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The 'Hutchinsonian niche' as an assemblage of demographic niches: implications for species geographic ranges

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Hutchinson defined the ecological niche as a hypervolume shaped by the environmental conditions under which a species can 'exist indefinitely'. Although several authors further discussed the need to adopt a demographic perspective of the ecological niche theory, very few have investigated the environmental requirements of different components of species' life cycles (i.e. vital rates) in order to examine their internal niche structures. It therefore remains unclear how species' demography, niches and distributions are interrelated. Using comprehensive demographic data for two well-studied, short-lived plants (*Plantago coronopus*, *Clarkia xantiana*), we show that the arrangement of species' demographic niches reveals key features of their environmental niches and geographic distributions. In *Plantago coronopus*, opposing geographic trends in some individual vital rates, through different responses to environmental gradients (demographic compensation), stabilize population growth across the range. In *Clarkia xantiana*, a lack of demographic compensation underlies a gradient in population growth, which could translate in a directional geographic range shift. Overall, our results highlight that occurrence and performance niches cannot be assumed to be the same, and that studying their relationship is essential for a better understanding of species' ecological niches. Finally, we argue for the value of considering the assemblage of species' demographic niches when studying ecological systems, and predicting the dynamics of species geographical ranges.

Introduction

The concept of the niche is fundamental to ecology and evolution (Chase and Leibold 2003, Wake et al. 2009), although it remains controversial (McInerny and Etienne 2012). Built on seminal observations and ideas (Johnson 1910, Grinnell 1917, Elton 1927 among others), G. Evelyn Hutchinson (1957) first defined it as 'an n-dimensional hypervolume […], every point in which corresponds to a state of the environment which would permit [a] species […] to exist indefinitely'. This influential approach further inspired a new generation of ecologists and biogeographers

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to represent ecological niche hypervolumes based on species occurrence points and various environmental variables (i.e. so-called 'ecological niche' or 'species distribution' models, SDMs; Elith and Leathwick 2009).

On the other hand, Maguire (1973) extended Hutchinson's definition by incorporating a demographic vision, describing the niche as a hypervolume composed of different demographic hypervolumes. To this end, he first proposed a reproduction hypervolume (i.e. the environment permitting the species to reproduce), and a survival hypervolume. From this perspective, the overall niche of a species (the population growth hypervolume) would be defined as a combination of these two hypervolumes (i.e. the environment permitting the species to survive and reproduce). This was congruent with earlier observations of distinct environmental requirements for the different demographic rates of species (Salisbury 1926, Costlow et al. 1960). In his inspiring textbook on 'Introduction to population ecology', Hutchinson (1978) described Maguire's idea as 'doubtless the most important contribution to the concept of the niche since the death of Robert MacArthur'. Indeed, such an approach based on species demographic processes would account for populations' performance and dynamics unlike a niche based on simple observations of species presence.

Subsequent authors reinforced the view that the overall niche of a species is formed by the combination of possibly divergent niches of different demographic rates at different life stages. In the context of plant community dynamics, Grubb (1977) proposed the concept of the 'regeneration niche' to describe the requirements for the replacement of the individuals of one generation by those of the next one. Such a niche definition clearly emphasized that mature and juvenile plants of the same species may not have the same environmental requirements. Similarly, Holt (2009) distinguished the requirements for populations to grow at low density (i.e. 'establishment niche') and survive at high density (i.e. 'persistence niche'). However, empirical descriptions of a complete internal demographic niche structure considering all species' vital rates and life-stages lag behind theory.

Moreover, the lack of theoretical and empirical work relating species' demographic niches to their distributions is striking (Schurr et al. 2012, Ehrlén and Morris 2015). Pulliam (2000) used landscape simulation models to examine the relationship between hypothetical demographic niches and species' distributions, but very few studies applied this approach to datasets. Several recent empirical studies demonstrated the singularity of the regeneration niche, and insisted on its importance in defining an overall species' niche and geographical distribution (Bykova et al. 2012, Bell et al. 2014, Cochrane et al. 2015). By studying the responses of different vital rates of the South African shrub species, *Protea repens*, across large environmental and geographical gradients, Merow et al. (2014) represents one of the very few analyses considering the niches and distributions of most components of a species life cycle (see also Merow et al. 2017).

Defining the internal demographic structure of the niche of a species therefore requires describing the particular arrangement of all its demographic hypervolumes in the environmental hyperspace, and characterizing the species' response within each hypervolume (i.e. how does each species' demographic rate vary across populations as a function of the variation in the environmental axes of the niche). Both Hutchinson (1957) and Maguire (1973) expected that species' demographic performance would decrease from an optimal part of the niche towards its limits. Such an expectation inspired the 'abundant-centre' or 'central-marginal' model, which predicts species' abundance or demographic rates to decline gradually from the centre towards the edge of the niche (and, consequently, from the centre to the edge of the geographical distribution) (Hengeveld and Haeck 1982, Brown 1984, see Pironon et al. 2016 for a review). However, the 'central-marginal' hypothesis has not been widely supported by field observations (Sexton et al. 2009, Pironon et al. 2016).

Several authors recently suggested that demographic compensation could explain such discrepancy (Villellas et al. 2013a, Pironon et al. 2015). Demographic compensation is the phenomenon whereby the different life-history components of a species, such as survival, growth or fecundity, change in opposite directions across populations, in response to environmental gradients. Originally proposed as a mechanism for species to maintain relatively stable population growth rates across ranges (Doak and Morris 2010), it commonly occurs in nature and may have the potential to facilitate range expansion and alter responses to climate change (Villellas et al. 2015). It is therefore important to consider all demographic niche components of a species' life cycle (and not only an occurrence, survival or regeneration niche) in order to understand the dynamics of a species' niche and geographic range.

However, not all components of the life cycle contribute equally to the population growth rate (de Kroon et al. 1986), so that the overall niche of a species should be mostly determined by the niches of the most influential vital rates. The relative importance of different vital rates can vary even among populations of a species (Morris and Doak 2005). Thus, besides analyzing variation in actual vital rates, a comprehensive way to analyze and interpret intraspecific demographic variation, and understand the whole dynamics of a species' niche, is to determine which life cycle components have a higher influence on population performance across a species' range (Caswell 2001).

Using extensive and complete demographic information for two plant species, collected during multiple years across most of their geographical and environmental ranges, we determined for the first time: 1) whether the demographic niche structure envisioned previously is confirmed by field observations, with the niches of different demographic rates (survival, growth, fecundity, and recruitment of different life stages) diverging from each other and from a niche built on species' occurrences, 2) if demographic rates decrease systematically from an optimal part of species' occurrence-based niches to their boundaries, and 3) whether considering the entire species' life cycle is necessary to capture the dynamics of the overall species niche and geographic range.

