DEMOGRAPHY BEYOND THE POPULATION

Advancing environmentally explicit structured population models of plants

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Summary

1. The relationship between the performance of individuals and the surrounding environment is fundamental in ecology and evolutionary biology. Assessing how abiotic and biotic environmental factors influence demographic processes is necessary to understand and predict population dynamics, as well as species distributions and abundances.
2. We searched the literature for studies that have linked abiotic and biotic environmental factors to vital rates and, using structured demographic models, population growth rates of plants.
3. We found 136 studies that had examined the environmental drivers of plant demography. The number of studies has been increasing rapidly in recent years. Based on the reviewed studies, we identify and discuss several major gaps in our knowledge of environmentally driven demography of plants. We argue that some drivers may have been underexplored and that the full potential of spatially and temporally replicated studies may not have been realized.
4. We also stress the need to employ relevant statistical methods and experiments to correctly identify drivers. Moreover, assessments of the relationship between drivers and vital rates need to consider interactive, nonlinear and indirect effects, as well as effects of intraspecific density dependence.
5. *Synthesis.* Much progress has already been made by using structured population models to link the performance of individuals to the surrounding environment. However, by improving the design and analyses of future studies, we can substantially increase our ability to predict changes in plant population dynamics, abundances and distributions in response to changes in specific environmental drivers. Future environmentally explicit demographic models should also address how genetic changes prompted by selection imposed by environmental changes will alter population trajectories in the face of continued environmental change and investigate the reciprocal feedback between plants and their biotic drivers.

Key-words: demography, distribution, environmental change, environmental drivers, environmental stochasticity, non-stationary environments, plant population and community dynamics, stage-structured models, vital rates

Introduction

Quantifying the links between environmental factors and population growth rates is fundamental to understanding and predicting abundances and distributions, to elucidating the mechanisms by which natural selection operates and to making informed management decisions for species in changing environments. Yet, much of the existing theory that attempts to explain how environmental variation will affect the rate of population growth does not consider which environmental factors cause vital rates (survival, growth, reproduction and recruitment) to vary in space and time (Lewontin & Cohen 1969; Tuljapurkar 1990; Caswell 2001; Crone 2016). Instead, when calculating stochastic population growth rates, vital rates are assumed to have stationary distributions with fixed means, variances and covariation between rates. While this methodology has greatly enhanced our general understanding of how environmental variability will affect populations, its

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applicability to the real and pressing problem of predicting how populations will respond to ongoing environmental changes is limited. Without identifying which environmental factors are most responsible for differences in vital rates, we cannot begin to predict the population consequences of anticipated future changes in, for example, climate, disturbance, habitat fragmentation and the introduction of species. The assumption that vital rate distributions are stationary breaks down in the face of ongoing changes, in which the means and variances, and even the covariances, of vital rates are likely to change as a consequence of changes in the environmental factors that govern these rates. The ability to investigate population dynamics in non-stationary environments by allowing the environmental factors that shape demography to change over time is an essential ingredient for predicting the consequences of a continually changing world.

Consequently, an attractive alternative to stochastic population models with stationary vital rate distributions is to identify the relationships between the vital rates and specific environmental factors (hereafter 'drivers') that cause vital rates to vary. For plant populations, important drivers of vital rates may be abiotic factors (e.g. climate, soil nutrients, and natural or anthropogenic disturbances such as fires, hurricanes and mowing) or biotic factors (e.g. competitors, herbivores, pathogens and mutualists such as pollinators, mycorrhizal fungi and rhizobial bacteria). Once we have identified the relationships between vital rates and environmental drivers, we can use future values of the drivers to predict the vital rates and thus the change in population sizes and geographical distributions of species in the future (Merow *et al.* 2014; Ehrlén & Morris 2015). Applying such environmentally explicit demographic models to multiple co-occurring species also provides a means to predict how interspecific differences in responses to particular drivers will shape the relative abundances and continued coexistence of species in communities (Adler, Dalgleish & Ellner 2012). Moreover, differences among individuals in traits that govern their responses to particular drivers are the grist for natural selection, and such traits may thus be essential for understanding how evolutionary change will alter the future trajectories of populations experiencing environmental changes (Knight, Barfield & Holt 2008).

