3. The null model (site only) was not included in the set of models with $\text{dAICc} < 2$ for any traits, meaning that some of our predictors at least were informative in all cases. For SLA, the best models were model D (land use and temperature), A (suitability, $\text{dAICc} = 0.91$), F (elevation, $\text{dAICc} = 1.87$), C (temperature, $\text{dAICc} = 1.97$). For LA, the best models were F (elevation, $\text{dAICc} = 0$), C (temperature, $\text{dAICc} = 1.15$) and A (suitability, $\text{dAICc} = 1.29$). For Seed Mass the best models

were C (temperature, dAICc = 0) and F (elevation, dAICc = 0.19). For seed number, the best model was model A (suitability), and no other model had a dAICc lower than 2.

Relationship between vital rates and predicted suitability

The relationships between functional traits and predicted suitability are shown in Figure 3.1. SLA (slope 0.11, 95%CI = [0.05:0.17]), LA (0.33 [0.18:0.48]), and Seed Number (0.34 [0.2,0.49]) all increased with suitability. Seed Mass tended to decrease with the suitability gradient, but the trend is inconclusive (-0.31 [-0.71:0.08]). The relationship between functional traits and elevation can be seen in Figure S3.3.1

Effects of functional traits on survival

Overall, the linear term for LA in the survival model was negative (estimate = -0.44968, 95% CI [-0.83,-0.07]) and the interaction term between LA and suitability was positive (0.61, 95% CI [0.36,0.86], Figure 3.2). As a result, the relationship between LA and probability of survival was positive in high suitability areas, whereas it was negative in low SDM-suitability areas. This means that broad leaves are beneficial for survival in high suitability areas, but detrimental in harsh conditions. The model explained about a third of the variance in survival ($R^2_m = 0.18$, $R^2_c = 0.35$). Similarly, the linear term for SLA was negative (-0.43, 95% CI [-0.77:-0.08]), but the interaction between SLA and SDM-suitability was positive (0.55, 95% CI [0.21: 0.89]). As a result, the relationship between SLA and probability of survival was very unclear at high SDM-suitability values (positive estimate, but with a very broad confidence interval), but negative at low SDM-suitability (Figure 3.2B). This means that small, dense leaves were beneficial for survival in harsh conditions, but this was not true in high suitability conditions. Overall, the model explained about a third of the variance in survival ($R^2_m = 0.164$, $R^2_c = 0.35$, see S3.2 for detailed model outputs and S3.3 for similar plots using elevation).

3.5 Discussion

The best predictors of variance in the functional traits of *Plantago lanceolata* across the sampled gradient varied between traits, but elevation and suitability both consistently ranked in the top three models for all four traits and had similar average ranks (2 for elevation, 2.25 for suitability). Both elevation and suitability are complex compound metrics

of underlying environmental gradients and it is well known that elevational gradients are important for plant ecology (Hof, Jansson, and Nilsson 2012; von Humboldt et al. 2010). Here we focus on the far less well-known effects of suitability on trait variation. In high suitability sites plants were found to have larger, more cheaply constructed

leaves and produced more seeds per inflorescence, with LA and SLA having no effect on survival. In contrast, low suitability sites had smaller, more densely constructed leaves with a low number of seeds produced. The effects of LA and SLA on survival were strongly negative in these low suitability sites, demonstrating a mechanistic demographic driver for the trait patterns observed.

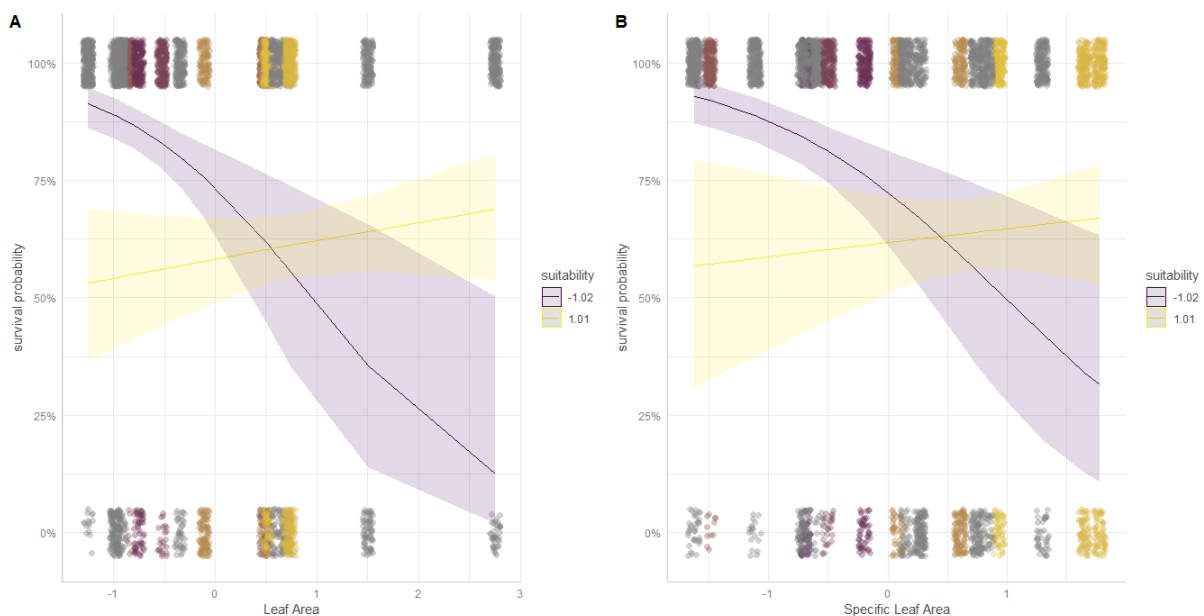


Figure 3.2 Relationship between LA (A) or SLA (B) on survival in interaction with the suitability gradient. Panel A shows the relationship between LA (x-axis) and survival probability (y-axis). Panel B shows the relationship between SLA (x-axis) and survival probability (y-axis). The interaction between the environmental gradient and the functional trait in explaining survival is represented by the two colored lines, where deep purple shows the relationship at the lowest suitability value observed in the study area. Light yellow shows the relationship at the highest suitability value. Points are coloured as per the lines. The shaded areas represent the 95% confidence interval for the predictions. Each observation is an individual from one of the 18 populations: points are shown with jitter to avoid overlap. Plots created using the *ggeffects* package (Lüdtke 2018) using the *viridis* colour-blind friendly colour maps (Garnier et al. 2021).

Evidence for a faster pace of life in high SDM-suitability areas

Higher SLA is typically associated with broader, thinner leaves, that produce a high photosynthetic income for a short period of time (Díaz et al. 2016; Moles 2018; Pérez-Harguindeguy et al. 2013). Similarly, high LA is associated with broad, leaves, representing a low cost of production, and usually a fast turnover (Díaz et al. 2016; Moles 2018; Pérez-Harguindeguy et al. 2013). We found that both LA and SLA increased with SDM-suitability (Figure 3.2). Both a high SLA and LA were associated with lower survival probability in low SDM-suitability, and higher survival probability in high SDM-suitability (Figure 3.3). Therefore, our results seem to indicate that *P. lanceolata* invests in the production of more durable leaves in low environmental suitability conditions (Moles 2018). Contrary to our expectation, the trend for seed mass to decrease towards higher SDM-suitability values was inconclusive. Nonetheless, we found an increasing seed number per inflorescence with SDM-suitability. This is in agreement with our expectations, and the findings of Baudraz et al (Chapter 2) who found a higher reproductive investment (summed millimetres of inflorescence produced over all stems of a genet) at higher SDM-suitability. The production of more seeds per reproductive event is usually correlated with a lower mass per seed (inconclusive in our study), and a shorter life span (Moles 2018; Moles and Westoby 2004). Following our expectations, the patterns we observed along the suitability gradient therefore describe a faster life cycle in higher SDM-suitability area. At low SDM-suitability values, we observed a higher investment in long-lived leaves (Wright et al. 2004), with few offspring being produced (Moles 2018; Moles and Westoby 2004). In high SDM-suitability, we observed large, thin, short lived leaves (Wright et al. 2004). In their analysis of direct demographic measurements of the same species along the same suitability gradient, Baudraz *et al.* (Chapter 2) found that a decrease in survival along the suitability gradient caused a shift in population life history strategies towards faster life cycles in higher SDM-suitability. We therefore can conclude that multiple measurements of several functional traits captured a qualitatively similar shift in life history strategies along the gradient.

Relationship between leaf functional traits and individual survival

We also attempted to test whether leaf functional traits could directly predict changes in one fitness component (survival). Functional traits typically tend to explain very little of the

observed changes in demographic rates (Wright et al. 2010). One suggested reason for this lack of relationship is that functional traits to demography relationships might vary depending on the climatic and biotic context (Yang et al. 2018). Despite a limited sample size at the level of the site (only 18 populations, visited for two yearly transitions each), we found a significant interaction between the environmental gradient and both LA and SLA for individual survival. The interaction was strong enough for the relationships to have different signs at opposite ends of our studied gradient (Figure 3.3). In less suitable conditions (\cong higher elevation), higher LA or SLA predicted a lower probability of survival, whereas in more suitable conditions (\cong low elevations) higher LA or SLA predicted a higher probability of survival. In other words, broader, thinner leaves are advantageous at high SDM-suitability, but becomes maladaptive in harsher conditions. Given our limited sample size, the results should be interpreted with caution, yet for a significant effect to be detected with only 18 populations in two yearly demographic transitions means that the magnitude of the effect is very strong. This is in agreement with the findings of other authors (Adler et al. 2014; Kelly et al. 2021), and stresses that climatic context is necessary to infer a relationship between functional traits and life history strategies in interspecific studies. Both our survival models explained about a third of the variance in individual survival ($R^2_c = 0.353$ and 0.350 respectively, Supplement S4), but functional trait values, environmental suitability and identity of the demographic transition (2017 - 2018 or 2018 - 2019) only explained less than a fifth of the variance ($R^2_c = 0.18$ and 0.164 , Supplement S3.2). This is higher than many studies and in agreement with the fact that we only use population average values rather than individual level trait measurement (Moles 2018; Wright et al. 2010), but highlights the complexity of the task of correctly inferring functionality and fitness components based on functional trait values alone.

Ability to capture the environmental gradient

In our study, temperature, elevation and SDM-suitability all performed reasonably well at capturing changes in functional traits along the gradient (Table 3.2), all being basically indistinguishable from the best predictor based on AIC for all traits except seed size (Burnham, Anderson, and Huyvaert 2011). Given the lack of spatial replication in demographic datasets and the relative scarcity of datasets measuring functional traits over repeated individuals or populations of the same species (but see examples such as Blonder

et al., 2018), there is a need for tools to summarise complex environmental gradients into meaningful metrics (Buckley and Puy 2021). In our study for example, despite the monitoring of over 1000 individuals per year, the number of populations limited us to investigating the interaction between functional traits and just one environmental driver to explain survival. By using SDM-suitability rather than elevation, it is our expectation that SDMs could help with transferability of other environmental gradients into an indicative and directly comparable metric. The relationship between SDM-suitability and patterns of functional traits was shown to be weak and species dependent (Thuiller et al. 2010). Nonetheless, common practice in SDM research is to build models based on one standard set of environmental variables for many species (Mod et al. 2016; Thuiller et al. 2010). In population ecology, much more focus tends to be put into fewer species known in detail, which in turn could benefit the choice of meaningful predictors for SDMs (Austin 2002; Austin and Van Niel 2011; Guisan et al. 2006; Mod et al. 2016). In our case, with careful choice of predictors for the SDM, we could make use of SDM-suitability to describe shifts in life history strategy along a complex environmental gradient, based on the measurement of functional traits in only 18 populations. We can only recommend other authors be as careful in their establishment of an SDM for the inference on population behaviours across gradients and geographic distances (Gurevitch et al. 2016).

3.6 Conclusions

The rare joint sampling of functional trait and demographic data from the same sites over broad environmental suitability gradients enabled us to test the effects of SDM-suitability on individual and population level functions. We found that suitability explains variance in the

functional traits of *Plantago lanceolata* that corresponds with previous findings of a slower life cycle in harsher environmental conditions. Given limited sample sizes of within-species demographic data at the level of the population, we need tools to summarize complex environmental gradients into one single meaningful environmental predictor. We found that elevation, and suitability derived from an SDM with predictors selected carefully to match the ecology of the species, both perform well at explaining variance across all traits. Using SDM-suitability to summarize the gradient, we found that SLA and LA explain individual

survival in interaction with environmental suitability. In harsher conditions (\cong higher elevation), higher LA predicted a lower probability of survival, whereas in more suitable conditions (\cong low elevations) higher LA predicted a higher probability of survival. Similarly, higher SLA predicted a lower probability of survival in harsh, but not suitable conditions. Our results stress the importance of including local environmental context when attempting to infer population level functionality based on individual functional trait measurements alone. Datasets of coupled demographic and functional trait information along quantified environmental gradients are rare. The present study therefore provides useful insights for the transferability of the relationship between functional traits to demography across populations and geographic areas (Catford et al. 2021; Shea et al. 2005).