Methods

Study species

Plantago coronopus (buck's horn plantain, Plantaginaceae) is a short-lived herb with a lifespan generally ranging from a few months to five years. It is gynodioecious (i.e. can be found as female or hermaphrodite individuals) and mainly wind-dispersed and outcrossing. It has a wide distribution from the Mediterranean Basin to the coasts of southern Scandinavia, and occurs across a wide variety of habitats such as coastal prairies, sand dunes, shrublands, or human-disturbed areas. Our study only focuses on the most common subspecies *Plantago coronopus* ssp. *coronopus*, later referred to as *P. coronopus* in this manuscript.

Clarkia xantiana ssp. *xantiana* (Onagraceae) is a winter annual. Its flowers are strongly protandrous (i.e. anthers mature before stigma) and herkogamous (i.e. stigma and anthers are spatially separated), which makes it primarily outcrossing, although it is self-compatible (Eckhart and Geber 1999, Runions and Geber 2000, Moeller et al. 2011). It is mainly pollinated by specialist solitary bees and large-bodied generalists (Moeller 2005). It is narrowly-distributed, endemic to southern California, United States, where it occurs mainly on steep, sandy slopes, in blue oak-gray pine woodlands, or open grassland. Hereafter, we will refer to this subspecies as *C. xantiana*.

Demographic information

Thousands of plants were monitored for four years in each of 11 populations of *P. coronopus* in Spain, France, Denmark, Sweden, and Scotland (Villellas et al. 2013b) and 20 populations of *C. xantiana* in the Kern River drainage, California, United States (Eckhart et al. 2011) (Supplementary material Appendix 1). Although it is impossible to monitor all populations of both species across their whole ranges during multiple years and the same time period, this sampling represents one of the most extensive found in the literature (see also Doak and Morris 2010, Sheth and Angert 2017) and it captured a large part of the environmental variability across most of the species distributions. Indeed, we monitored populations across most of the latitudinal range of *P. coronopus*, except its southern margin in north Africa. For *C. xantiana*, the populations cover the northeastern half of the species' range, where populations are more frequent and accessible than in the southwestern half of the range.

To assess the niche dimensions of each species, we extracted all the vital rates (fecundity, recruitment, growth, survival) of each population from previous studies (Eckhart et al. 2011, Villellas et al. 2013b). For *P. coronopus*, survival is represented by the proportion of plants that remained alive from one year to the next, and has been measured for seedlings (s1), and small (s2), medium (s3), and large (s4) plants older than one year. We considered an age-based first stage (seedlings), since the first year is crucial for the performance of this species and shows distinct rates than the following years (JV and MBG unpubl.). Growth is the probability of growing from seedlings (g1), small (g2), or medium (g3) plants to any larger class conditional on surviving. Annual mean fecundity was estimated for seedlings (f1), small (f2), medium (f3), and large plants (f4) by multiplying the number of inflorescences of each reproductive individual by the number of seeds per inflorescence. Finally, recruitment corresponds to the number of new seedlings in a given year divided by the number of seeds dispersed the previous year (r). For further details on vital rates estimation, see Villellas et al. (2013b).

For the annual *C. xantiana*, seed survival in the seed bank was estimated during the germination period, between November and January (s1 for the first year, s3 for one year-old seeds, and s5 for two years-old seeds), and between January and October (s2 for the first year, s4 for one year-old seeds, and s6 for two years-old seeds). The mean annual seedling survivorship to fruiting was also estimated (si). Fecundity is represented by the number of fruits produced per plant (ff), and the number of seeds produced per fruit (fs). Finally, recruitment corresponds to the germination rate in the first year (r1), of one year-old seeds (r2), and of two years-old seeds (r3). For further details on vital rates estimation, see Eckhart et al. (2011).

Stochastic population growth rates (L) of each of the 11 and 20 populations of *P. coronopus* and *C. xantiana* were estimated using matrix projection models (Caswell 2001) that accounted for temporal variability and correlations among vital rates (Eckhart et al. 2011, Villellas et al. 2013b). For *P. coronopus*, we projected the populations 50 000 yr to calculate L, by randomly choosing one of the three annual matrices in each time step, assuming that each annual environmental state (i.e. each annual matrix) is independent of previous states (Caswell 2001). We used the same approach to estimating L for *C. xantiana* populations, randomly sampling from each of the annual matrices (Eckhart et al. 2011). We calculated the relative contribution of each vital rate to spatial variation in population growth rates, using a Life Table Response Experiment (LTRE) analysis (Caswell 2001, Villellas et al. 2015), which accounts for both the potential influence of vital rates on population growth rate (i.e. sensitivities; Caswell 2001) and their variation among populations. Specifically, the mean contribution (C_i) of each vital rate i across populations was estimated as $C_i = \frac{\sum_{n=1}^{N} \left| \left(x_{i,n} - \overline{x_i} \right) \times S_i \right|}{N}$, where n is the population considered, N is the total number of monitored populations, x_i is the vital rate in the considered population, $\overline{x_i}$ is the mean vital rate across all populations, and S_i is the sensitivity of the population growth rate to changes in the i-th vital rate. Sensitivities were calculated on a reference matrix for each species (obtained by averaging annual transition matrices for each population, and then obtaining a mean matrix across populations).

Environmental information

We considered different sets of environmental variables in order to characterize the ecological niches of both species.

For *P. coronopus*, we used the finest (~1 km resolution) climate, land cover and soil information available across its range. We selected eight climatic variables from the WorldClim database (Hijmans et al. 2005): annual mean temperature and precipitation, temperature and precipitation seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, maximum precipitation of the wettest month, and minimum precipitation of the driest month. We chose these eight variables in order to represent mean, variability and extremes in climatic conditions, which potentially impact the physiology of *P. coronopus*. Land cover variables were extracted from Tuanmu and Jetz (2014), which provide consensus information on the worldwide prevalence of 12 land cover classes. From this database, we selected the eight variables that vary across *P. coronopus*' distribution: evergreen/deciduous needleleaf trees, deciduous broadleaf trees, mixed/other trees, shrubs, herbaceous vegetation, cultivated and managed vegetation, regularly flooded vegetation, barren, and open water. Finally, we selected eight soil variables from the SoilGrids database (ISRIC 2013): bulk density, percentage of coarse fragments, cation exchange capacity, soil organic carbon concentration, soil pH, clay, silt, and sand content at a 2.5 cm depth. A total of 24 environmental variables were used for this species.