For threatened species, environmentally explicit models have the advantage of identifying particular factors that could be managed to improve the conservation status of the species. More than 20 years ago now, Graeme Caughley (1994) argued for a perspective on species conservation in which such knowledge is necessary, stating 'The declining-population paradigm ... focuses on ways of detecting, diagnosing and halting a population decline. By this paradigm the problem is seen as a population in trouble because something external to it has changed, the current size of the population being of no great relevance'. In a world that is to an ever-increasing extent characterized by anthropogenic, directional environmental change, linking population dynamics to changes in such external factors has clearly become a major task for conservation.

Because of the growing realization of these advantages of environmentally explicit population models, many

demographic studies in recent decades have examined how particular abiotic or biotic drivers affect one or more vital rates in populations structured by size, age or life stage. Because structured populations have multiple vital rates, and because those rates do not contribute equally to the overall rate of population growth, for such organisms structured population modelling should be considered as an essential tool for providing a mechanistic understanding of the effects of changing drivers on one to many vital rates, and for translating those effects into the rate of population growth. Projection matrix models and integral projection models (IPMs) have become standard tools to represent the demography of organisms with stage-structured life cycles, such as plants (e.g. Griffith *et al.* 2016). Here, we review all the papers we could find, published in the last 20 years (1995–2015), that quantified the impact of one or more environmental drivers on one or more vital rates for plant populations, and then used a structured population model to evaluate impacts on the population growth rate.

Overall, we find that much progress has been made and that our knowledge of the environmental determinants of plant demography is rapidly increasing. Nonetheless, major gaps in our knowledge remain. The major part of the paper focuses on some important limitations of much of this recent work, including studies of our own, and how future studies could be designed to further improve our ability to link vital rates and population growth rates to environmental drivers. In particular, we discuss the importance of examining relevant factors over appropriate spatial and temporal scales, the need to complement correlative studies with experimental manipulations, the limitations of past experimental studies and the potential advances to be made by incorporating effects of intraspecific density, indirect effects of environmental changes and nonlinear and interactive effects of drivers. We also identify some directions where we see exciting future possibilities to develop demographic models for plants: in particular models that account for current genetic variation, feedback effects of environmentally induced genetic changes, and reciprocal feedbacks between plants and their biotic and abiotic drivers.

Literature review

We performed a literature survey of peer-reviewed scientific articles presenting results of empirical studies of vascular plants in which the effect of one or several environmental drivers on vital rates and the structured population growth rate had been estimated. We searched Web of Science (http://www.webofknowledge.com) using the search: TS = (plant* OR tree*) AND TS = (demographic model OR demography OR projection matrix OR integral projection model OR stage-structured model OR individual-based model) AND TS = (environmental factor* OR environmental driver* OR abiotic factor* OR biotic factor* OR herbivory OR competition OR pollination OR seed predation OR light availability OR disturbance). In addition, we searched citation lists from previous reviews on plant demographic studies (Menges 2000; Maron & Crone 2006; Crone *et al.* 2011). Lastly, we added a

number of studies of which we knew but that were not identified using the above methods. We included only studies published or in press in the last 20 years (from January 1995 to May 2015) that used demographic models covering the whole plant life cycle and that estimated population growth rate using structured population models. Our review is almost certainly not exhaustive, as we were unable to design a literature search that would find all the relevant papers of which we knew, and we did not include other relevant studies published as book chapters. Nevertheless, the studies we found should provide a good indication of how studies examining relationships between environmental drivers, vital rates and population growth rates have been carried out in the recent past.

To regard a study as linking an environmental driver to vital rates or population growth rate, we used the criterion that the relationship should be based on at least two levels of one or several specified environmental factors and at least two corresponding estimates of vital rates and the population growth rate. We included three types of studies: (i) studies that obtained a quantitative measure of the driver across years or sites and typically regressed vital rates against that driver; (ii) studies (often experimental) that involved categorical levels of a putative driver (e.g. presence vs. absence of herbivores, or ambient vs. elevated levels of nitrogen) and typically tested for an effect of the driver using a categorical test (e.g. a t-test); and (iii) studies that combined sites and years to reconstruct a chronosequence of time since disturbance to examine how disturbance affected demography. We did not include studies that examined 'habitat types' when the environmental factors that differed between habitats were not identified. We did, however, include studies that compared ambient (but unquantified) levels of herbivory with no herbivory. Lastly, we did not include studies that examined effects of harvesting only. Our survey focused on studies and not on species, so studies including more than one species were counted once. If two papers clearly used the same species in the same place (often using the same population model to examine effects of different drivers), we combined them as one 'study' in our review. Most of the studies focused on perennial plants, but we included studies of annuals if they used a structured model (e.g. if they tracked age classes in the seed bank).