3.7 Acknowledgement:

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Chapter 4: Evidence for a slower life cycle in low SDM-predicted probability of occurrence areas in the perennial herb *Plantago lanceolata* L.

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4.1 Abstract

Species Distribution Models (SDM) predict the probability of occurrence of a species as a function of environmental drivers. SDMs can be used to quantify suitability gradients along niche dimensions. It remains an open question whether and how readily available measures of environmental “suitability” inferred from SDM are associated with variation in species demography and life history strategies. There is evidence for perennial plants to delay reproduction and slow down their life cycle in harsher environmental conditions. Here, we test for a slower life history strategy in low SDM-suitability areas using 39 populations from the native range of the perennial herb *Plantago lanceolata*. We find evidence of a longer life span, longer generation length, a higher yearly reproductive rate, a higher reliance on shrinkage and lower rates of progressive growth in low SDM-suitability areas. These results were reliant on the selection of environmental predictors closely related to the ecology of the species. An SDM built using generic predictors, commonly used to predict the distribution of multiple plant species, produced weaker or non-detectable trends in life history strategies. Our results demonstrate that SDM-suitability can provide meaningful information for intraspecific changes in life history strategies, provided appropriate methodological choices are made.

4.2 Introduction

Most demographic data is poorly replicated spatially (Abeli et al. 2014; Salguero-Gómez et al. 2015), although notable exceptions exist (Merow, Bois, Allen, Xie, Silander Jr., et al. 2017; Römer et al. 2021; Villellas, Morris, and Garcia 2013). This complicates the transferability of demographic data from one location to another (Coutts et al. 2016) and we rarely have access to detailed demographic information needed to address pressing management issues in the appropriate climatic conditions (Crouse et al. 1987; Kerr et al. 2016; Ramula 2017; Ramula et al. 2008). We therefore need to develop proxies of demographic performance enabling us to make inferences based on limited demographic information (Buckley and Puy 2021), and to assess their performance using highly replicated systems.

Predicted probability of occurrence from Species Distribution Models (SDMs) is an example of such potential proxies. SDMs are correlative models explaining the occurrence of species in space as a function of environmental predictors, attempting to capture the species realized niche (Araújo and New 2007; Elith et al. 2006; Guisan et al. 2017; Hutchinson 1957). A high probability of occurrence as predicted by SDMs is often interpreted as a high suitability (hereafter, SDM-suitability) of the environmental parameters for the species (Guisan and Thuiller 2005; Guisan et al. 2017; Vanderwal et al. 2009). SDM predictions are regularly used for applied purposes in conservation, climate change or invasive species management (Araújo and Williams 2000; Breiner et al. 2015, 2017; Guisan et al. 2013; Lagos et al. 2020; Petitpierre et al. 2012; Velazco et al. 2020). The applied use of SDM is mediated by assumptions on population performance and the demographic pathways thereof (Bohner and Diez 2020; Csergő et al. 2017). For instance, to favour high SDM-suitability sites for conservation measures, one assumes a higher probability of population persistence in higher SDM-suitability areas (Csergő et al. 2017; Pulliam 2000). This assumption is intuitive, though more and more discussed (Bohner and Diez 2020; Csergő et al. 2017). SDMs use the large amount of occurrence data available together with detailed environmental data to estimate the probability of occurrence as a suitability metric. Environmental suitability is useful as an explanatory variable in the analysis of demographic data, as it reduces the dimensionality of complex environmental gradients to a single value. That value is more likely to be meaningful for the ecology of species than other dimension reduction techniques

that do not use species specific occurrence information, such as PCA of multiple environmental gradients (Blonder et al. 2018).

A major focus in the use of SDM is to predict the shift of species distributions under climate change scenarios, and much of the literature linking SDMs with life history or demography has focused on refining such predictions (Fordham et al. 2018; Schurr et al. 2012; Swab et al. 2012). Nonetheless, SDMs capture the result of demographic processes in currently existing ecological conditions (Hutchinson 1957; Maguire, 1973). Occurrence is only possible where values of the vital rates (the rates of growth, fecundity and mortality) of a species enable it to complete its life cycle frequently enough to ensure replacement of dying and aging individuals (Caswell 2001; Stearns 1992), though immigration of individuals can rescue some populations (Lieury et al. 2016). Many types of life history strategies can lead to population persistence (Cole 1954). Just in plants, at the interspecific level, life expectancy can vary from just a few days to several centuries (Salguero-Gómez et al. 2016; Stearns 1992). Different populations of the same species also vary in their demographic strategies to adapt to local conditions (Csörgő et al. 2017; Dahlgren, Bengtsson, and Ehrlén 2016; Ehrlén et al. 2016; Villellas et al. 2015, 2021). As SDMs capture realized variations in the probability of occurrence, they reflect the consequences of variation in vital rates, together with dispersal ability of individuals (Schurr et al. 2012). An important question is whether the SDM suitability metric can be generally applied to be a useful proxy for demographic performance (Buckley and Puy 2021; Csörgő et al. 2017; Pironon et al. 2017).

Many studies linking SDM-suitability to population ecology in existing environmental conditions have focused on abundance (Weber et al. 2017), population density (Thuiller et al. 2014) or population growth rates (Greiser et al. 2020), partly due to their direct implications for conservation purposes (Ehrlén and Morris 2015). In addition, one can infer a population abundance or population growth rate on the basis of only one or two visits to a site, making data relatively easy to collect for model building, or validation (Morris and Doak 2002). In comparison, obtaining individual level demographic measures of survival, fecundity and growth is much more time consuming (Caswell 2001). For this reason, work which breaks down the expectations from SDMs or niche suitability models for demographic pathways are rare but insightful (eg Csörgő et al., 2017; Pironon et al., 2017). These works are however poorly replicated at the within-species level, as studies of demographic

processes in a replicated way along quantified environmental gradients are sparse (Abeli et al., 2014; Pironon et al., 2017; but see Oldfather and Ackerly, 2019; Pironon et al., 2018; Römer et al., 2021; Smith et al., 2020; Jesus Vilellas et al., 2013 for recent progress on the topic). To fill this gap PlantPopNet (www.plantpopnet.com) was set up as a collaborative science project which monitors the demography of the perennial herb *Plantago lanceolata* L. in >60 populations at a global scale (Buckley et al. 2019).

Potential links between SDM-suitability and demography are not straight forward (Bayly and Angert 2019; Csergő et al. 2017; Greiser et al. 2020; Thuiller et al. 2014). Some find that SDM and population models each tell a meaningful, but slightly different story (Bayly and Angert 2019; Greiser et al. 2020). Others find no trend between population growth rate and SDM-suitability (Csergő et al. 2017), or varying and even opposing trends between both population growth and carrying capacity and SMD-suitability depending on geographic areas (Thuiller et al. 2014). Despite their power and amount of available data, SDMs have limitations. They assume equilibrium between a species and its environment, and exclude biotic interaction when inferring distribution based on climatic drivers (Guisan et al. 2017; Soberón and Nakamura 2009). As a consequence, they can only capture the realized niche of a species (Hutchinson 1957; Soberón et al. 2017). In addition, the lack of explicit consideration of biotic interactions makes SDM blind to density dependent feedbacks, which are known to strongly determine local abundance (Courchamp et al. 2008; Holt 2009) and population growth rates (Reed et al. 2013; Reed, Gienapp, and Visser 2015) through impacts on different vital rates (Buckley et al. 2001; Sletvold 2005).

Perennial plants have been demonstrated to have slower life cycles and delayed reproduction in harsh climatic circumstances (Harper 1977). For instance, *Liastris aspera* was shown to complete its life cycle in two years in optimal garden circumstances, but reach a life expectancy of >40 years in the wild (Harper, 1977, chapter 19, pp. 557). Similarly, in a study of the demographic pathways along SDM gradients of 93 populations of 34 species, Csergő et al. (2017) found a correlation of lower SDM-suitability with retrogression, a conservative life cycle strategy (Salguero-Gómez and Casper 2010). Finally, more specifically for *Plantago lanceolata* along a steep climatic gradient in the Swiss Alps, Baudraz et al. (Chapter 2) found that the pace of life of the species slows down in lower SDM-suitability areas. This is expected where the suitability gradient follows an elevation gradient, as alpine

species often display much slower life cycles than temperate or tropical species (Kelly et al. 2021; Körner 2003; Salguero-Gómez et al. 2016). Slower pace of life history strategies come with a higher reliance on the survival of adult individuals and a longer time frame at which past or ongoing threats can affect populations (Crouse et al. 1987; Mace et al. 2008). Therefore, a systematic link between low SDM-suitability and slower life cycles within species could have consequences for the conservation of species.

Here, we test whether the hypothesis of a slower life cycle at lower SDM-suitability, evidenced at regional scale by Baudraz et al. (Chapter 2), generalizes at continental scale. We focus on the same species, *Plantago lanceolata* L., using data from the collaborative science project PlantPopNet (Buckley et al. 2019; Smith et al. 2020; Villellas et al. 2021), and species occurrence data from GBIF (GBIF.org 2021). This perennial herb is native to Europe but now spans five continents due to repeated introductions (CABI 2019; Smith et al. 2020). The species is documented to experience a shift in niche components and demographic drivers between its native and invasive niche, correlated with differences in genetic diversity, due to admixture in the non-native range (Petitpierre et al. 2012, 2017; Smith et al. 2020). We therefore focus first on the native range of the species. We produced population models for 39 populations of the species, and assessed whether the pace of life of the species increases towards high suitability values. As SDMs can be fitted with many techniques (Elith et al. 2006; Guisan et al. 2017; Norberg et al. 2019), which choice was shown to affect demographic inference (Fordham et al. 2012), we test this using two contrasting SDM methods.

4.3 Methods

Overview

We developed a site-specific population model without any environmental information, and used it to derive a series of life history metrics describing the species' pace of life at each site. In parallel, we built two candidate SDMs. One is a generic one for the field ("generic-SDM"), reproduced from a paper testing the relationship between SDM and demography across 34 species (Csörgő et al. 2017). The other is more specific to our species ("species specific-SDM"). In particular, it uses environmental predictors that are expected *a priori* to capture the ecology of the species, and the fitting algorithm, cross-validation and pseudo-

absence selection strategies were developed to best capture the distribution of this very widespread species, expected to be often overlooked (CABI 2016; Meusel and Jäger 2011). We used generalized linear models to test for the existence, direction and strength of a correlation between SDM suitability on life history metrics.

Species

Plantago lanceolata L. is a perennial, short-lived, rosette forming herb (Kuiper and Bos, 1992; Sagar and Harper, 1964), increasingly used as an ecological model organism (Penczykowski and Sieg 2021). Each individual (genet) is composed of one to several rosettes (ramets). Small flowers in linear inflorescences are arranged on a variable number of flowering stems per rosette (Sagar and Harper 1964). Each flower produces up to two seeds (Lauber et al. 2018). The plant is variable in size and shape, with leaves ranging from 2 to 45 cm in (Sagar and Harper 1964). The species inhabits disturbed areas, especially agricultural ones, to the point where it was used as an indicator of human settlement and change of agricultural practices from early human settlers (Erdtman, Berglund, and Pragłowski 1961; Kozáková et al. 2015). Native to Eurasia, it is now widespread throughout the globe due to several introduction events (Smith et al. 2020).

Demographic modelling

Data sources

We used the spatially distributed demographic network PlantPopNet (www.plantpopnet.com, Buckley et al. 2019). PlantPopNet gathers information on populations of *P. lanceolata* on three continents (Figure 4.1, see Figure 1.1 for the distribution of the entire network, including non-native range). 39 of these are in the native range of the species and were included in the present study. Each population consists of an initial minimum of 100 individuals, marked within plots, which are re-visited yearly at the peak of the flowering season. The area of the site is given by the number of plots needed to monitor at least 100 individuals in the first year. The number of leaves, flowering status (flowered, not flowered), as well as survival or death of each plant was recorded each year.