For *C. xantiana*, we also used the finest environmental information available (100 m resolution), extracted from Eckhart et al. (2011). In total, we employed eight climatic and geological variables measured during the demographic monitoring period. We considered five climatic variables: the mean February–June (spring; *C. xantiana*'s primary growing season) temperature and precipitation, the coefficient of variation of spring precipitation, and the mean and coefficient of variation of November–January (winter) precipitation (germination plus early growth period). Finally, we also used the three following geological variables: slope aspect and inclination, and surface material. Slope aspect is represented by the degree to which the slope faces northward (i.e. linear azimuth). We transformed the categorical variable of surface material into an ordinal variable representing an index of soil particle size (Kramer et al. 2011), with alluvium surfaces having the smallest particles (assigned value of zero), metasedimentary surfaces having intermediate particle size (assigned value of one), and igneous surfaces (granodiorite and gabbro) having the largest particles (assigned value of two). All environmental variables used for *P. coronopus* could not be applied to *C. xantiana* given their too coarse resolution, and those used for *C. xantiana* were not available across *P. coronopus* distribution.

Niche analyses

We used a multivariate, co-inertia analysis called the outlying mean index (OMI), also called 'marginality index', to characterize the structure of the niches of both species (Dolédec et al. 2000). By maximizing the variance in data points along ordination axes obtained from several environmental variables, the OMI assesses the distance between a group centroid (here, the mean habitat conditions, weighted by one of the demographic rate of a species) and the origin of the hyperspace (the mean habitat conditions occupied by the species). In the context of this study, it therefore estimates the tendency of a demographic rate to rely on a specialized environment. Unlike more traditional canonical correspondence analysis (CCA) or redundancy analysis (RDA), the OMI does not rely on expected relationships between the entity of interest (vital rates) and environment. For each species, we constructed an environmental hyperspace by considering each monitored population as a point determined by values of the environmental variables described previously. The 24 and 8 resulting axes (for *P. coronopus* and *C. xantiana*, respectively) were then reduced to the first two principal components of the OMI analyses. Built from simple occurrence points, these hyperspaces are similar to species' niches estimated by 'ecological niche' or 'species distribution' models (SDMs; Elith and Leathwick 2009).

Within these hyperspaces, we then identified distinct demographic niches for all the vital rates of the two species (s1–4, g1–3, f1–4, and r for *P. coronopus*; s1–6, si, ff, fs, and r1–3 for *C. xantiana*). To differentiate them based on the same occurrence data (i.e. the 11 and 20 monitored populations), we weighted each of these points by their associated vital rate value. Vital rates were normalized (between 0 and 1) in order to make them comparable and use positive values for weighting. Aside from the estimate of survival, growth, fecundity, and recruitment niches, we also repeated this procedure to identify overall demographic performance niches based on stochastic population growth rates (L). The OMI allowed us to identify the relative positions of all the demographic niches along the two environmental axes by measuring distances between the centroids of these niches and the hyperspace centre. Finally, we used a permutation test (1000 permutations) to examine the null hypothesis that the position of the niche centroid of each demographic rate on each of the two principal component axes does not differ from the position of the centre of the environmental hyperspace (i.e. niche defined by occurrences of the monitored populations). All of these analyses were performed using the 'ade4' package in R (R Development Core Team).

In addition to estimating the relative positions of the centroids of the different demographic niches within the environmental hyperspace, we represented their distributions across both niche and geographical spaces by relating the normalized demographic rates with the two OMI axes using multiple linear regressions. We used linear regressions for simplicity and because higher-order polynomial regressions did not improve the fit significantly. Finally, we projected these models in the niche spaces identified previously (such as in heat maps), as well as across each species' distributions. To do the latter, we first collected maps of both species

distributions from Eckhart et al. (2011) and Pironon et al. (2015). Then, we extracted the environmental conditions (24 and 8 variables used previously) at all the sites (grid cells) located within the ranges of both species. We projected these sites in the environmental hyperspace defined previously and extracted their coordinates along the two OMI axes. Finally, we projected the linear models on the OMI coordinates of each site located within the range of both species. We did not produce such spatial projections in order to predict in detail the demographic performance of the species across their ranges. Given the relatively low number of monitored populations and the impossibility of evaluating such predictions, we rather intended to illustrate conceptually what could potentially be the impact of the species' niche structures on their geographic distributions. For this reason, we also kept the normalized values of the vital rates for these analyses. The latter were performed using the 'lm' and 'predict' functions in R.

Results

The outlying mean index (OMI) analysis allowed the observation of a separation among the different demographic niches of the two species and a deviation of some of these from their respective environmental hyperspace centre. The first OMI axis explained most of the variability: 70% for *P. coronopus* and 79% for *C. xantiana*. It was mainly driven by gradients of aridity (i.e. maximum temperature of the warmest month and precipitation of the driest month) for *P. coronopus*, and gradients of spring climatic conditions (i.e. mean temperature, and mean and variation in precipitation) for *C. xantiana* (Supplementary material Appendix 2). The second OMI axis explained substantially less variation: 18% for *P. coronopus* and 9% for *C. xantiana*.

For both species, the first axis of the OMI discriminated among most of the demographic hypervolumes (Fig. 1, Supplementary material Appendix 3). For *P. coronopus*, all fecundity rates (f1–4), recruitment (r), and seedling growth (g1) deviated significantly from the centre of the hyperspace ($p < 0.05$) (Fig. 1–2, Supplementary material Appendix 3). *Plantago coronopus* had higher fecundity and juvenile growth in regions with warm and dry conditions over the year, whereas recruitment was higher in cold and wet conditions. Fecundity and recruitment were the demographic rates that contributed most to differences in population growth rate. Survival, growth of small, medium, and large individuals, and overall population growth did not diverge from the hyperspace's centre along the first OMI axis ($p > 0.05$). Finally, survival rates contributed the least to the population growth (s2–4) and diverged significantly from the hyperspace's centre along the second axis of the OMI ($p < 0.05$).

For *C. xantiana*, the number of fruits per plant (ff), first winter seed survival (s1), first year's germination (r1), and population growth (L) deviated significantly from the hyperspace's centre along the first OMI axis ($p < 0.05$) (Fig. 1–2). All of these demographic rates were higher in areas of the range with warmer and wetter springs and coarser soils, except recruitment r1, which was higher in parts of the range with contrasting conditions. The vital rates that contributed the most to the overall population growth rate were the ones found to be higher in warm and wet conditions (s1 and ff). All other vital rates (s0, s2–6, fs, r2–3, and densities) did not diverge from the hyperspace's centre along the first OMI axis ($p > 0.05$). Finally, none of the vital rates diverged significantly from the hyperspace's centre along the second OMI axis ($p > 0.05$).