For each study, we extracted the following information: (i) study species, (ii) spatial and temporal replication, (iii) environmental drivers considered, (iv) whether the levels of the drivers were quantified, (v) whether driver effects on underlying vital rates were examined (vs. whether only effects on population growth were quantified), (vi) whether LTRE analysis (or equivalent) was performed to better understand how driver effects on vital rates affected population growth, (vii) whether the study included any kind of experimental manipulation of the driver, (viii) whether the study accounted for effects of intraspecific density, (ix) whether the study accounted for indirect effects, (x) whether the study accounted for interactive effects of two or more drivers, (xi) whether the study considered nonlinear effects of the driver(s) on vital

rates or the population growth rate, (xii) whether reciprocal feedbacks with biotic drivers were considered, and (xiii) whether the possibility that the vital rate/driver relationship might evolve was assessed. The criterion for regarding a study as including effects of intraspecific density was that some measure of density was included as an additional predictor in a regression of the vital rate against the environmental drivers, or at least that some test for effects of density on the vital rate was included. A study was only considered to include indirect effects of a given driver if the direct effects were also assessed simultaneously. For example, disturbances such as fire often have indirect positive effects on fire-adapted species by reducing competition with other plants. However, we did not classify most fire studies as quantifying indirect effects, because they did not measure effects of fire on competitor abundance and effects of competitor abundance on the focal plant's vital rates. The criterion we used to regard studies as having examined interactive effects was that the linear model for the vital rates included an interaction term involving two or more environmental factors. Similarly, the criterion for nonlinear relationships was that the fit of nonlinear functions (e.g. quadratic relationships) was assessed for individual vital rates or population growth rates vs. the driver. Studies finding nonlinear effects because of changes in population structure or in sensitivities, or because of indirect effects, were thus not counted. Drivers examined were classified into six different driver 'types': (i) climatic drivers (e.g. temperature and precipitation), (ii) abiotic drivers not measuring climate directly (e.g. soil nutrients and organic matter), (iii) competitive interactions with other plant species (including effects of canopy cover and vegetation biomass), (iv) disturbance (e.g. fires, hurricanes, fragmentation, land management in terms of grazing and mowing regimes, and succession after disturbance [studies of succession were included if they estimated the actual time since disturbance, but were not included if they referred only to 'early' vs 'late' in succession]), (v) herbivory (including seed predation and grazing if the focal plant species was a preferred food plant; otherwise grazing was classified as a disturbance), (vi) mutualistic interactions (including pollinators, mycorrhizas and defending ants) and (vii) pathogens.

Review results

In total, we found 136 studies that met our criteria (Table S1 in Supporting Information). The number of studies increased from 2.6 per year during 1995–1999 to 10.6 per year in 2010–2014 (Fig. 1).

The number of annual transitions per study ranged from 1 to 29, but the distribution was highly right-skewed, and the median was only three transitions. Similarly, the number of populations per study varied from 1 to 63 (Table S1), but the median number of populations per study was only 2. It is worth noting, however, that comparing the number of populations between studies was difficult, both because different studies use different definitions of what constitutes a population (in Table S1, we equated 'site' with population in most

cases) and because definitions of sites and populations were not always clearly specified in the papers.

The two drivers most often investigated in demographic studies in the past two decades are herbivory (47 studies) and disturbance (45 studies), 25.8% and 24.6% of all drivers examined, respectively (Table 1). This result reflects the connection between the plant demography literature and the plant–animal interaction literature, in which a major goal is to quantify the impacts of natural enemies on plant populations in order to quantify the potential fitness benefits of plant defences or to gauge the efficacy of biological control agents. It also indicates a long tradition in plant ecology of studying the demographic effects of fire, the predominant disturbance in the studies we reviewed.

Of the 136 studies in Table S1, 96 studies (70.6%) examined only one type of driver. Of course, this does not mean that we only know about the impact of a single driver for all of these species, as different drivers may have been examined in different publications, and in some cases, a single study examined more than one driver of the same type.