Reproductive

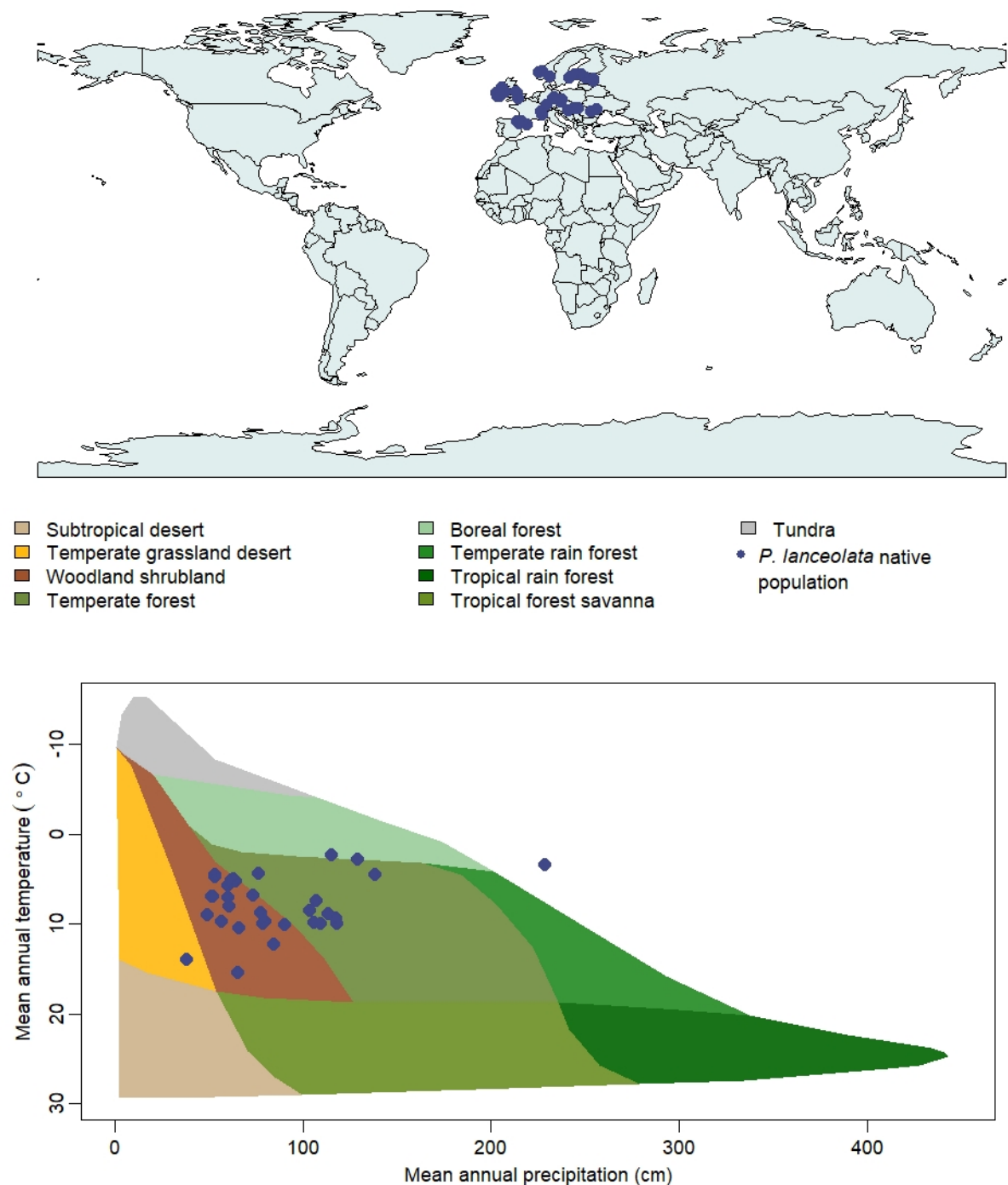


Figure 4.1 The distribution of the native populations of *Plantago lanceolata* included in this study in geographical space (A) and in environmental space (B). Panel A shows which biomes of the world *P. lanceolata* occurs in (Whittaker 1970). The biomes are classified by their mean annual precipitation values and mean annual temperature. Plots were developed with the BiomePlot (Kunstler 2014) and rworldmap packages (South 2011).

effort is estimated as the number of flowering stems and the length of the inflorescence of the longest stem (Villellas et al. 2021). In this paper we focused on the first two transitions of the PlantPopNet database (i.e., the first three years of data, Supplement S4.1). As only the individual (genet) identities are recorded at all sites following the PlantPopNet protocol (Buckley et al. 2019), this study was performed at genet level and the number of leaves for each ramet in the genet was summed to give a total genet size. For additional information on the PlantPopNet protocol see Buckley et al. (2019).

Life cycle and vital rates models

The life cycle of *Plantago lanceolata* is illustrated in Figure S2.2.1. Notation used are presented in Table 4.1. Overall, adult individuals of size z_t at time t contribute to the pool of individuals in the next year if they survive and grow (or remain or shrink) to a size z_{t+1} the following year, or if they reproduce. All individuals have a probability of flowering, and produce a varying number of seeds. Each seed has a probability of contributing to the pool of recruits entering the population the next year with a size given by the recruit size density function. This life-cycle assumes that all recruits are produced sexually, ignoring clonal reproduction (Kuiper and Bos 1992). Each life cycle component was modelled through a generalized linear mixed model, with the size of the individual in the first year as fixed effects, and the site of origin, the plot, the transect and the year in which the data was measured as random effects (Table 4.2). Size was measured as the number of leaves in a genet (Chapter 1). We estimate the number of seeds using a proxy, which is millimetres of inflorescence produced (length of inflorescence on the longest flowering stem x number of flowering stems).

Size transitions were estimated using the number of leaves at time t , z_t , predicting the number of leaves the following year z_{t+1} as a negative binomial model with constant variance and square root link function using the `nb1n2` family in the `glmmTMB` package (Brooks et al. 2017; Hardin and Hilbe 2018). Probability of survival and flowering were modelled using a binomial error model with logistic link function. Reproductive effort was log transformed and modelled as a Gaussian process. These mixed effects models were built in R version 3.6.3, using the `lme4` library (Bates et al. 2015; R Core Team 2020).

As per the field monitoring protocol and study design (Buckley 2019), year of sampling, site, transect nested within site and plot nested within transect were included in mixed effects models as random effects. For all of random factors, we attempted to fit a random intercept and slope (and quadratic if applicable) to the relationship between plant size and the vital rates, and only diverted from this structure to avoid model convergence issues, where simpler random effects structures were fitted. The resulting models and random structures are detailed in Table 4.2.

Table 4.1: Notations used

Symbol	Name		Definition
z_t	Size of individuals (number of leaves) at time t		Measured in number of leaves, with min(z) = 2 as the smallest individuals entering the matrix have 2 leaves and max(z) = 69.
y	year		Year at which the demographic data was sampled (from 2015 to 2019)
w	site		Locations of the populations
u	Plot identity		Identity of any given 50 cm x 50 cm plot used to map and monitor <i>P. lanceolata</i> L. individuals within sites
t	time		t = the time point at the start of a transition, t+1 = the time point at the end of a transition. In this case, time intervals are yearly intervals.
a	area		The number of 0.25 m ² plots covered by the population.
r	number of recruits		Measured at the site level
Vital rates models and functions used to parametrize the matrices			
Vital rate	Function	Name	Definition
s	$s(z_t, w)$	Survival probability	$s(^{\circ})$ predicts the probability of survival of an individual of size z_t with the appropriate attributes
g	$g(z_{t+1}, z_t, w)$	Growth, stasis or shrinkage	$g(^{\circ})$ predicts the probability for an individual of size z_t to transition to a size z_{t+1} , conditional on survival.
h	$h(z_t, w)$	Flowering probability	$h(^{\circ})$ predicts the probability of flowering of an individual of size z_t with the appropriate attributes

Table 4.1, continues

o	$o(z_t, w)$	Reproductive effort	$o(^{\circ})$ predicts the reproductive effort (mm of reproductive material) of an individual of size z_t with the appropriate attributes, conditional on flowering
c	$c(z_{t+1}, w)$	Size distribution of recruits	$c(^{\circ})$ Predicts the probability of a recruit to be of size z_{t+1} upon entering the population (at size w in transition T).
b	$b(w)$	Recruitment	$b(^{\circ})$ predicts number of new recruits expected to enter a population.
The functions predict the homonymous vital rates models described in Table 4.2 for an average plot \hat{u} , transect \hat{t} and year \hat{y} . The functions were applied on the range of sizes z_t (0 to 95) and z_{t+1} (0 to 95) to populate the site-specific matrices.			

Recruitment

There was no obvious linear relationship between the reproductive effort and the number of recruits entering the population in the next year. Several candidate recruitment models were attempted, corresponding to different density dependence regimes: compensatory density dependence, density independence and constant recruitment models. The models were compared using AICc (MuMIn package, Bartoń, 2018), and the best fit model was the constant recruitment model. The number of recruits emerging at each site was modelled as negative binomial process in a generalized linear mixed model with a fixed intercept, and the site of origin and year as random effects. Recruits were only monitored from size 2-leaves onwards in the PlantPopNet network, to avoid tagging-induced mortality. The size of the recruits was modelled as a negative binomial process, fitted on $(z_t - 2)$. The probability of a recruit of $z_{t+1} < 2$ to enter the population was set to 0. These two negative binomial models were fitted using the glmmTMB package with a nbinom2 family with log link (Brooks et al. 2017).

Population model

We used the vital rates models to predict the probability of transition of individuals from any size class z_t (one leaf sized bins) to any other size class z_{t+1} in the following year. We did this by building predictive functions that applied the vital rates model on a range of sizes (individuals from 0 to 95 leaves, the maximal value observed in the PlantPopNet dataset), ignoring the plot, transect and year random effects. This effectively populated a series of

site-specific Matrix Population Models. These matrix models were of size 96 x 96. Effectively, populating these matrix models was done as in an IPM of kernel

$$s(z_t, w) g(z_{t+1}, z_t, w) + h(z_t, w) o(z_t, w) \frac{b(w)}{\sum_0^{95} h(z_t, w) o(z_t, w) n_{z_t}} c(z_{t+1}, w) \quad \text{equation 1}$$

where $s(z_t, w)$ is the probability of survival of an individual of size z_t in site w , $g(z_{t+1}, z_t, w)$ the probability of an individual of size z_t in site w to grow (or shrink) into an individual of size z_{t+1} the following year, $h(z_t, w)$ the probability of flowering of an individual of size z_t in site w , $o(z_t, w)$ the reproductive effort (number of stems multiplied by mm of inflorescence) that an individual of size z_t is expected to produce in site w , $b(w)$ the number of recruits that are expected yearly at site w , n_{z_t} the number of individuals of size z_t in the population at time t , making $\sum_0^{95} h(z_t, w) o(z_t, w) n_{z_t}$ the total expected amount of reproductive effort produced by the entire population at time t . $\frac{b(w)}{\sum_0^{95} h(z_t, w) o(z_t, w) n_{z_t}}$ is hence the contribution of any unit of reproductive effort to the predicted pool of recruits.

Life history metrics and life cycle pace

We projected the matrices on the same starting population until stable stage distribution of the population was reached (500 iterations). The stable stage matrices were used to compute life history metrics. We computed generation length, reproductive life expectancy, mean reproductive rate and rates of progressive and retrogressive growth as in (Kelly et al. 2021). Packages used to compute the life history strategy metrics are expm (Goulet et al. 2021), ineq (Zeileis 2014), MASS (Venables and Ripley 2002) and popbio (Stubben and Milligan 2007). Functions were extracted from package Mage (currently maintained as Rage (Jones et al. 2021) and adapted by Kelly et al. (2021). We computed the generation length based on the survivorship table ($Generation\ time = \sum_{x=1}^{500} x\ l_x\ m_x / \sum_{x=1}^{500} l_x\ m_x$, where l_x is the survivorship until age x , m_x the mortality at time x) based on (Caswell 2001; Healy 2021).

Relationship with SDM suitability

The relationship between LHS metrics and SDM-suitability was assessed through a series of linear models (one per LHS metric as response variables). The models were fitted using the stats package in base R (R Core Team 2020).