None of the vital rates of the two species exhibited a unimodal distribution, with an intermediate maximum, along their hyperspace's axes (Fig. 3–4). In *P. coronopus*, linear regressions confirmed the previous observations that fecundity and growth of juveniles decreased from warm and dry to cold and wet environments (from south to north of the geographic range), whereas recruitment increased (Fig. 3, Supplementary material Appendix 4–5). Similarly, the number of fruits per plant, the first winter seed survival, and the population growth rate of *C. xantiana* decreased from warm and wet to cold and dry conditions (from west to east), whereas first year's germination increased (Fig. 4, Supplementary material Appendix 4–5). Finally, it is important to note that the remaining demographic parameters did not respond to the environmental gradients considered (Fig. 3–4, Supplementary material Appendix 4–5).

Discussion

Early studies considered the niche to be a property of the environment (i.e. a place in the environment that can support a species) (Grinnell 1917). Later, while defining the hypervolume niche, Hutchinson (1957) rather attributed it to be a property of the species (i.e. environmental requirements of a species). Although Hutchinson already had a demographic outlook in his definition of the niche, Maguire (1973) was the first to specifically attribute niches to species' vital rates (i.e. environmental requirements for survival and reproduction). Here, by reanalyzing extensive demographic information collected in the field across the whole life cycles of two herbaceous plants, we provide for the first time natural evidence of the ecological niche as an assemblage of different demographic niches.

Indeed, the niches of the different demographic rates of *P. coronopus* and *C. xantiana* do not all share the same position within the environmental hyperspace, and are therefore not completely overlapping. For instance, the environmental associations of *P. coronopus*' fecundity and recruitment are highly divergent: seed production is higher in arid regions, whereas recruitment is higher in wet ones. In *C. xantiana*, early seed survival and fruit production are both higher in regions with warm and wet springs, but germination in young seed is higher in areas with cool, dry springs (though it should be noted that, throughout the range, recruitment

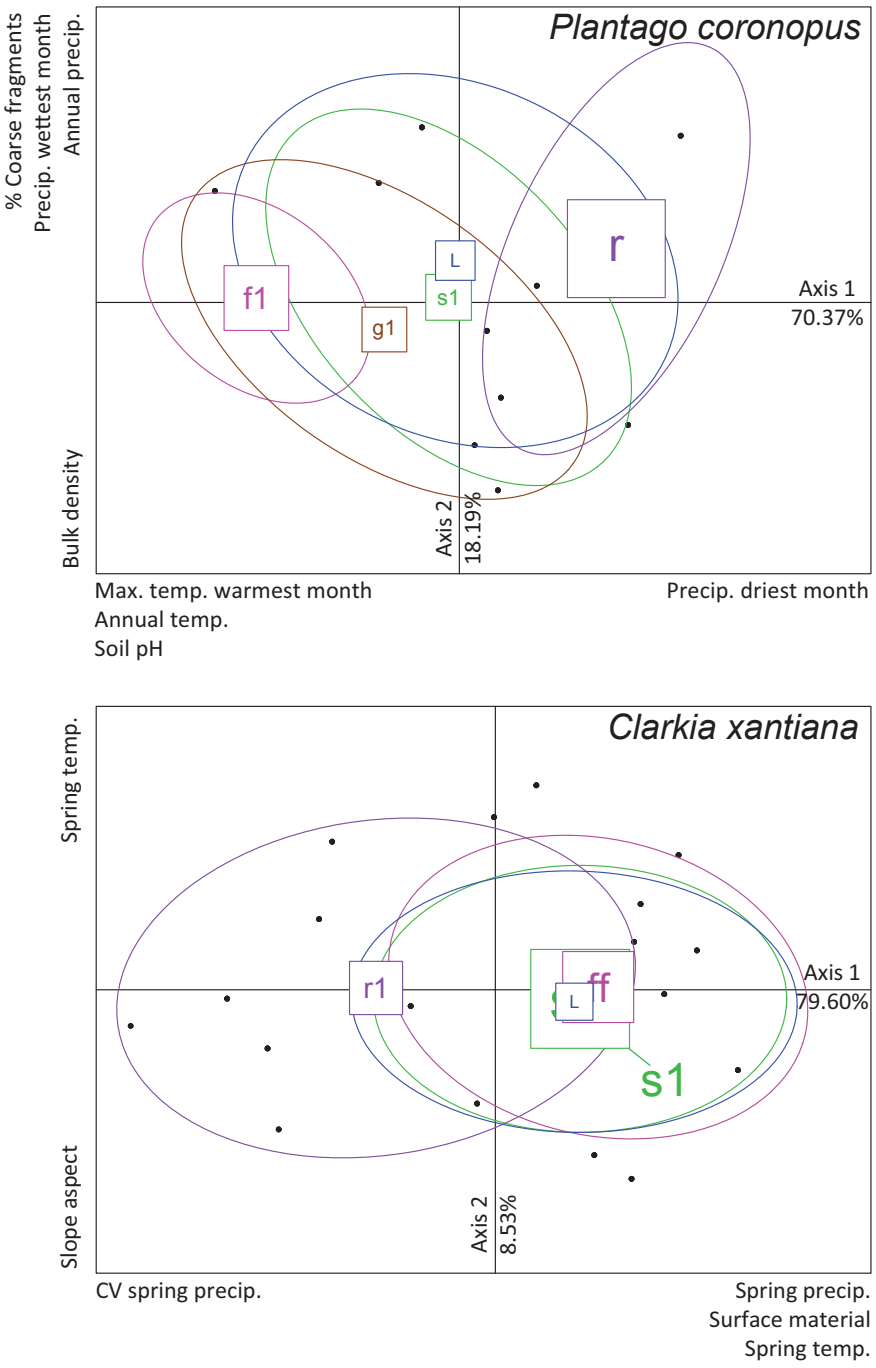

Figure 1. The internal demographic niche structures of *P. coronopus* and *C. xantiana*. The environmental hyperspaces are defined by the climatic, land use and geological variables described in the Methods. The most important variables are displayed on the two axes of the OMI analyses (canonical coefficients in Supplementary material Appendix 2). The positions of the monitored populations are represented by black dots. The different demographic niches are represented by 1.5 inertia ellipses and their centroids by squares. The size of the squares is proportional to the contribution of the vital rates to differences in population growth rate (L) and remains constant for the latter. The population growth niches (L) are represented in blue, fecundities (f) in pink, growths (g) in brown, survivals (s) in green, and recruitments (r) in purple (more details on the vital rates in the Methods). For clarity, we displayed only the survival, growth, fecundity, and recruitment rates with the highest contributions to differences in population growth rates (f1, g1, s1, r for *P. coronopus*; ff, s1, r1 for *C. xantiana*). All the demographic rates are represented in Supplementary material Appendix 3.