A surprising outcome of our review of published studies is that the impact of biotic drivers, particularly herbivory and competition, has received more attention in the demography literature (80 studies, 47.3% of all drivers examined; here we have omitted biotic disturbances such as grazing) than have abiotic drivers, mostly climate and soil characteristics (45

studies, 26.9% of drivers examined). A total of 45 studies (24.6% of drivers examined) quantified effects of disturbance. This result is in sharp contrast with the literature that has used species distribution models to predict future geographical ranges of species under climate change, which has focused almost exclusively on abiotic drivers and largely ignored both biotic drivers and disturbance. Mutualist effects were investigated in 10 studies, representing only 5.5% of the driver types examined in the 136 studies, and only two studies (1.1%) investigated pathogens as a driver.

Across the 136 studies, there were 188 cases that we could classify as to whether the driver was experimentally manipulated and the level of the driver was quantified (some of these cases involve different aspects of the same type of driver, so the total here does not equal the total in Table 1). In less than half of these cases (71 of 188) was the level of the driver quantified; in the other cases, drivers were excluded or elevated experimentally or natural variation in the presence/absence of the driver was exploited, without quantifying the actual level of the driver in the 'present' or 'ambient' scenario. Not surprisingly, a significantly lower proportion of the experimental cases (12 of 71 cases, or 16.9%) quantified driver levels, compared to cases that employed a purely correlational approach (59 of 117 cases, or 50.4%; Fisher's exact test: $P = 3.0 \times 10^{-6}$).

Researchers used a variety of response variables to assess the influence of potential drivers (Table S1). Seven studies (5.1%) performed no formal statistical tests for driver effects that we could discern and 6 studies (4.4%) tested for effects on only one vital rate (and not also on the population growth rate), but 100 studies (73.5%) tested effects on two or more vital rates or matrix elements. Forty-five studies (33.1%) tested for differences in deterministic population growth rate (λ) among plots or populations that differed in the driver. A wide array of other response variables (including stochastic population growth rate λ_s, entire matrix elements, transient population growth rate, even dispersal distance) was also assessed.

To assess overall effects of the drivers on population growth, 114 (83.1%) of the 136 studies in Table S1 used projection matrices, 22 (16.2%) used IPMs, and one used an individual-based model. The metric of population growth was λ in 120 (88.2%) studies, λ_s in 27 (19.9%) studies and extinction probability/time in 19 (14.0%) studies. Other metrics included transient population growth rate, population size and invasion speed. To further explore the mechanisms underlying overall driver effects, 58 (42.6%) studies used LTRE analysis.

In summary, our review of published plant demographic studies from the past two decades shows that a wide range of drivers has been examined for a diversity of plants and using a variety of approaches, and highlights the fact that we have now learned quite a bit about the influence of several of these drivers, notably herbivory, competition, disturbance, climate and soil characteristics. Nevertheless, significant gaps in our knowledge remain. We now discuss nine aspects of plant demographic studies that we think are important to consider to fill these gaps (Table 2, Fig. 2).
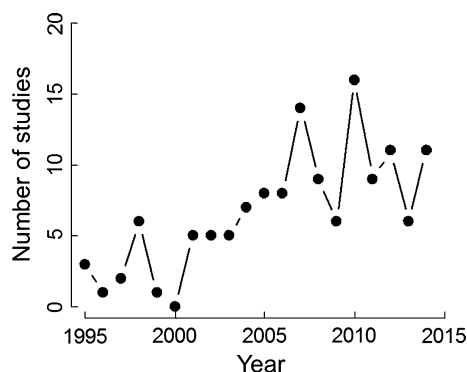

Fig. 1. The number of published studies in each of the past 20 years that examined the impact of environmental drivers on vital rates and population growth rates of structured populations. (Two studies published in 2015 by the time of writing were excluded).

Table 1. The number of times each type of environmental driver was examined in the studies listed in Table S1. The sum of cases (181) exceeds the number of studies (136), because some studies included more than one driver type

| Driver type	Number of cases
Herbivory	47
Disturbance	45
Competition	29
Climatic factors	28
Other abiotic factors	22
Mutualists	10
Pathogens	2

Table 2. Nine challenges associated with the identification of environmental drivers of plant population dynamics identified in this article, recommendations for how to deal with those challenges and examples of studies that have addressed parts of the challenges