Species Distribution Models

Overview

Many different techniques can be used to fit SDMs (Elith et al. 2006; Guisan et al. 2017; Norberg et al. 2019). To assess the generalizability of our findings, we produced two different types of SDM: one “generic-SDM”, applicable to many species, and one “species specific-SDM” (described below). As a generic procedure, we reused the SDM-building technique of Csergő et al. (2017) which compared the relationship between suitability and demographic metrics across several species using an ensemble model including several techniques (Thuiller et al. 2016), with climatic predictors known to drive the ecology of plant species. As a species-specific technique, we built a random boosted regression tree (GBM; Elith et al. (2008) and used environmental predictors specific to match the ecology of *P. lanceolata*. Both model approaches (generic and species-specific) were built using the same set of occurrences (extracted from GBIF; GBIF.org (2021) as the response variable. We hereafter detail the cleaning process of the GBIF data, common to both models, followed by the details of each SDM approach.

Occurrence data and cleaning

Data for all *P. lanceolata* records were downloaded from the Global Biodiversity information facility (GBIF.org; download <https://doi.org/10.15468/dl.1rzpk0>) and then restricted to the native range of the species only for the current project. Records with no coordinates, fossil data, taxonomy issues or co-ordinate issues were dropped. Records with coordinate uncertainty of more than 10km were dropped, except where these records were from unique locations otherwise unrepresented in the data. We visually examined all points flagged as being in the sea, and dropped all data appearing to be nonsensical i.e. more than 10km off the coast. We verified our manual cleaning approach by using the CoordinateCleaner package on the cleaned dataset (Zizka et al. 2019). As this package flagged just 1078 GBIF occurrences as problematic, (less than 0.0016% of the data), we deemed the remaining occurrence records to be usable.

Generic SDM procedure.

Csergő et al. (2017) built an ensemble of four different techniques to obtain robust Species Distribution Models for all species in their study. They created an ensemble of generalized

linear models, generalized boosted regression models, random forest and maximum entropy modelling using the biomod2 package (Thuiller et al. 2016). We used the same techniques, but for Maxent, where we used the Maxent.Phillips algorithm due to an update in the package. As Csergő et al. compared species with very different ranges and dispersal limits, they selected pseudo-absences only in climatic conditions analogous to those of known occurrences of the native range of each species using a Multivariate Environmental Similarity Surface (MESS) analysis (Elith, Kearney, and Phillips 2010). Although we focus only on the native range of *P. lanceolata* in this study, we applied the same process for direct comparability. We also used the same set of eight environmental predictors commonly used for modelling the distribution of plant species than Csergő et al.: annual mean temperature, temperature seasonality (Coefficient of Variation), mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of wettest quarter, as well as annual means and seasonality (standard deviation of monthly values) of global potential evapo-transpiration.

We extracted the most up to date version of the same climatic layers from WORLDCLIM (<http://www.worldclim.org/bioclim>; Fick and Hijmans (2017) and CGIAR Consortium for Spatial Information (Trabucco and Zomer (2019)). We downloaded the maps at 5 arc-minutes resolution (~10 km in the temperate regions), similarly to Csergő et al. (2017). We applied this method to the *Plantago lanceolata* occurrences extracted from GBIF, and selected pseudo-absences in same quantity as occurrences. Models were calibrated with 70% of the data. The remaining 30% were used for model evaluation. The procedure was repeated 25 times, with random training and evaluation datasets, producing 100 models (4 techniques x 25 runs each). Model prediction performance was assessed using the area under the receiver operating characteristic curve (AUC) (Hosmer and Lemeshow 2000), and the maximization of Cohen's Kappa (i.e. max-Kappa; Cohen (1960) and of TSS (i.e. max-TSS; Allouche et al. (2008). See Guisan et al. (2017) for the maximization procedures for both these metrics. The final ensemble model was constructed from selected models with the evaluation metric max-TSS larger than 0.7, and by taking a max-TSS-weighted average of the predicted probabilities of occurrence.

Species-specific SDM procedure.

For our species-specific SDM, we focussed on one modelling algorithm, and addressed several ecological particularities of *P. lanceolata*. We focused on random boosted regression trees (using gradient boosting machine, GBM) as they were shown to perform well compared to other single algorithm techniques and are highly flexible in the type of relationships to environmental drivers that can be fitted (Elith et al. 2006, 2008). We selected predictors to best match the known ecology of the species. In particular, a main driver of the ecology of *P. lanceolata* is that it is a species of disturbed areas, particularly agricultural land. Hence, we selected several human pressure and land use predictors as candidate variables. As a non-showy perennial herb, *P. lanceolata* is expected to be heavily under-recorded. This is an issue when modelling commonly available presence-only data, as non-occurrences are often absences of record and not true absences (Barbet-Massin et al. 2012). We therefore selected our pseudo-absences so as to minimize sampling bias. Following Barbet-Massin et al. (2012), we informed the distinction between true absences and absence of presence by using another, broader taxon as an indication of sampling bias in GBIF. We extracted all known occurrences from the *Plantae* kingdom (including groups such as algae, bryophytes, pteridophytes, gymnosperms, angiosperms and others) between 1850 and 2020. We selected pseudo-absences in approximately the same number (same order of magnitude, Barbet-Massin et al. (2012) as presences, from sites with at least one known *Plantae* occurrence.

Predictor selection

We selected predictors to best match what is known of the ecology of the species (Kuiper and Bos 1992; Penczykowski and Sieg 2021; Sagar and Harper 1964). Details of the GIS layers that were used, and rationale to do so, are as follows.

We selected the ‘human footprint’ index as a combined metric of Anthropogenic impacts on the environment (Venter et al. 2016). This index is a compound metric of eight variables: extent of built environments, crop land, pasture land, human population density, night-time lights, railways, roads, and navigable waterways (Venter et al. 2016). As the roads and streets data tends to be of variable quality depending on the area of the globe, we also used a simple human population density estimate. We added the UN WPP-Adjusted Population

Density, v4.11 (CIESIN 2018) as a potential predictor. We extracted the 2015 human population density measurement as representative of the study period. As *P. lanceolata* is strongly linked to agriculture and human land use, we also used GlobCover (ESA and UCLouvain 2010) as a categorical predictor. This map classifies land cover for the whole globe into 22 categories based on vegetation type, including forests with different percentages of broadleaf trees, grasslands, artificial surfaces, and gives a good insight of the type of land experienced by plants in each area of the world.

P. lanceolata is a very tolerant species in terms of most climatic predictors (Kuiper and Bos 1992). Nevertheless, some candidate climatic drivers emerged from the literature: water availability, temperature and light availability (Kuiper and Bos 1992; Mook et al. 1992; Villellas 2021, McKeon, Finn and Buckley, in prep). At a local scale, the species was also found to be very tolerant of soil conditions (Haeck et al. 1992; Haeck, van Tongeren, and van der Maarel 1985). Additionally, soil moisture emerged as a potential predictor (Kuiper and Bos 1992) and there was little information about the importance of soil properties for *P. lanceolata*'s distribution outside the very narrow range of soil types present on European shores (Haeck et al. 1985; Sagar and Harper 1964). A local study in the Swiss Alps found slope to be an important predictor of the distribution of the species in the region (Chapter 2). Given this, the following edaphic predictors should be included in our models: slope, soil sand content and moisture information.

To represent this set of species-specific ecologically-meaningful predictors, we used the following available layers: mean annual temperature, average yearly precipitation and precipitation seasonality were extracted as worldclim layers (<http://www.worldclim.org/bioclim>; Fick and Hijmans (2017)). We used the CHILL layer (Theobald et al. 2015) as a proxy for light availability and solar radiation. We represented edaphic factors as surface soil sand content (Hengl 2018) and surface soil moisture layers (Entekhabi et al. 2010; NASA-USDA 2015). The slope was computed based on the SRTM 90m DEM Digital Elevation Database version 4 (Jarvis et al. 2008) using the `ee.Terrain.slope` function in Google Earth Engine (Gorelick et al. 2017). All layers were accessed through the Google Earth Engine catalogue on January 10th, 2020. Layers were exported at a 10 km x 10 km scale and handled in R (R Core Team 2020). We assessed

correlations between the predictors in the models using the `corrgram` package in R (Wright 2021) and did not discard any predictor based on this analysis.

GBM-Modelling

We fitted boosted regression trees (Elith et al. 2008; Friedman 2001; Greenwell et al. 2018) using the `'gbm.step'` function in the `'dismo'` R package (Hijmans et al. 2020) and evaluated them by 5-fold spatial block cross-validation (Roberts et al. 2017). We used a learning rate of 0.008 and a tree depth of 4 for boosted regression tree models, and used the `gbm.step` function to optimize the number of trees to use for each model by sequentially adding trees and monitoring out-of-sample error. We assessed model prediction performance on data in cross-validation test folds using the area under the receiver operating characteristic curve (AUC) (Hosmer and Lemeshow 2000) and maximized Cohen's Kappa (Cohen 1960) and maximized TSS (Allouche, Tsoar, and Kadmon 2006). We used the reduction in squared error attributable to each variable in the boosted regression trees as a measure of variable importance (Friedman 2001, supplement S4.2).

4.4 Results

Evaluation of the Species Distribution Models

Both our Species Distribution Model techniques yielded very good evaluation metrics. The generic-SDM yielded a max-Kappa = 0.849, max-TSS= 0.857 and AUC = 0.983. The species-specific-SDM yielding a max-Kappa = 0.75, max-TSS = 0.75 and AUC =0.94. The predicted distribution maps were qualitatively similar (Figure 4.2). As the predictors used for the more detailed species-specific SDM are less readily available at a large scale, more pixels had missing values for this model than for the generic-SDM. As a consequence, we needed to attribute the nearest non-NA value from the raster for three PlantPopNet populations with the species-specific SDM, against only one for the generic-SDM.

Qualitatively, both SDMs predicted a similar distribution for the species, with the generic-SDM predicting larger areas of high suitability than the species-specific model, especially in Spain, Italy, the west of the island of Ireland and Sweden. The importance of the various environmental predictors in each SDM are displayed in supplement S4.2.

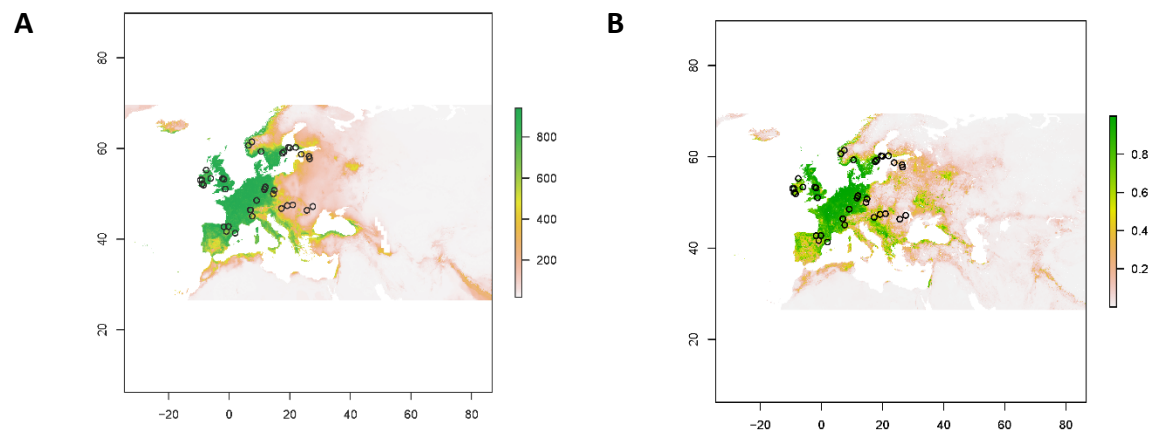


Figure 4.2 map of the predicted suitability values from (A) the generic-SDM (biomod ensemble model including general environmental predictors) and (B) the species-specific SDM (boosted regression tree model with species-specific environmental predictors). The black circles represent PlantPopNet populations.

Vital rates and population models

The vital rates models and their respective percentage of explained variance are displayed in Table 4.2. Overall, the amount of deviance in the raw data that could be explained by each model was high with R^2c ranging between 0.48 (recruitment) and 0.71 (flowering probability). The use of random factors to explain the variance between populations makes the information provided by the fixed effects of the models of relatively low value, but the respective R^2m of these models were 0.2 (model h, flowering, which contains the size of individuals in the previous year as a fixed effect) and 0 (model b, recruitment, which includes no fixed effect).