of young seed increases with winter rainfall, Eckhart et al. 2011). The above findings therefore support the view of Maguire (1973) and Grubb (1977) that the ecological niche of a species is made of an ensemble of demographic

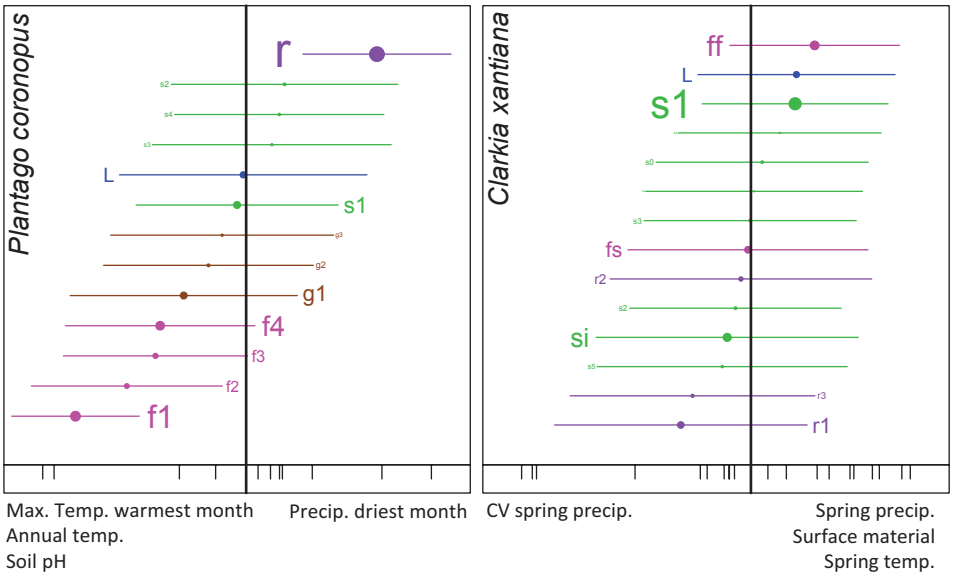

Figure 2. Position of the demographic niches along the first axes of the OMI analyses. Tick marks on the axes correspond to the positions of the monitored populations. The dark vertical line represents the position of the centre of the environmental hyperspace (i.e. centroid of the niche based on occurrence records). Dots represent the position of the centroids of the different demographic niches. The size of the dots and of the names of the demographic rates is proportional to the contribution of the vital rates to differences in population growth rates. Their size for population growths is constant. Horizontal bars represent the standard deviation (i.e. niche breadth). The population growth niches are represented in blue, fecundities in pink, growths in brown, survivals in green, and recruitments in purple (more details on the vital rates in the Methods).

niches that potentially occupy different positions along environmental axes. Given the examples of *P. coronopus* and *C. xantiana*, and additional observations of diverging environmental requirements for different vital rates made on other species (Salisbury 1926, Doak and Morris 2010, Diez et al. 2014, Sheth and Angert 2017), it is clear that such internal demographic niche structure represents a common pattern across taxa.

Several previous studies found a relatively good concordance between species occurrence and performance niches (VanDerWal et al. 2009, Martínez-Meyer et al. 2013, Van Couwenberghe et al. 2013, Osorio-Olvera et al. 2016), and others further assumed this relationship for conservation purposes (Oliveira et al. 2009). Nevertheless, such concordance has only been described for species abundance, and very few tests assessed its validity for species vital rates or population growth (Thuiller et al. 2014, Csergő et al. 2017, Merow et al. 2017). Based on an extensive analysis of the literature, Pironon et al. (2016) recently proposed that the concordance between species' occurrence and performance niches would not hold for such finer demographic processes. The results of our study confirm this proposition as most demographic niches (based on vital rates and population growth) of *P. coronopus* and *C. xantiana* diverged from their environmental hyperspace centres defined by occurrence records. We conclude that our understanding of the ecological niche would gain much from additional analyses of the relationship between occurrence and performance niches, and that in no way they should be assumed to be the same.

Hutchinson (1957), in his conceptual definition of the niche, 'supposed that all points in each fundamental niche imply equal probability of persistence of the species, all points outside each niche, zero probability of survival of the relevant species'. Interestingly, he later qualified this view stating 'ordinarily there will however be an optimal part of the niche with markedly suboptimal conditions near the boundaries'. Similarly, the so-called 'central-marginal hypothesis' later proposed that species' demographic performance should decrease from the centre towards the edges of a species niche (and geographic distribution) (Hengeveld and Haeck 1982, Brown 1984). However, our results support the conclusions of many previous empirical studies showing that all demographic parameters of a species do not systematically follow the same central-marginal model (Sexton et al. 2009, Pironon et al. 2016).

Our data allowed us to estimate the relative positions of the different demographic niches, but fell short in identifying precisely their breadths. Instead of vital rates showing linear responses to environmental axes (e.g. f1, g1 and r in *P. coronopus*, or s1 and ff in *C. xantiana*), they should in fact follow curvilinear distributions, in the view of Hutchinson (1957) and the central-marginal hypothesis. Monitoring hardly accessible populations at the southwestern edge of *C. xantiana*'s range would, for instance, help to fully identify whether its overall demographic performance follows a centered or highly skewed curvilinear distribution. At the same time, we found that some other demographic rates (most of them contributing little to the population growth