Challenge	Recommendation	Examples of studies
1. Vital rates are simultaneously influenced by multiple drivers	Measure multiple drivers and use appropriate statistical techniques to assess their relative importance (AIC, lasso regression, etc.)	Eckhart *et al.* (2011), Dalgleish *et al.* (2011), Nicolè *et al.* (2011), Adler, Dalgleish & Ellner (2012), and Louthan *et al.* (2014)
2. Data from a large number of populations or many years may often be difficult to collect	Use mixed model regression to efficiently utilize both temporal (among-year) and spatial (among-population) variation to assess effects of drivers	Doak & Morris (2010), Eckhart *et al.* (2011)
3. Observed correlations between drivers and vital rates may not reflect causal relationships	Supplement correlative approaches with experimental manipulations	Fröborg & Eriksson (2003), Ehrlén (2003), Dangremond, Pardini & Knight (2010), Scanga (2014)
4. Relationships between drivers and vital rates depend on intraspecific densities	Measure intraspecific densities and explore effects of density and drivers simultaneously in statistical models, or manipulate densities experimentally	Gornish (2013), Dahlgren, Ostergard & Ehrlén (2014)
5. Environmental factors may influence vital rates both directly and indirectly, via other environmental factors and biotic interactions	Assess both the direct effects and indirect effects via different paths leading from a focal driver to vital rates	Kolb, Leimu & Ehrlén (2007), Adler, Dalgleish & Ellner (2012), von Euler, Ågren & Ehrlén (2014)
6. The effect of an environmental driver on vital rates may depend on the level of other drivers	Design studies so that interactive effects among drivers on vital rates can be examined	Maschinski *et al.* (2006), Nicolè *et al.* (2011), Diez *et al.* (2014)
7. Relationships between drivers and vital rates may be nonlinear	Strive to include extreme values of drivers and use regression models	Doak & Morris (2010), Diez *et al.* (2014), Scanga (2014)

(continued)

Table 2. (Continued)

Challenge	Recommendation	Examples of studies
	that allow nonlinear relationships	
8. Effects of biotic drivers on plant vital rates may feedback to the driver	Build reciprocal feedbacks between plants and their biotic drivers into population models	Adler, Dalgleish & Ellner (2012)
9. Drivers may induce evolutionary changes in plant populations	Incorporate evolutionary responses to changes in environmental drivers into population models	Rose, Louda & Rees (2005), Knight, Barfield & Holt (2008)
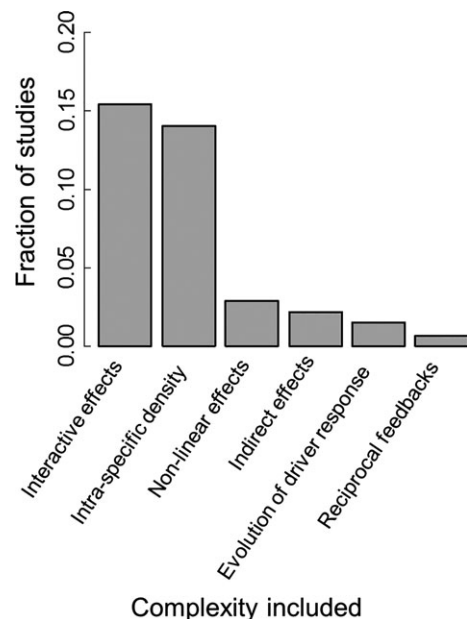
Fig. 2. The fraction of 136 studies examining the effects of environmental drivers of plant demography, listed in Table S1, that addressed six different complexities in assessing the relationship between drivers and vital rates.

Under-explored drivers and relative impacts of multiple drivers

Papers that have identified environmental drivers of demography rarely provide much information about how the driver or suite of drivers was chosen for investigation. From our own work, we suspect that demographers most often base their decision about which drivers are likely to be most important, and thus most worthy of investigation, on their knowledge of the ecology of the species and the ecosystem it inhabits. For example, for desert plants that possess apparent adaptations for drought tolerance (e.g. small or fleshy leaves, deep roots