Life History Metrics

The relationships between all life history strategy metrics and the suitability predicted by the generic-SDM were nearly completely flat (Figure 4.3): survival over reproductive life span (slope = $-4.94 \cdot 10^{-5}$, 95% confidence interval $[-1.9 \cdot 10^{-4}; 8.9 \cdot 10^{-5}]$), Reproductive life span ($-3.1 \cdot 10^{-4}$ $[-1.2 \cdot 10^{-3}; 5.8 \cdot 10^{-4}]$), generation time ($-2.9 \cdot 10^{-4}$ $[-1.4 \cdot 10^{-3}; 7.8 \cdot 10^{-4}]$), retrogression ($-2.03 \cdot 10^{-5}$ $[-1.2 \cdot 10^{-4}; 7.9 \cdot 10^{-5}]$), progression ($-1.72 \cdot 10^{-5}$ $[-7.9 \cdot 10^{-5}; 4.4 \cdot 10^{-5}]$), yearly reproductive rates ($2.9 \cdot 10^{-4}$ $[-6.7 \cdot 10^{-4}; 1.2 \cdot 10^{-3}]$). There were more PlantPopNet populations in high suitability areas than in low suitability areas, with very few populations at mid-range values (note that the range displayed in Figure 3 and 4 only expands to where PlantPopNet populations were observed). When using the suitability

predicted by the species-specific SDM, trends in life history metrics with suitability were apparent (Figure 4.4). Reproductive life span ($-0.87 [-1.51;-0.22]$), generation time, retrogression ($-0.07 [-0.15;-1.6 \cdot 10^{-3}]$) and progression ($-5.1 \cdot 10^{-2} [-9.6 \cdot 10^{-2};-4.6 \cdot 10^{-3}]$) decreased with suitability, whereas the yearly reproductive rates ($0.15[0.1;0.27 \cdot 10^{-3}]$) and survival over the reproductive life span ($0.06, [-0.04;0.17]$) tended to increase with suitability, the later inconclusively. These results are consistent with a faster life cycle in higher suitability areas.

As the relationships between LHS and SDM-suitability were so distinct between the two SDMs, we ran each SDM using the environmental predictors of the other to check whether

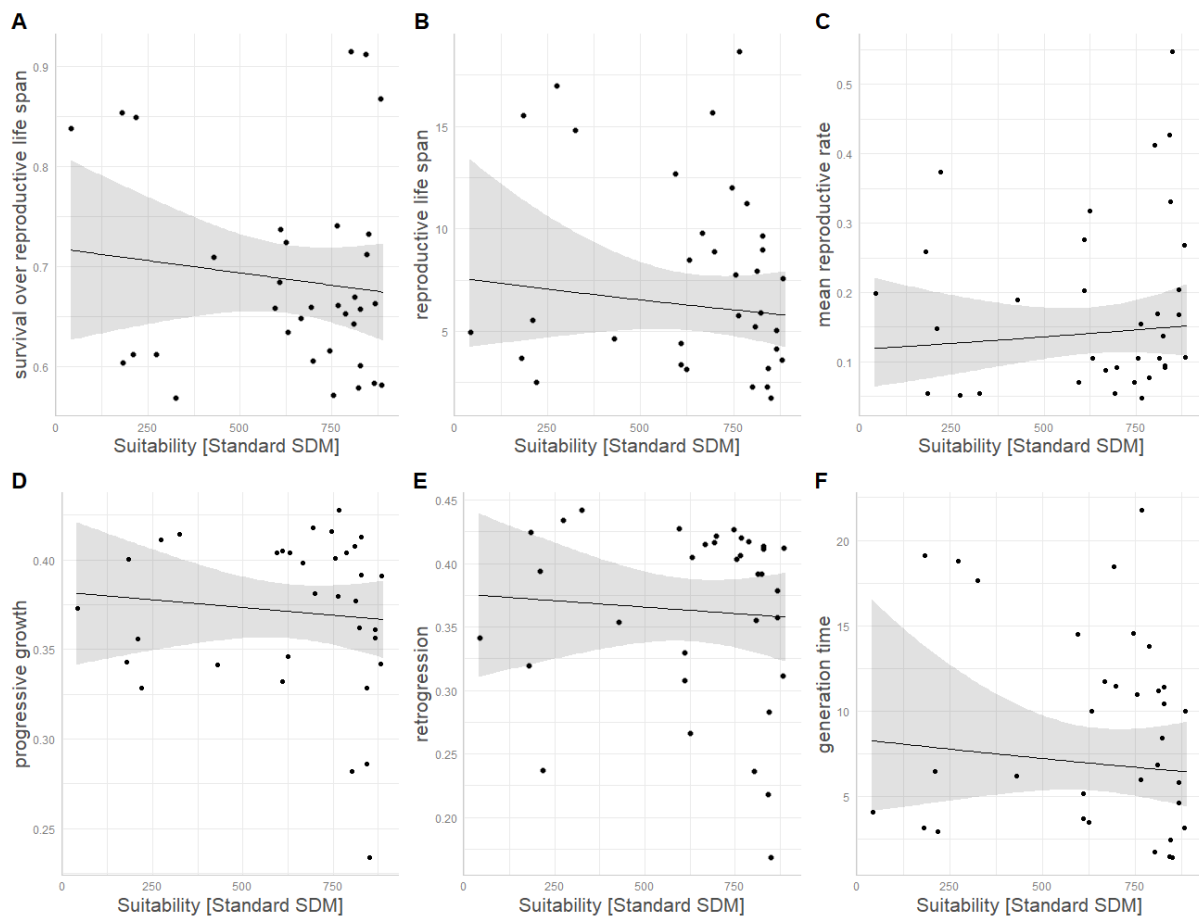


Figure 4.3 Life history metrics of *Plantago lanceolata* over the suitability predicted by the generic SDM. Each point is a PlantPopNet population. Shaded areas are bounded by 95% confidence intervals from a glm predicting each life history strategy metric separately as a function of SDM-suitability. LHS values were derived from the site-specific Matrix Population Model described in Table 4.1. A) survival over reproductive life span (probability) B) reproductive life span (years) C) average yearly reproductive rate D) progressive growth, i.e. the probability for individuals to transition to a bigger size the following year E) retrogression, i.e. the probability for individuals to transition to a smaller size the following year F) generation time (years)

Table 4.2: vital rate models (A) and predictive functions (B) used to build the population models.

Panel A

Rate	Response	Link	Error	Model equation	Random structure	correlation	R^2c	R^2m
s	$P(\text{survival})$	Logit	$E_{w,u,i} \sim \text{binomial}$	$(0.1 + b0_u + b0_t + b0_y + b0_w) + (0.28 + b1_w)z + E_{w,u,t,y,i}$	$b0_u \sim N(0, 0.58)$ $b0_t \sim N(0, 0.14)$ $b0_y \sim N(0, 0.56)$ $b0_w \sim N(0, 0.43)$ $b1_w \sim N(0, 0.03)$	$b0_w$ $b1_w (0.26)$	0.67	0.26
g	z_i	log	$E_{w,u,t,y,i} \sim \text{neg binomial}(\mu_1, \sigma_1 = 0.523)$	$(1.91 + b0_u + b0_t + b0_y + b0_w) + (0.09 + b1_t + b1_w)z + E_{w,u,t,y,i}$	$b0_u \sim N(0, 0.01)$ $b0_y \sim N(0, 0.02)$ $b0_t \sim N(0, 0.06)$ $b0_w \sim N(0, 0.11)$ $b1_w \sim N(0, 0.001)$	$b0_w$ $b1_w (-0.83)$	0.65	0.41
h	$P(\text{flowering})$	logit	$E_{w,u,t,y,i} \sim \text{binomial}$	$(-8 + b0_u + b0_t + b0_y + b0_w) + (4.36 + b1_w)z + E_{w,u,t,y,i}$	$b0_u \sim N(0, 0.13)$ $b0_y \sim N(0, 2.85)$ $b0_t \sim N(0, 0.31)$ $b0_w \sim N(0, 1.32)$ $b1_w \sim N(0, 0.03)$	$b0_w$ $b1_w (-0.36)$	0.71	0.20
o	$\log(\text{reproductive effort})$	Identity	$E_{w,u,y,i} \sim \text{gaussian}$	$(2.61 + b0_u + b0_y + b0_w) + (0.04)z + E_{w,u,t,y,i}$	$b0_u \sim N(0, 0.002)$ $b0_y \sim N(0, 0.0003)$ $b0_w \sim N(0, 0.39)$	NA	0.57	0.13
c	$z_i - 2$	Log	$E_{w,u,i} \sim \text{neg binomial}(\mu_2, \sigma_2 = 2.62)$	$(0.62 + b0_u + b0_y + b0_w) + E_{w,u,y,i}$	$b0_u \sim N(0, 0.17)$ $b0_y \sim N(0, 0.02)$ $b0_w \sim N(0, 0.43)$	NA	0.49*	0.0
b	number of recruits	Log	$E_{y,w} \sim \text{negbinomial}$	$2.26 + b0_y + b0_w + E_{w,u,i}$	$b0_y \sim N(0, 0.46)$ $b0_w \sim N(0, 0.84)$	NA	0.48	0.0

Panel B

Density function	Equation	Terms definition
Adult genet size density function	$P(z_{t+1}) = \text{neg. binomial}(\text{mean} = \mu_1, \text{dispersion parameter} = \sigma_1)$ with constant variance parametrization (Hardin et al. 2018)	where μ_1 is the prediction of model g and σ_1 is the dispersion parameter of model g
Recruits size density function	For $z_{t+1} > 1$, $P(z_{t+1}) = \text{neg. binomial}(\text{mean} = \mu_2, \text{dispersion parameter} = \sigma_2)$ For $z_t + 1 < 2$, $P(z_{t+1}) = 0$ as the minimal size in our model is 2 leaved individuals	where μ_2 is the prediction of model c and σ_2 is the dispersion parameter of model c

it was a methodological or predictor related difference. Results are displayed in supplement S4.3. We find that applying the generic-SDM method on the species-specific environmental predictors (hybrid 1, Figure S4.3.1) produces similar trends to those of our species-specific SDM (Figure 4.4), although with lesser strength of the signal and broader confidence intervals. Applying the species-specific SDM method on the generic environmental predictors (hybrid 2, Figure S4.3.3) produces trends between LHS and SDM-suitability very similar to those obtained with our generic-SDM (Figure 4.3). The spread of the suitability values covered by PlantPopNet populations in hybrid 2 technique was uneven, with

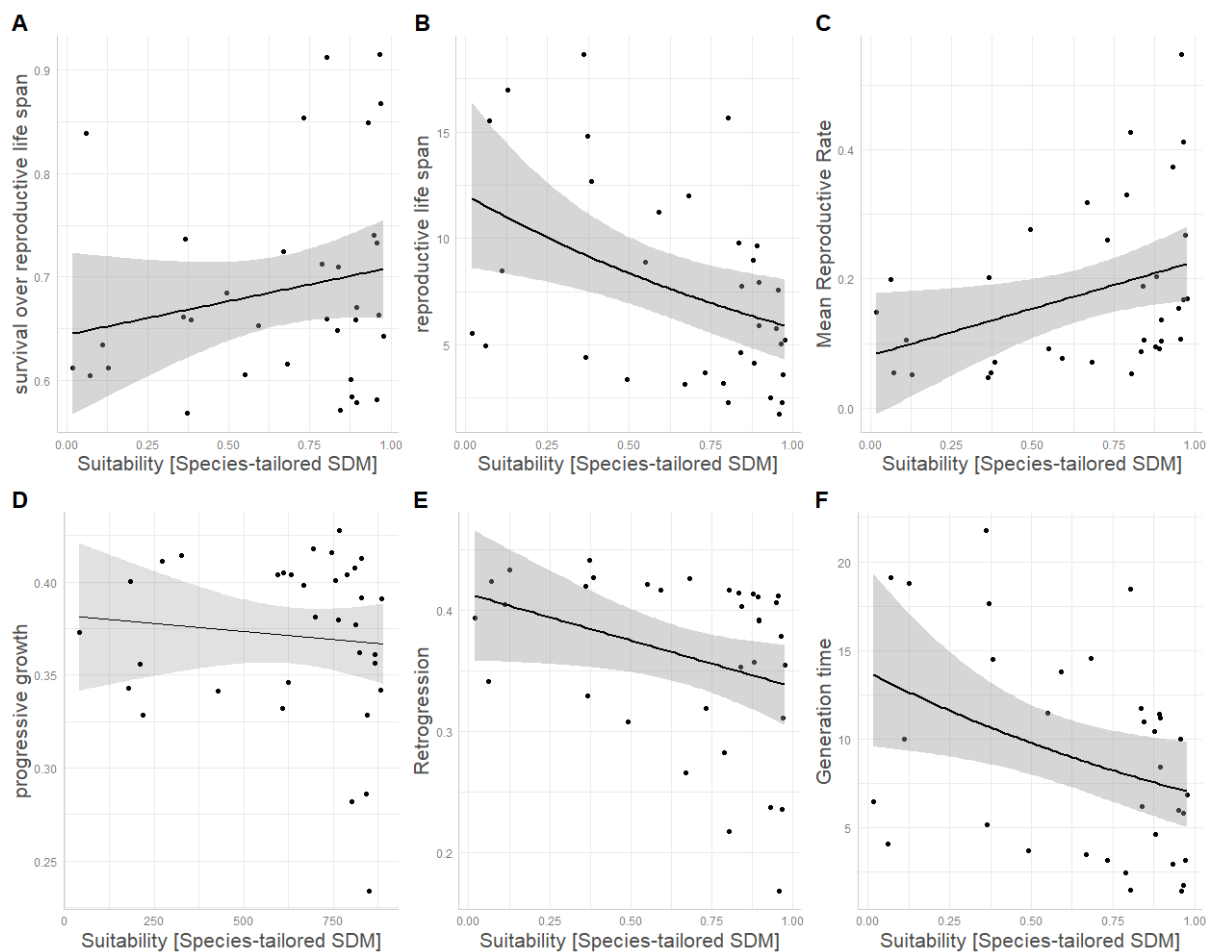


Figure 4.4 Life history metrics of *Plantago lanceolata* over the suitability predicted by the species-specific SDM. Each point is a PlantPopNet population. Shaded areas are bounded by 95% confidence intervals from a glm predicting each life history strategy metric separately as a function of SDM-suitability. LHS values were derived from the site-specific Matrix Population Model described in Table 4.1. A) survival over reproductive life span (probability) B) reproductive life span (years) C) average yearly reproductive rate D) progressive growth, i.e. the probability for individuals to transition to a bigger size the following year E) retrogression, i.e. the probability for individuals to transition to a smaller size the following year F) generation time (years). Reproductive life span, mean reproductive rate and generation time were log transformed in the models.