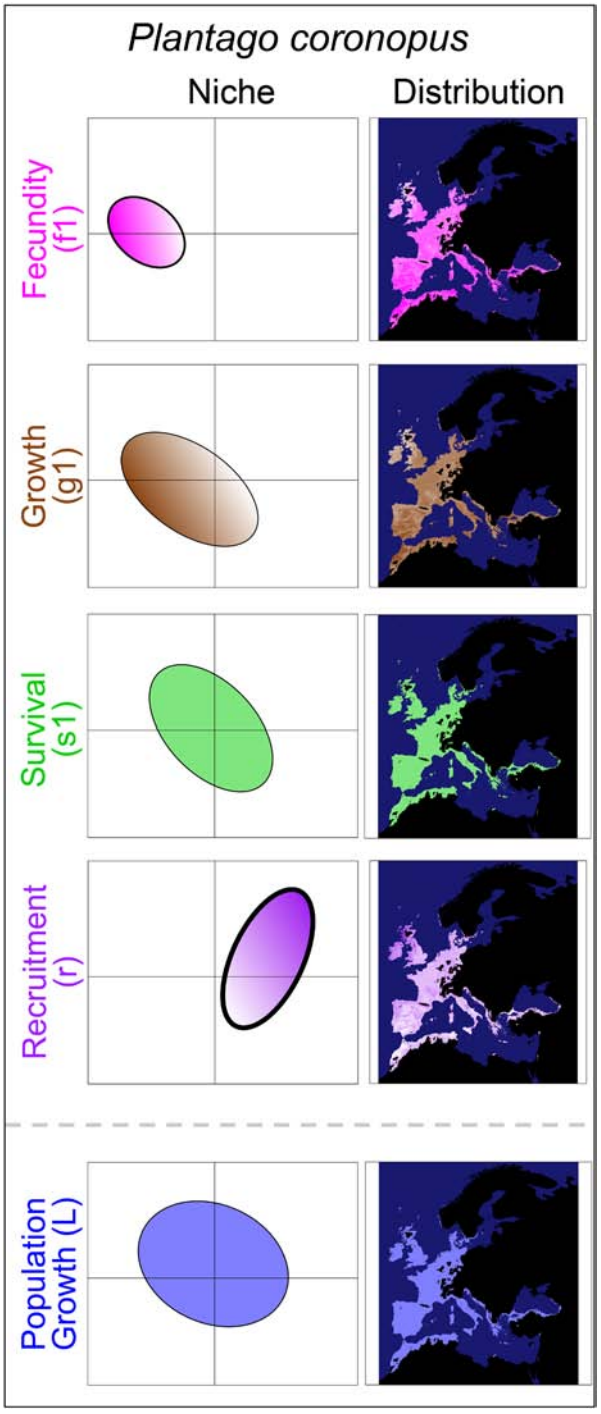

Figure 3. Modeled demographic response of *P. coronopus* within its niche and distribution. For each demographic rate, low values are represented in white and high values in pink (fecundity), brown (growth), green (survival), purple (recruitment), or blue (population growth). Colors fluctuate across niches and distributions for significant models (f1, g1, and r), but remain constant for the non-significant models (s1, L). Detailed results of the multiple linear models for all the demographic rates are given in Supplementary material Appendix 4. The width of the ellipses is proportional to the contribution of the vital rates to differences in population growth rates (the width of the ellipse of population growth rate being constant). For clarity, we displayed only the survival, growth, fecundity, and recruitment rates having the highest contributions (f1, g1, s1, r). Unsuitable areas are represented in black, and Oceans and Seas in dark blue. Maps are also provided with another color gradient in Supplementary material Appendix 5.

of both species) did not respond to the niche axes at all. Such results do not necessarily conflict with the central-marginal model, but could rather suggest that our analyses ignored niche axes that would better explain variation in these rates such as biotic interactions or other microhabitat characteristics. Species' demographic rates (survival, growth, fecundity, recruitment) might therefore decrease from one optimal part of their niches towards their boundaries, but this optimum is not always centrally located, and each rate potentially responds to different niche axes, as envisioned previously by Pironon et al. (2016). Additionally, it is important to note that our study did not account for density-dependence, which could interact with environmental factors and affect species' vital rates. If so, it could potentially reshuffle the assemblage of species demographic niches and affect their overall niche dynamics. Further studies will be needed in order to properly investigate the influence of density-dependence.

The concept of demographic compensation has recently been proposed for plant species that exhibit crossing demographic rates along environmental or geographic gradients (Doak and Morris 2010, Villellas et al. 2015), and similar trade-offs in vital rates across populations have been reported for animals (Martone and Micheli 2012). Such processes can easily be envisioned in the context of the internal demographic niche structure, as the presence of one vital rate niche at one end of an environmental axis could compensate for the absence of another, and vice-versa at the other end. A pattern of compensation could result in a constant niche of overall population growth, as found in the widespread *P. coronopus*, for which the demographically-important fecundity and recruitment rates compensate for one another at the two extremes of the aridity gradient. By contrast, the key stages of early seed survival and fruit production in the endemic *C. xantiana* have relatively similar environmental requirements. These patterns of demographic response lead the overall demographic performance of *C. xantiana* to be unbalanced towards warmer and wetter spring conditions. The niche of a species is therefore made of the arrangement of all its demographic niches, their relative contribution to the overall population growth, and the intensity of demographic compensation present among vital rates. It is thus essential that the niches of all the components of a species life cycle (survival, growth, fecundity, recruitment at different life-stages) be considered in order to fully understand its overall niche (that of population growth) and range dynamics (Doak and Morris 2010, Diez et al. 2014, Swab et al. 2015).

While collecting (experimentally or observationally) complete demographic information on any species across large environmental gradients requires a considerable