or an annual life history with a long-lived seed bank), precipitation or soil moisture is an obvious choice for an abiotic driver likely to be important (Martorell 2007; Eckhart *et al.* 2011). For arctic or alpine plants, temperature, snow depth and growing season length (e.g. snow-free period) are equally obvious choices (Doak & Morris 2010; Griffith & Loik 2010). For plants in fire-prone ecosystems, time since the last fire is likely to be an important driver of demography (e.g. Menges & Quintana-Ascencio 2004). To the extent that multiple drivers have been examined, they are often ones that might be expected a priori to be causally related (e.g. the effect of precipitation is influenced by slope or aspect (Nicolè *et al.* 2011), or by soil permeability). Visual evidence of interspecific interactions (e.g. herbivore damage or pathogen attack) suggests biotic drivers worthy of study. An obvious limitation of focusing on the drivers that are, a priori, most likely to be important is that we may fail to collect the data on other potential drivers to evaluate whether the a priori ones really do exert more influence on the vital rates, and this failure may leave us with an incomplete picture of the full set of drivers. Reliance on visual evidence of interactions may cause us to miss important drivers that are not easily observed (e.g. fungal pathogens in the soil that affect seed survival). Only two of the studies in Table S1 examined effects of pathogens, and none quantified below-ground biotic factors (e.g. root pathogens, mycorrhizal fungi or rhizobial symbionts).

Of course, collecting data on many potential drivers, especially ones not easy to observe, may not often be feasible, and we may have little choice but to rely on natural history knowledge to determine which drivers are likely to be most important. In addition, examining multiple potential drivers that lack an a priori reason to suspect they might be important could be risky, as it may increase the chance that we accept as 'drivers' factors that are non-causally correlated with vital rates.

If we do manage to obtain measures of multiple potential drivers, we would need a protocol to determine which of them actually exert a significant influence on vital rates. One way to do this is to use information from multiple populations. Several studies in Table S1 combined data among spatial locations that differed in levels of environmental factors in order to test for relationships between drivers and vital rates. While using spatial variation in potential drivers and vital rates has the advantage that we do not need to wait for the results from a long-term study in a single population, we must use caution as populations along an environmental gradient may differ in factors – some extrinsic and some intrinsic – other than the putative driver. One way to use information from multiple populations to examine effects of drivers is to fit a series of models, each regressing a vital rate against a different combination of potential drivers, and then chose the most parsimonious model using an information criterion approach, such as AICc (Burnham & Anderson 2002). Studies in Table S1 that used this approach include Eckhart *et al.* 2011; Dalgleish *et al.* 2011; Adler, Dalgleish & Ellner 2012 and Louthan *et al.* 2014;. The number of potentially important drivers will frequently be large in rela-

tion to the number of data points (i.e. years or sites), which makes parameter estimation and selection based on model comparisons less reliable. Instead, techniques such as model averaging or parameter shrinkage using ridge regression, lasso regression or the elastic net could be used (Dahlgren 2010). For environmental drivers that are continuously monitored, such as climatic variables, and where the response to the driver is a smooth function of distance in time or space, functional linear models constitutes an alternative (Teller *et al.* 2016). When there are multiple potential drivers, we must also recognize that some of them may be highly correlated, and the statistical model selection procedures have no way of distinguishing between them so that we cannot say which of them are true drivers and which are simply correlated with drivers. In this case, it may make sense to apply principal components analysis to the potential drivers and then correlate the vital rates with the orthogonal principal components. For example, Doak & Morris (2010) regressed the vital rates of two tundra plants against two drivers (mean July temperature and snow-free period) separately. But as the drivers were partially positively correlated, they used the first principal component to represent an axis from cooler, shorter summers to warmer, longer summers and showed that the population growth rate (integrating the separate responses of different vital rates to July temperature or snow-free period) showed a unimodal relationship with this principal component.

Combining spatial and temporal environmental variation to identify drivers

Several of the studies in Table S1 collected demographic and driver data not only in multiple populations but also for several years in each of these populations. When putative drivers vary temporally and are not fully synchronized among populations, one option in these cases would be to use a mixed model regression, with the putative driver included as a fixed effect and population and position along the gradient (if there are replicate populations at each position) included as random effects (cf. Doak & Morris 2010; Eckhart *et al.* 2011). By including the random effects as variation in the intercept of the vital rate vs. driver regression, the random effects capture among-population differences in the mean of the vital rate due to unknown environmental factors unrelated to the putative driver. In addition to external factors such as additional drivers, populations may also differ in intrinsic factors, such as intraspecific density or level of inbreeding, that generate among-population variation in vital rates, and the influence of these factors would also be captured by the random variation in intercepts in a mixed model regression. But a limitation of incorporating unmeasured variation in intraspecific density as random variation among populations is that we would not be able to explicitly model the effect of density on vital rates, or how the effects of density and drivers interact (see section 'Differences in intraspecific density are rarely taken into account'). We must also recognize that even when we exploit purely temporal variation within populations, con-

founding factors may still come into play, as other, unmeasured drivers may vary among years independently of – and thus obscuring the effects of – the focal driver. Experimental manipulation of drivers may get around these confounding problems with exploiting both spatial and temporal variation (see the next section).