populations clustered at extreme SDM-suitability values. Consequently, an experimenter might have used a quadratic shape to describe the relationship between LHS and SDM-suitability (Figure S4.3.2).

4.5 Discussion

In this paper, we investigated the relationships between demography and habitat suitability as predicted by Species Distribution Models (SDM) (Guisan et al. 2017). We tested the hypothesis of a slower life cycle in harsher conditions. We found that an SDM built using environmental predictors tailored to the ecology of the species predicted a faster pace of life at higher SDM predicted suitability (SDM-suitability). An SDM built using a set of environmental predictors used for studies across multiple plant species (see for instance Broennimann et al. (2007); Petitpierre et al. (2012); Thuiller et al. (2005) produced no clear trends with suitability.

Slower pace of life at low SDM-suitability

At higher SDM-suitability, we found a shorter life span and generation length and a higher yearly rate of sexual reproduction (Figure 4.4). These trends are coherent with a shift towards a faster pace of life along the fast slow axis of plant life history strategies (Cole 1954; Salguero-Gómez et al. 2016; Stearns 1992). In addition, we find a lower rate of retrogressive growth (probability of transitioning to a smaller size class the following year). Shrinkage is known to play an important role in increasing the ability to buffer times of hardship, and therefore individual survival and longevity (Csörgő et al. 2017; Salguero-Gómez and Casper 2010). Thus, when using an SDM with predictors and fitting a species-specific model, we found a coherent pattern between six life history metrics, describing a shift towards a slower life cycle in low SDM-suitability areas. For perennial plants to delay reproduction and rely more on survival in suboptimal conditions is well documented (Harper 1977). A systematic link between low SDM-suitability and slower life cycles at the within species level would have consequences for the conservation of species. Red listing of species, for instance, relies on the use of generation length as a measure of a meaningful time frame for population declines (IUCN 2001; IUCN Standards and Petitions Subcommittee 2014). We found some support for this hypothesis in our study, with faster population turnover in higher probability of occurrence areas.

The choice of environmental predictors in SDMs

Given the extremely wide range of available SDM techniques (Norberg et al. 2019), we wanted to compare the results obtained by a generic SDM (our generic SDM) and one built specifically for the species (our species specific SDM). When using our generic-SDM technique, with predictors meant to capture the ecology of many plant species, no clear trends were detectable between SDM-suitability and life history metrics at a continental scale (Figure 4.3). Applying this same generic-SDM method on environmental predictors selected to match more specifically the ecology of the species (that is, our hybrid 1) yielded results similar to our species-specific SDM (Supplement S4.2). Therefore, the result of our swap in predictors between the two methods clearly indicate that the choice of environmental predictors is important (Supplement S4.2). When attempting to compare numerous species, previous works attempting to link SDM and demography did not focus on optimizing the choice of predictors for each studied species (Csergő et al. 2017; Thuiller et al. 2014). There are good reasons to focus on a set of generic predictors such as was done in these studies. First, it facilitates the comparability between species. Second, one major use of SDMs is to predict the effects of climate change on the future distribution of species (Csergő et al. 2017; Egan et al. 2018; Guisan et al. 2013; Scherrer, Massy, et al. 2017). This implies the projection of SDMs based on environmental predictors derived from various climate change scenarios (Moss et al. 2010). Yet, not all predictors are available under such scenarios. And finally, not all predictors are available as georeferenced layers at the same quality for all scales, as is illustrated by our result of needing to infer the suitability value from the nearest value for three of our populations in the species-specific technique. It is therefore not surprising that this approach (of using a generic set of environmental predictors across several species) has mostly been used so far. Nonetheless, it is widely known that the choice of environmental predictors in an SDM can change the quality of the predictions in terms of distribution (Mod et al. 2016; Petitpierre et al. 2017). There have been several calls to optimize environmental predictors selection for target species, especially in conservation studies (Austin 2002; Austin and Van Niel 2011; Guisan et al. 2006). Our results indicate that this step may be critical to allow for inference on life history strategies based on SDM predictions. In our study, despite attempting several land use and human exploitation predictors, precipitation seasonality seems to be the most important

predictor in our species-specific technique, which was not included in the generic-SDM (Supplement 4.2).

Density dependence and its consequences

The recruitment in our system was modelled as strongly density-dependent (Table 4.2). The recruitment model that best fitted our data represents a scenario where only a limited number of microsites or resources will be available for recruit emergence, more limiting for recruitment than the number of propagules produced (Ellner et al. 2016; Kachi and Hirose 1985; Reed et al. 2013). Adult individuals will be in competition with each other for these few recruitment opportunities. This implies a strong intra-specific competition regime, potentially due to inter-specific competition limiting the available resources. A consequence of this density dependent regime in our system is that, without perturbations, the population growth rate would quickly converge to one (constant size of the population, Supplement S4.4). Therefore, no relationship between SDM-suitability and population growth rates can be detected in our system. This matches the results of other authors, who found no relationships, or differing relationships depending on geographic areas, between population growth rates and SDM-suitability (Csergő et al. 2017; Thuiller et al. 2014). It is widely known that interactions with co-occurring species will affect the distribution and local performance of focal species (Ehrlén and Morris 2015; Holt 2009) and that biotic interactions are usually only be implicitly included in SDMs (Ehrlén and Morris 2015; Soberón and Nakamura 2009; Soberón et al. 2017). Nonetheless, density dependence and intraspecific interactions are also a form of biotic interactions, and these processes are often overlooked while inferring on population performance (particularly abundance or population growth rate) based on distribution and probability of occurrence alone (Ehrlén and Morris 2015; Holden et al. 2021). Our population models hence illustrate one type of biotic interactions occurring in the wild that could explain counterintuitive population behaviour along probability of occurrence gradients, and that SDMs fail to capture (Soberón and Nakamura 2009).

Simple models of multiple populations

Importantly, our vital rate models do not include any environmental information, and we use one single, time averaged model per site. This contrasts with outstanding work of the

second decade of the 21st century attempting to parse out the causal drivers of variance in vital rates along geographic gradients (Evans et al. 2016; Merow, Dahlgren, et al. 2014; Römer et al. 2021; Treurnicht et al. 2016; Villellas et al. 2015). In the present study, we aimed to assess the usability of SDM-suitability as a simple, but meaningful, environmental proxy to complement detailed demographic studies for the inference on demography across space (Buckley and Puy 2021; Gurevitch et al. 2016). The incorporation of environmental variables (such as temperature or precipitation) into the vital rates models was therefore contrary to our objectives. It is a general point of tension when studying population ecology across large scales that environmental predictors are replicated at the level of the site (or population), whereas demographic studies are based on the study of vital rates at the level of individuals within site (Gelman and Hill 2007). Each population (i.e., each geographical site) represents hours or days of active monitoring over the span of several years, and represents hundreds of degrees of freedom (individual observations) for population studies. It is hence understandable that over 50% of plant studies that do build full Matrix Population Models include only three or less populations (Salguero-Gómez et al. 2015). Here, we seek to develop environmentally-based proxies of population performance (Buckley and Puy 2021) in order to apply them to the hundreds of existing demographic models where we cannot assess the effect of even one environmental predictor due to lack of replication across relevant gradients. The choice of not including environmental drivers is facilitated by our use of generalized linear mixed models to capture vital rates (Bolker 2019; Bolker et al. 2009; Buckley et al. 2003; Gelman and Hill 2007). Mixed models will draw intercepts (and slopes) from normal distributions to best fit the patterns observed in each site or year (Gelman and Hill 2007; Zuur et al. 2013). This enabled us to model a slightly different relationship between vital rates and plant size in any given site and year (the random effects), without having to determine the reasons for these changes. This approach offers flexibility in the climatic relationships driving demography as it does not imply for us to choose the most important driver nor the shape of the relationship (Doak et al. 2021).

Spread of the populations

In Figures 4.3 and 4.4, we observe a cone-shaped spread of reaction in several panels. In Figure 4.3C-D or Figure 4.4A, 4.4C-E, for instance, there may be a wider breadth of reactions at higher SDM-suitability values. Two causes can lead to this observed pattern. On the one

hand, more PlantPopNet populations were sampled in high suitability areas for the species. This is to be expected, as there was no a-priori directed sampling of the selection of populations in the suitability space. Populations drawn randomly from the map without stratified sampling are likelier to come from a high probability of occurrence site (Guisan et al. 2017). On the other hand, this cone shape could be due to a higher breadth of demographic strategies in higher suitability areas, as was found by (Csergő et al. 2017). As there was no stratified sampling of the PlantPopNet populations in the suitability space, it is impossible to distinguish between these potential causes in our data, at least with 39 time-averaged observations per life history strategy metric.

4.6 Conclusions

In this study, we built spatially-replicated population models for 39 populations of the species *Plantago lanceolata* in its native range and found two key findings. First, our results support the hypothesis of a slower life cycle in populations with a lower SDM-predicted probability of occurrence. Second, that the previous findings are reliant on how SDMs were developed, with more species-specific environmental predictors showing a stronger relationship with life history strategies. When more generic predictors were used, such as those often used to infer the effects of climate change on the distribution of multiple plant species in one single study, signals were weak and not detectable. These results demonstrate that SDM predictions can provide meaningful information for life history and population performance within species, provided appropriate methodological choices.

4.7 Acknowledgements

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Chapter 5. Discussion and perspectives

5.1 Synthesis

In this thesis, we established ways forward to model multiple populations of the study organism *Plantago lanceolata* at a local, continental and global scale. By using multiple sources of information such as functional traits and occurrence data (Adler et al. 2014; Buckley and Puy 2021; Guisan et al. 2017; Gurevitch et al. 2016; Pistón et al. 2019), we provided valuable insights on spatial patterns in population performance and functionality across environmental and geographical gradients (Bohner and Diez 2020; Gurevitch et al. 2016; McGill et al. 2006; Pironon et al. 2017), and proposed ways forward for the development of macroecological population models (Buckley and Puy 2021). We will highlight some of the main findings here, and their potential impact for the inference of population performance across scales and gradients (Gurevitch et al. 2016).

5.2 Size matters

The relationship between size and fitness forms the basis of most of our understanding of the variation in individuals' life history and fitness through space (Stearns 1992; Villellas et al. 2021). Size is the most important predictor of plant fitness (Easterling et al. 2000; Salguero-Gómez and Casper 2010; Silvertown and Charlesworth 2007). The causes of variation in individual performance are expected to be multiple, and to differ across scales (Gurevitch et al. 2016; Kuppler et al. 2020; Moles et al. 2007). Yet were these changes to be mediated by a different relationship to size or its components, for instance as selective pressures differ in space, our ability to capture the effect of environmental drivers would be diminished by our inability to understand the effects of changes in size. Studies focusing on the relationship between size and vital rates across large geographic distances are therefore an important stepping stone towards a more systematic understanding of the drivers of plant demography and fitness across varying scales and environmental conditions.