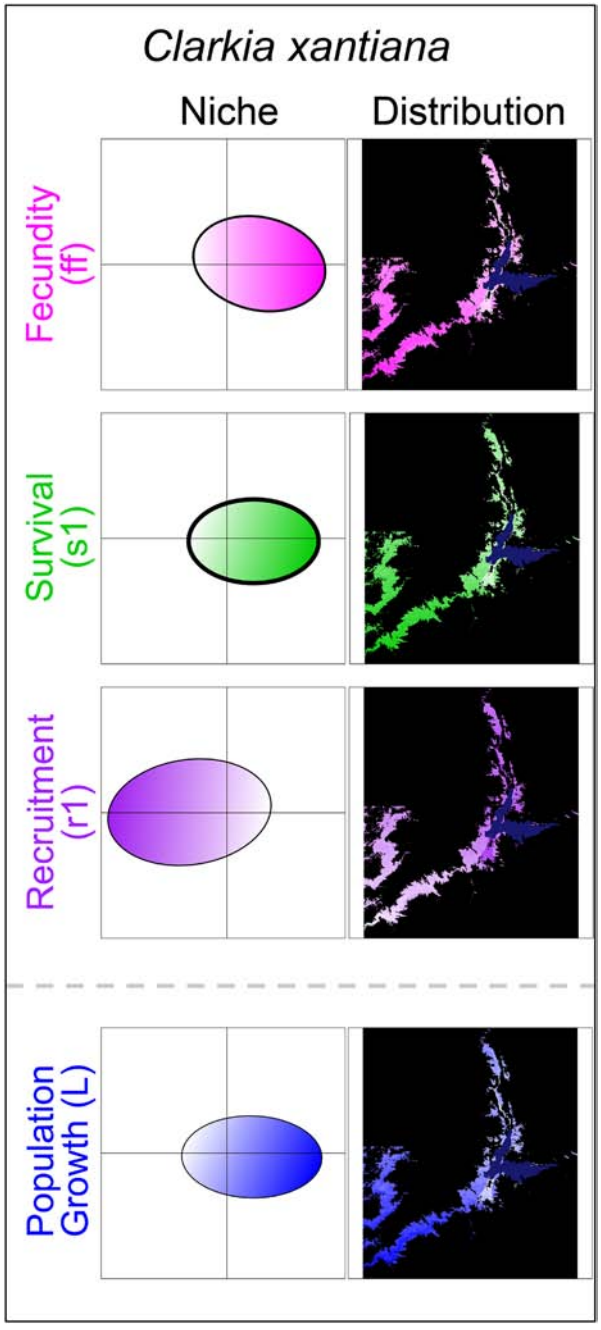

Figure 4. Modeled demographic response of *C. xantiana* within its niche and distribution. For each demographic rate, low values are represented in white and high values in pink (fecundity), green (survival), purple (recruitment), or blue (population growth). Colors fluctuate across niches and distributions for significant models (ff, s1, r1, and L). Detailed results of the multiple linear models for all the demographic rates are given in Supplementary material Appendix 4. The width of the ellipses is proportional to the contribution of the vital rates to the population growth rate (the width of the ellipse of population growth rate being constant). For clarity, we displayed only the survival, growth, fecundity, and recruitment rates having the highest contributions (ff, s1 and r1). Unsuitable areas are represented in black, and the Isabella Lake in dark blue. Maps are also provided with another color gradient in Supplementary material Appendix 5.

effort, one possible short-cut would involve focusing on the demographic rates with the strongest influence on population growth, something determined by species' life-history (e.g. short- vs long-lived plants; Silvertown et al. 1996). Another possibility would be to assume that some easier-to-measure functional traits are good proxies for quantifying demographic parameters (Adler et al. 2014). Finally, the standardized and coordinated monitoring of demographic rates of multiple populations across large spatial and temporal scales could potentially be executed within the scientific community (Fraser et al. 2012), or with the help of citizen science programmes (Devictor et al. 2010).

Plantago coronopus and *C. xantiana* have two different niche structures leading potentially to two different range dynamics: a relatively stable one for *P. coronopus*, and a west-to-east directional one for *C. xantiana* (i.e. rear-leading edge dynamic, Hampe and Petit 2005). Recently, Thuiller et al. (2014) evaluated whether the probability of occurrence computed from species distribution models (SDMs) for 108 tree species could be a relevant proxy for their intrinsic population growth rate. Overall, they found an unexpected negative correlation between these two variables and called for caution when linking demographic performance to SDM outputs. Their study accounted for the overall species' demographic niches (population growth) without considering the underlying assemblage of individual vital rates' niches and the potential for demographic compensation. Here, the centre of the hyperspace of *P. coronopus* or *C. xantiana* represents the centre of the niche defined by the occurrences of our monitored populations, which is therefore analogous to the niche centre computed by any SDM. Consequently, finding a negative relationship between the probability of occurrence and the population growth rate would mean that the centre of the overall demographic niche diverges from the centre of the hyperspace, such as is the case for *C. xantiana*. We would therefore expect that most of the 108 tree species considered in Thuiller et al. (2014) have unbalanced demographic niches (no compensation pattern), and therefore ranges with rear-leading edge dynamics (i.e. with an eroding edge at one end, and a growing, colonizing one at the other). Such unbalanced niche and range dynamics could therefore be relatively common in nature (see also Purves 2009, Bell et al. 2014, Sheth and Angert 2017).

Although predictions from SDMs might not reflect species' demographic performance, their combination with demographic data might be useful in better understanding the dynamics of species ranges. Moreover, new methods have been recently developed in order to account for the arrangement of the different demographic niches when predicting species' distributions (Pagel and Schurr 2012, Merow et al. 2014, 2017). Such demographic distribution models (DDMs), coupled with information on species' dispersal ability, could greatly improve predictions made by SDMs, and ultimately help conservation planning.

Given the recent and urgent call for the integration of demography into biogeographical studies (Wake et al. 2009, Higgins et al. 2012, Normand et al. 2014, Ehrlén and

Morris 2015), it seems particularly appropriate to go back to the basics of the niche theory to better understand how species' demographic niches are shaped in nature. In this context, the internal demographic niche structure described here has important biogeographic and ecological implications. Outstanding questions include: how is the ensemble of demographic niches impacted by temporal environmental fluctuations over the short- or long-term (also discussed by Maguire (1973))? How, in return, do responses of the demographic niches modify the environment (Chase and Leibold 2003)? How are different assemblages of demographic niches interrelated within a community (species interactions)? Does demographic compensation explain the unexpected persistence (or extinction debt, (Kuussaari et al. 2009)) of populations facing global change (Doak and Morris 2010)? All these questions, among others, would surely benefit from a more systematic demographic dissection of the niche. With this approach, "the total environment of a species, a population, or an individual is thus examined through its 'biological eyes', and its observed biological response is a function of what it 'sees'" (Maguire 1973).

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References

Adler, P. B. et al. 2014. Functional traits explain variation in plant life history strategies. – Proc. Natl Acad. Sci. USA 111: 740–745.

Bell, D. M. et al. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. – Global Ecol. Biogeogr. 23: 168–180.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.

Bykova, O. et al. 2012. Temperature dependence of the reproduction niche and its relevance for plant species distributions. – J. Biogeogr. 39: 2191–2200.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. – Sinauer Associates.

Chase, J. M. and Leibold, M. A. 2003. Ecological niches. – Chicago Univ. Press.

Cochrane, A. et al. 2015. Will among-population variation in seed traits improve the chance of species persistence under climate change? – Global Ecol. Biogeogr. 24: 12–24.

Costlow, J. D. et al. 1960. The effect of salinity and temperature on larval development of *Sesarma cinereum* (bosc.) reared in the laboratory. – Biol. Bull. 118: 183–202.

Csergő, A. M. et al. 2017. Less favourable climates constrain demographic strategies in plants. – Ecol. Lett. 20: 969–980.

de Kroon, H. et al. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. – Ecology 67: 1427–1431.

Devictor, V. et al. 2010. Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. – Divers. Distrib. 16: 354–362.

Diez, J. M. et al. 2014. Probabilistic and spatially variable niches inferred from demography. – J. Ecol. 102: 544–554.

Doak, D. F. and Morris, W. F. 2010. Demographic compensation and tipping points in climate-induced range shifts. – Nature 467: 959–962.

Dolédec, S. et al. 2000. Niche separation in community analysis: a new method. – Ecology 81: 2914–2927.