In chapter 1, we established that simple size metrics such as leaf number captured patterns in vital rates similarly across populations, climatic gradients and both the native and invasive range of the species. Our study was designed to investigate whether the choice of size metric impacted our ability to capture changes in demographic output (growth, survival, flowering

probability and reproductive effort) at a global scale. In addition, we interrogated the goodness of fit of the candidate metrics across the temperature and precipitation gradients covered by PlantPopNet populations at the global scale. We found that while demographic outputs in some populations were captured with varying degrees of success, there was no consistent effect of the choice of size metric in specific areas, neither in the geographic nor the climatic space.

This is important and welcome news for the study of demography and individual performance across ever larger scales (Buckley and Puy 2021; Gurevitch et al. 2016; Smith et al. 2020; Villellas et al. 2021). The most powerful and flexible techniques to date to describe changes in fitness among individuals, within one or several populations, are continuous population models (Easterling et al. 2000; Ellner et al. 2016), or matrix projection models parametrized based on models of vital rates as a function of size (Caswell 2001; Morris and Doak 2002). Continuous population models rely heavily on the relationship between fitness and size, particularly for plants (Easterling et al. 2000; Ellner et al. 2016; Silvertown and Charlesworth 2007). The thorough investigation of the effects of the size variable on the ability to capture demography in one study organism such as *Plantago lanceolata* is a first methodological step towards the building of models of multiple populations across large scales (Römer et al. 2021; Treurnicht et al. 2016), which will hopefully provide insights allowing for other species to be modelled in the future.

Finally, the lack of effect of the choice of size metric is also important for the comparability of existing demographic datasets (Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Queded, and Wardle 2010; Salguero-Gómez et al. 2015). The collation and comparison of species average values gathered through different projects has been shown to yield powerful insights on the functionality and variety of species life history strategies, be it in their relationship to functional traits (Adler et al. 2014), the organisation of life histories and the breadth of the existing spectrum of average strategies (Salguero-Gómez et al. 2016), or their relationship to climate and phylogeny (Kelly et al. 2021). Likewise, within-species comparisons (although as of now much less developed) are likely to shed light on the many processes enabling species to adapt to varying local conditions throughout their niche, be it genetically or through plasticity (Maguire, 1973; Pironon et al. 2018; Römer et al. 2021; Smith et al. 2020; Villellas et al. 2021). These will only be possible under the

assumption that the choice of size metric to structure the population model does not affect the parametrized demographic transitions. For all these purposes, the fact that the first chapter of this PhD was so monotonously boring is incredibly good news for science.

5.2 Ways of summarizing gradients

Intraspecific demographic and functional information is rare, and most often suffers from a severe lack of spatial replication (Abeli et al. 2014; Csergő et al. 2017; Pironon et al. 2017; Salguero-Gómez et al. 2015). Yet the drivers of individual performance and fitness are multiple and interact in complex ways (Pistón et al. 2019; Römer et al. 2021). Therefore, there is a strong need to develop ways to summarize complex ecological gradients into meaningful currencies, comparable across species (Buckley and Puy 2021).

In Chapters 2, 3 and 4, we made use of environmental suitability predictions from species distribution models (Csergő et al. 2017; Guisan et al. 2017) to summarize multi-driver environmental gradients into one metric, the predicted probability of occurrence of the species. This metric offers several advantages in addition to summarizing complex gradients; it pulls information from the readily available occurrence information for species (GBIF.org 2021) and offers a common currency comparable across species (Buckley and Puy 2021; Csergő et al. 2017). Though the latter is not exploited in the present thesis (where only one species was studied), it is important for the development of future uses of SDMs to predict demography in the current, realized niche of species (Gurevitch et al. 2016; Holt 2009; Hutchinson 1957).

In Chapters 2 and 3, we investigated the ability of SDM-suitability to capture the variance in demographic processes (Chapter 2) and functional traits (Chapter 3) along a steep environmental gradient in the Swiss Alps. We found a faster life cycle in areas with higher SDM-predicted probability of occurrence (low elevation). The generation length and reproductive life expectancy were shorter, but the yearly reproductive rate was higher and populations relied less on retrogression. We demonstrated that these changes were mostly caused by a lower probability of survival in high suitability areas. Functional traits showed similar patterns, with populations producing more acquisitive, short-lived leaves (high Leaf Area and Specific Leaf Area) and more seeds per inflorescence in high suitability areas (Díaz et al. 2004, 2016; Moles 2018; Salguero-Gómez et al. 2016). In Chapter 4, we tested for the

repeatability of such a pattern (shift to slower strategies in low probability of occurrence areas) across the Eurasian native range of *P. lanceolata* (CABI 2019; Meusel and Jäger 2011). In this case, the environmental gradient captured by the SDM was not strongly linked to elevation (Baer and Maron 2019; Körner 2003). We found a similar pattern of an increased pace in the life cycle of *P. lanceolata* in high probability of occurrence areas.

There have been several calls for the use of SDM-suitability as a predictor to infer drivers of spatial variance in demography (Buckley and Puy 2021; Gurevitch et al. 2016). However, predictions of the relationship between occupancy and demography remain unclear, and mostly predicted to be species- and gradient-specific (Pironon et al. 2017). We provided evidence across two very distinct scales and ecological gradients for a shift from a slow life history in low probability of occurrence areas to a faster life cycle in high probability of occurrence areas. This pattern does not therefore seem to be strongly gradient-specific, although testing across more examples of gradients would be needed. One question remains: is this pattern species specific, or could it be expected to be generalizable to other species as well? *Plantago lanceolata* is a species of disturbed lands (Lauber et al. 2018; Sagar and Harper 1964). Its common name in one of the native languages of the area, *Spitzwegerich*, even translates in “Pointed[-leaved] king of paths” (Ganz 2014), a reference to the shape of its leaves and its main habitat (*Weg* means path in German). We could expect the species to mostly occur where disturbance is frequent, possibly with a shortened life span as a consequence. Populations could only persist where a shorter life span can be compensated by a higher seed production, the latter probably requiring good climatic and soil conditions. These patterns are compatible with our results, especially in the Alps, where we know the SDM-suitability gradient to be correlated with elevation, which in turn drives the agricultural practices in the area (Lachat et al. 2011; Randin et al. 2009), and would be specific to the ecology of the species. The species is globally linked to agriculture, to the point that its pollen is used as a marker of early human settlements (Kozáková et al. 2015). To successfully adapt such a realized niche (Hutchinson 1957; Soberón and Nakamura 2009), the species must have evolved strategies enabling it to deal with situations in which (human-induced) disturbance can cause strong reductions in life expectancy. As the species’ realized niche is linked to disturbed habitats, the species needed to adapt to faster life cycles in its optimum realized habitat. One could argue that this specificity is what drives our finding of

a faster life cycle in areas of high predicted probability of occurrence, rather than a generalizable mechanism. In this case, the relationship between SDM-suitability and Life History Strategies would only apply to species of similar ecology, or be species-specific.

However, it is not certain that disturbance would cause a lower survival in *P. lanceolata* (Villellas et al. 2021, Chapter 2), whereas there is ample evidence for species to delay reproduction and slow down their life cycle in harsh environmental conditions (Harper 1977). Increased investment into vegetative growth and reproduction was shown to strongly increase longevity and fitness in extremely challenging conditions (Ottaviani et al. 2017; de Witte and Stöcklin 2010) and *Poa alpina* was for instance shown to increase its investment in vegetative and clonal growth towards the highest elevation parts of its range (Hautier et al. 2009). Clonal patches of common grasses such as *Festuca rubra* or *Festuca ovina* can then be found of >1000 years of age (de Witte and Stöcklin 2010). If SDMs do capture the “suitability” of the environment, there is reason to believe these shifts in life history strategy could be predicted by SDM gradients. Indeed, Csergő et al., (2017) found in a study of 93 populations of 34 species that populations occurring in low SDM-predicted probability of occurrence areas relied more on the ability to retrogress to smaller sizes. These results align with the possibility of a link between slower life history and harsher SDM-suitabilities across several species and multiple gradients. More information about more species along occupancy-gradients caused by varying ecological drivers most definitely ought to be collected. Nonetheless, it is useful to ask ourselves the following: is there a potential mechanism that could provoke a slower life cycle in harsher conditions across multiple species?

A first step here is to define “harsher conditions”. Species Distribution Models tend to define harsher conditions as a low probability of occurrence or occupancy. This may differ from demographic suitability (Figure 5.1). In optimal *demographic* conditions, environmental conditions are such that all parts of the life cycle of the species can be performed optimally (Figure 5.1, panel A-B, Maguire, 1973). The population is, if not growing in size (Ehrlén and Morris 2015; Holt 2009), stable and able to buffer perturbations with ease (Capdevila et al. 2020; Reed et al. 2013). A point in the climatic niche space could deviate from optimal *demographic suitability* through either of two pathways (Figure 5.1, panel B). In the first pathway, the survival-growth part of the life cycle could be constrained (Figure 5.1B, strategy

α on panels C-D). For a population to exist where survival is constrained, one would need to have this short life span compensated by a high production of recruits (Cole 1954; Stearns 1992). In many species, especially perennial plants such as our study organism, dispersal mostly happens at the level of the propagule (but see for instance Scherrer, Stoll, & Stöcklin, 2017). A higher production of seeds could therefore imply a higher probability of dispersal (Figure 5.1C1-C2). Therefore, neighbouring habitat patches (or habitat patches accessible by the species from this point) are likely to be occupied by at least one individual of the species (Araújo, Williams, and Fuller 2002). The same is likely to occur in any habitat patches with a similar set of climatic conditions anywhere on the map. Following this reasoning, this pathway to a *low* “demographic suitability” is likely to be correlated with a *high occupancy* in the area, and therefore a *high* SDM-suitability.

The second pathway is for fecundity to be limited (Figure 5.1B, strategy γ on panels C-D). In such cases, for a population to exist, adult individuals would need to live long enough to be able to reproduce, or reproduce often enough to compensate this low reproductive output (Cole 1954; Stearns 1976, 1992). Any occurrence in those low “demographic suitability” areas of the map are likely to be of persistent populations. Propagules that could lead to a recent and transient colonization of unsuitable neighbouring habitat patches are rare (Figure 5.1C1-C2). If full colonization of all demographically suitable habitat in the area has not happened yet (Soberón and Nakamura 2009), their colonization is lower, as fewer propagules exist in those areas to reach each habitat patch. Once dispersal equilibrium has happened, transient colonization of habitat patches under the demographic habitat suitability limit (“sink populations”) would be rare, and re-colonization after the eventual disappearance of a population would be slow (Lieury et al. 2016). Consequently, this one pathway to *low* “demographic suitability” would be correlated with a *low* occupancy (and consequently SDM-suitability).

A new spatially explicit hypothesis emerges, where only part of the possible scenarios for “low demographic suitability” can be captured by SDM-suitability (Figure 5.1E). Areas of *high demographic suitability* (Figure 5.1C-D, strategies β) and *low demographic suitability due to constraints on survival* (Figure 5.1C-D, strategies α) are *both* captured by Species Distribution Models as high suitability areas. On the other hand, areas of *low demographic suitability due to constraints on fecundity* (Figure 5.1C-D, strategies γ) are linked to a low SDM-suitability.

The emerging hypothesis in Figure 5.1 could be tested using a spatially explicit model including demographic strategies and dispersal within the kernel, such as those known as dynamic range models (Schurr et al. 2012). It would be an important contribution to landscape demography and population macroecology (Buckley and Puy 2021; Gurevitch et al. 2016) to establish, refine and test such mechanistic hypotheses of the drivers of a relationship between probability of occupancy and demographic pathways.

Were this hypothesis shown to hold true, we could fine tune the applied use and implications of the powerful tool that are SDMs. At high suitability predicted by SDMs, one of two things could accordingly happen: an optimal, non-constrained life cycle where populations can rely on survival of established members as much as the reliable, steady flow of incoming new recruits, or a fast, boom and bust life history strategy, prone to dealing with disturbance or local extinctions of populations through means of (re)colonization. The following consequences would emerge: meta-populations at high SDM suitability values are likely to be able to buffer environmental changes, as is currently expected, but only if enough habitat patches are available to allow for colonisation-extinction mechanisms to come into play. If there are not enough habitat patches available, then persistence would not be guaranteed in some of the demographic pathways captured as high SDM-suitability. On the other hand, at low SDM-suitability values, populations *must* be able to rely on the high survival probability of individuals to persist. The instinctive applied use of SDM for conservation is maintained, and populations are expected to be less likely to buffer disturbance and environmental changes, unless these changes relax the pressures on the reproductive part of the life cycle. This was at least true for *Plantago lanceolata* in the two settings we studied.