Eckhart, V. M. and Geber, M. A. 1999. Character variation and geographic distribution of *Clarkia xantiana* A. Gray (Onagraceae): flowers and phenology distinguish two subspecies. – Madroño 46: 117–125.

Eckhart, V. M. et al. 2011. The geography of demography: long-term demographic studies and species distribution models reveal a species border limited by adaptation. – Am. Nat. 178: S26–S43.

Ehrlén, J. and Morris, W. F. 2015. Predicting changes in the distribution and abundance of species under environmental change. – Ecol. Lett. 18: 303–314.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Elton, C. S. 1927. Animal ecology. – Sedgwick and Jackson.

Fraser, L. H. et al. 2012. Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. – Front. Ecol. Environ. 11: 147–155.

Grinnell, J. 1917. The niche-relationships of the California trasher. – Auk 34: 131–135.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. – Biol. Rev. 52: 107–145.

Hampe, A. and Petit, R. J. 2005. Conserving biodiversity under climate change: the rear edge matters. – Ecol. Lett. 8: 461–467.

Hengeveld, R. and Haeck, J. 1982. The distribution of abundance. I. Measurements. – J. Biogeogr. 9: 303–316.

Higgins, S. I. et al. 2012. Special issue: the ecological niche as a window to biodiversity. – J. Biogeogr. 39: 2089–2089.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – Int. J. Climatol. 25: 1965–1978.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. – Proc. Natl Acad. Sci. USA 106: 19659–19665.

Hutchinson, G. E. 1957. Concluding remarks. – Cold Spring Harb. Symp. Quant. Biol. 22: 145–159.

Hutchinson, G. E. 1978. An introduction to population ecology. – Yale Univ. Press.

ISRIC 2013. A World soil information. SoilGrids: an automated system for global soil mapping. – <http://soilgrids1km.isric.org>.
Johnson, R. H. 1910. Determinate evolution in the color-pattern of the lady-beetles. – Carnegie Inst. of Washington, Washington, D.C.
Kramer, H. A. C. et al. 2011. Environmental and dispersal controls of an annual plant's distribution: how similar are patterns and apparent processes at two spatial scales? – Plant Ecol. 212: 1887–1899.
Kuussaari, M. et al. 2009. Extinction debt: a challenge for biodiversity conservation. – Trends Ecol. Evol. 24: 564–571.
Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. – Am. Nat. 107: 213–246.
Martínez-Meyer, E. et al. 2013. Ecological niche structure and rangewide abundance patterns of species. – Biol. Lett. 9: 20120637.
Marton, R. G. and Micheli, F. 2012. Geographic variation in demography of a temperate reef snail: importance of multiple life-history traits. – Mar. Ecol. Prog. Ser. 457: 85–99.
McInerny, G. J. and Etienne, R. S. 2012. Ditch the niche – is the niche a useful concept in ecology or species distribution modelling? – J Biogeogr. 39: 2096–2102.
Merow, C. et al. 2014. On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. – Ecography 37: 1167–1183.
Merow, C. et al. 2017. Climate change both facilitates and inhibits invasive plant ranges in New England. – Proc. Natl Acad. Sci. USA 114: E3276–E3284.
Moeller, D. A. 2005. Pollinator community structure and sources of spatial variation in plant–pollinator interactions in *Clarkia xantiana* ssp. *xantiana*. – Oecologia 142: 28–37.
Moeller, D. A. et al. 2011. Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. – Ecology 93: 1036–1048.
Morris, W. F. and Doak, D. F. 2005. How general are the determinants of the stochastic population growth rate across nearby sites? – Ecol. Monogr. 75: 119–137.
Normand, S. et al. 2014. Demography as the basis for understanding and predicting range dynamics. – Ecography 37: 1149–1154.
Oliveira, G. de et al. 2009. Conservation biogeography of mammals in the Cerrado biome under the unified theory of macroecology. – Acta Oecol. 35: 630–638.
Osorio-Olvera, L. A. et al. 2016. Sobre la relación entre idoneidad del hábitat y la abundancia poblacional bajo diferentes escenarios de dispersión. – Rev. Mex. Biodivers. 87: 1080–1088.
Pagel, J. and Schurr, F. M. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. – Global Ecol. Biogeogr. 21: 293–304.

Supplementary material (Appendix ECOG-03414 at <www.ecography.org/appendix/ecog-03414>). Appendix 1–5.

Pironon, S. et al. 2015. Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? – Global Ecol. Biogeogr. 24: 611–620.
Pironon, S. et al. 2016. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. – Biol. Rev. doi: 10.1111/brv.12313
Pulliam, H. R. 2000. On the relationship between niche and distribution. – Ecol. Lett. 3: 349–361.
Purves, D. W. 2009. The demography of range boundaries versus range cores in eastern US tree species. – Proc. R. Soc. B 276: 1477–1484.
Runions, C. J. and Geber, M. A. 2000. Evolution of the self-pollinating flower in *Clarkia xantiana* (Onagraceae). I. Size and development of floral organs. – Am. J. Bot. 87: 1439–1451.
Salisbury, E. J. 1926. The geographical distribution of plants in relation to climatic factors. – Geogr. J. 67: 312–335.
Schurr, F. M. et al. 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. – J. Biogeogr. 39: 2146–2162.
Sexton, J. P. et al. 2009. Evolution and ecology of species range limits. – Annu. Rev. Ecol. Evol. Syst. 40: 415–436.
Sheth, S. N. and Angert, A. L. 2017. Demographic compensation does not rescue populations at a trailing range edge. – bioRxiv: 117606.
Silvertown, J. et al. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. – Conserv. Biol. 10: 591–597.
Swab, R. M. et al. 2015. The role of demography, intra-species variation, and species distribution models in species' projections under climate change. – Ecography 38: 221–230.
Thuiller, W. et al. 2014. Does probability of occurrence relate to population dynamics? – Ecography 37: 1155–1166.
Tuanmu, M.-N. and Jetz, W. 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. – Global Ecol. Biogeogr. 23: 1031–1045.
Van Couwenberghe, R. et al. 2013. Can species distribution models be used to describe plant abundance patterns? – Ecography 36: 665–674.
VanDerWal, J. et al. 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. – Am. Nat. 174: 282–291.
Villellas, J. et al. 2013a. Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus*. – Ecography 36: 136–145.
Villellas, J. et al. 2013b. Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb. – Ecology 94: 1378–1388.
Villellas, J. et al. 2015. Demographic compensation among populations: what is it, how does it arise and what are its implications? – Ecol. Lett. 18: 1139–1152.
Wake, D. B. et al. 2009. Biogeography, changing climates, and niche evolution. – Proc. Natl Acad. Sci. USA 106: 19631–19636.