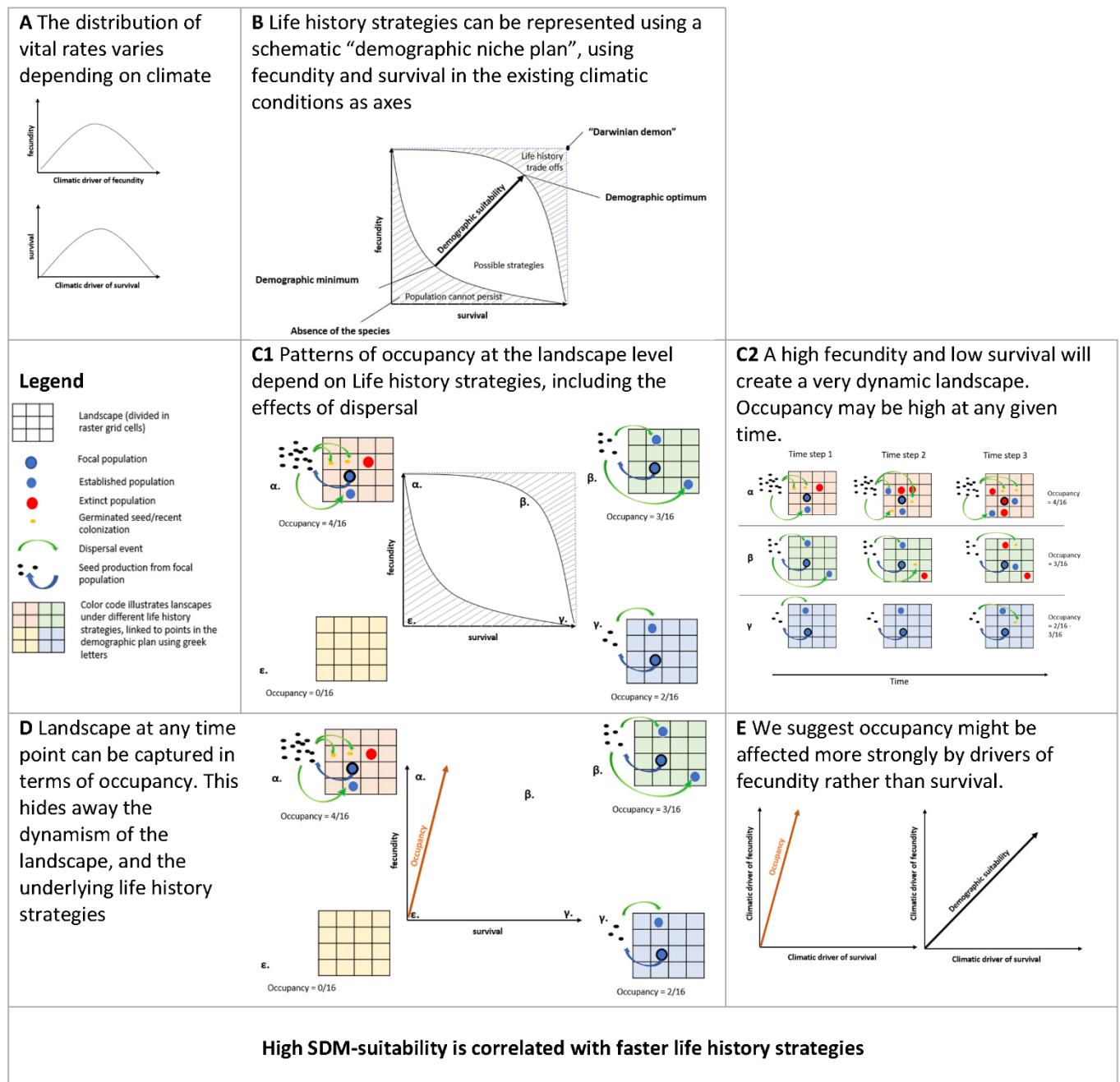


Figure 5.1: Scheme of the landscape-level hypothesis of the relationship between occupancy and life history strategies. References: panel A) Maguire, (1973); Pironon et al., (2018), panel B) our own, see Cole (1954); Harper (1977); Stearns 1992) for the use of the axes, Coste and Pavard (2020); Rees, Metcalf, and Childs (2010) for life history trade-offs, Cole (1954); Hutchinson (1957) for the lower limits of possible strategies. Panel C) our own, see Schurr et al. (2012) for a review on dynamic range models, panel D) our own, see Ehrlén and Morris (2015) for a reflexion and review on the topic, panel E) and conclusion: see the entirety of this PhD thesis. Possibilities to compare these predictions with works on other species include Baer and Maron (2019, 2020); Csergő et al. (2017); Eckhart et al. (2011).

5.3 The careful collaboration of different fields of ecology

Another powerful finding of Chapter 4 was that different SDM methods yielded different results in terms of relationship with demography. This is in agreement with the findings of other authors, especially in the context of estimating extinction risk due to climate change (Fordham et al. 2012). In Chapter 4, we could identify that not only the SDM fitting algorithm, but also the choice of predictors mattered for the ability of SDMs to predict patterns in demography. Yet it is not uncommon for SDM studies to model the distribution of large numbers of species in one single study (Scherrer, Massy, et al. 2017; Thuiller et al. 2014). It is therefore not uncommon to select predictors based on the general expectation of a relationship between environmental drivers and plant (or other taxa) ecology and dispersion in general (Csergő et al. 2017; Mod et al. 2016; Thuiller et al. 2014). On the other hand, population ecologists tend to focus on one single species. This increases the knowledge of the studied system. In our case, we gave careful consideration to the selection of predictors likely to driver the ecology of our one study organism. Our results highlight the importance of this step for the use of SDM-predictions with the objective to infer demography. We can only encourage future researchers to invest time into the acquisition and selection of meaningful environmental predictors to build SDMs.

The field of SDMs and biogeography can also largely inspire the building of demographic studies. In particular, the planning of sampling strategies and the description of selection criteria in demographic studies are often limited (Baer and Maron 2020; Oldfather 2018a; Oldfather et al. 2021). There is a known bias among demographic works to sample individuals in areas containing high numbers of individuals of the focal species (Baer and Maron 2020; Buckley, Ramula, Bomberg, Burns, Crone, Ehrlén, Knight, Pichancourt, Quested, and Wardle 2010). This creates a positive feedback loop as, the practice being common in the field, expert reviewers may not insist on sampling strategies and the adequate reporting of the criteria used for site selection for the publication of manuscripts. The choice of the sampling strategy nonetheless can have significant impacts on the ability to infer the effects of environmental drivers on studied processes (Guisan et al. 2017; Hirzel and Guisan 2002). As a concrete example, Baer & Maron, (2019) chose to establish populations in areas presenting enough individuals for the building of a population model,

discarding areas of too few individuals. In a follow up study, they investigated the relationship between SDM-suitability and abundance using the same populations (Baer and Maron 2020). The studies by Baer & Maron are full of insightful elements, and their use of multiple experiments, including transplant of individuals past the species niche limit of the species and the investigation of different sources of recruitment make it an informative study. Yet the choice of populations in the first place makes an investigation of the niche-abundance relationship hardly convincing.

In biogeographic works, and especially species distribution models, the thorough planning of a data-gathering campaign is normal. Multiple strategies are possible and described, such as random selection of points, the regular, grid based selection of points or, particularly, the random stratified approach (Guisan et al. 2017). In this approach, environmental conditions are divided in strata, with equal representation of the different categories in the final dataset, despite potentially very uneven representation in space (Baudraz et al. 2018; Dubuis et al. 2011; Dubuis, Rossier, et al. 2013). This enables the study of generalizable, unbiased processes with well-estimated species-environment response curves along entire environmental gradients. In the present work, Chapter 2 and 3 were undertaken using a random stratified design, where populations were selected randomly within known occurrences of the species in strata of SDM-suitability. In comparison, the sampling strategy in Chapters 1 and 4 was opportunistic, with collaborators selecting points in space based on accessibility (Smith, *pers. comm.*). Consequently, fewer populations stemmed from challenging conditions, and we could not infer whether the cone-shaped patterns we observed in life history strategies were due to an increased variance in life history strategies at higher SDM-suitability values, or an increase in data availability. Advancing the elucidation of the drivers of changes in the demography of species (using SDM-suitability or other predictors) will probably require the thorough rethinking of sampling strategies in future works. In general, the cross-over of different fields of ecology, particularly that of biogeographical methods into demography and vice versa, are immensely fertile (Ehrlén and Morris 2015) and we strongly recommend researchers starting a new project to invest time into the building of thorough sampling strategies, and reviewers to promote the correct documentation and report of site-selection strategies in upcoming publications.

5.3 The use of functional traits

Functional traits are expected to capture changes in the fitness of individuals (Violle et al. 2007). They are expected to be easier to measure than actual fitness components of individuals, such as its demographic pathways (the vital rates of growth, fecundity and survival). Nonetheless, studies investigating the relationship between functional traits and demographic performance typically find low correlations (McGill et al. 2006; Moles 2018; Wright et al. 2010). This makes inferring functionality based on functional traits alone a tricky endeavour (McGill et al. 2006; Salguero-Gómez et al. 2018).

In Chapter 3, we found that functional traits measured in repeated populations described a shift in life history strategy along a local, steep environmental gradient linked to elevation. Plants produced thinner and broader leaves in high suitability (\cong low elevation) areas, and many more seeds, with an uncertain trend towards a lower seed mass. These trends are compatible with a shift towards an acquisitive functional strategy (Díaz et al. 2004; Grime et al. 1997) or a faster life history strategy (Adler et al. 2014; Salguero-Gómez et al. 2016), similar to what we found studying demographic processes in Chapter 2. Most importantly, we tested for the ability of functional traits to explain survival, the principal driver of changes in life history strategies along the studied gradient (Chapter 2). We found that SLA and Leaf Area predicted survival in strong interaction with the climate. A higher SLA or Leaf Area were correlated with a lower probability of survival in low suitability (\cong high elevation) areas. In high suitability (\cong low elevation) areas, a higher Leaf Area increased the probability of survival, and SLA had no clear impact on survival.

Such results have strong implications for the use of functional traits as a proxy for individual fitness and population functionality (Salguero-Gómez et al. 2018). A strong interaction between functional traits and local climate is in agreement with the findings of several other authors in the case of interspecific comparisons (Adler et al. 2014; Kelly et al. 2021). Within a species, local climate affects the relationship between functional traits and the demographic pathways to fitness. When available to the level of microclimate, knowledge of local conditions was shown to increase the amount of variance in vital rates that can be explained by functional traits (Blonder et al. 2018). Such studies are extremely valuable, but hardly practicable at larger scales (Blonder et al. 2018). However, there is evidence for the

between population variance in functional traits to be driven by gradients in environmental drivers (Moles 2018). In our study, using just one population average trait value helped capture the ecological meaning of changes in leaf traits along the SDM-suitability gradient. This highlights that functional trait measurements remain a powerful surrogate for the inference of fitness and demographic pathways in cases or places where detailed, long-term monitoring of populations is not available. In such attempts, though, the interaction with local climatic and biotic conditions ought to be carefully taken into account (Kelly et al., 2021, Chapter 3).

5.4 Conclusions

This PhD thesis developed several methods for the inference of spatial patterns in demography and population performance across varying scales. Using one study organism, the ribwort plantain *Plantago lanceolata* L. (Penczykowski and Sieg 2021), we explored several approaches in detail, hoping to provide guidance for lesser known study organisms in future studies. The major take home messages are that environmental suitability as inferred from Species Distribution Models should be considered a useful predictor of shifts in life history strategies. It remains to be tested whether the direction of these changes will be the same for all species. We provide a hypothesized mechanism that could explain how multiple species could reliably see their life history slow down in lower occupancy areas, and suggest a way to test it. We find that functional traits are useful to infer changes in life history strategies along an elevation gradient, but that the correct inference of the evolutionary implications of changes in functional traits requires the careful consideration of local conditions. We observed that differences in the planning of the data-gathering phase between the fields of biogeography and demography hinder progress on the inference of the effects of environmental drivers on demography and population performance. We recommend the use of thorough site selection methods, and increase in the quality of the documentation of site-selection criteria in publications as promising ways forward for the fields of landscape demography and population macroecology.

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