Vital rate/driver relationships are mostly based on correlations, not experiments

Less than half of the studies in Table S1 used experimental manipulation of any of the putative drivers of demography. Instead, a correlative approach, exploiting natural variation in drivers across space or time, has more often been used. Variation over different spatial scales has been used to parameterize relationships with a large number of abiotic and biotic factors, such as herbivory, canopy cover and soil nutrients. For factors related to climate and weather, such as temperature, precipitation and hurricanes, relationships are most frequently parameterized using among-year variation. For disturbances such as fire, relationships between drivers and vital rates are most frequently parameterized using spatio-temporal variation, substituting space for time to capture a wide range of time since fire, but also incorporating variation across a limited number of years within sites (e.g. Quintana-Ascencio, Menges & Weekley 2003; Menges & Quintana-Ascencio 2004). Overall, correlational studies involved significantly more populations (mean = 6.3; median = 4) than did experimental studies (mean = 2.6; median = 1) (Wilcoxon rank-sum test, $P = 5.9 \times 10^{-5}$). This result implies that correlational studies have more often exploited among-population variation to quantify relationships between drivers and vital rates than they have exploited temporal variation in drivers within single populations.

Establishing relationships between environmental factors and vital rates in plants using some type of experimental manipulations is done relatively frequently [62 (45.6%) studies of which seven manipulated more than one driver category], albeit less commonly than using only natural variation (74 studies [54.4%]) (Table S1). Disturbance (27 studies) and herbivory (22) were the drivers most frequently manipulated. Disturbance experiments were mostly carried out to examine effects of different types of land use (13 cases, mostly involving different grazing and mowing regimes) or fire frequencies (eight cases). Effects of herbivory were examined experimentally by manipulating the abundance of the herbivore or seed predator (15 cases) or by applying artificial damage to plants (seven cases). Interactions with con- and heterospecific plant neighbours were examined experimentally in nine cases, mostly through removal of competitors. Effects of climatic factors were examined experimentally in three studies and effects of abiotic factors in two studies, which is infrequent given how often these drivers were examined in correlative studies. Mutualisms (4) and pathogens (1) were rarely examined in experimental studies, but this was true also for correlative studies. The vast majority of studies have manipulated environmental factors in existing populations and only two studies have transplanted plants into environments representing new combinations of environmental drivers (Eckberg, Tenhumberg & Louda 2014; Stevens & Latimer 2015). An interesting approach to examine how effects of a driver vary with other aspects of the environment is to carry out replicated experiments along an environmental gradient. For example, Miller *et al.* (2009) experimentally examined the effects of seed predators on plant population growth rates along an altitudinal gradient, and Roy *et al.* (2011) experimentally investigated the effects of herbivores and pathogens in the native vs. invaded range.

Using purely correlative approaches is problematic because environmental factors might be correlated to each other and to intraspecific density, and causal relationships might therefore be difficult to establish. The fact that past correlational studies primarily exploited among-population variation thus means that, while they may have uncovered drivers that are important across multiple populations of a species, they may also have been influenced more by confounding effects than past experimental studies that were made on smaller spatial scales. Moreover, to predict effects of environmental change, we are often interested in examining the effects of non-analogue environmental conditions that do not currently exist but are likely to occur in the future. An increased use of experimental manipulations of climatic factors is likely to be particularly valuable for predicting the effects of future climate change. In addition, the effects of biotic interactions between species that do not currently overlap in space but may soon do so due to climate-driven range shifts or expansion of exotic species can at present only be investigated by means of experiments.

Notwithstanding the usefulness of experimental manipulations, purely experimental approaches might be problematic for several reasons. Manipulating environmental factors in natural populations can be irrelevant to future conditions if the parameter combinations used are unlikely ever to occur naturally, even with environmental change. This is particularly true when plants grown in glasshouses or environmental chambers are exposed to variation in one or a few factors; such conditions typically exclude the influence of many biotic interactions that are likely to be important in the field and may modulate the effects of the drivers being experimentally manipulated. Moreover, while transplanting individuals into new environments enables us to explore plant responses to a broader set of environmental conditions, it does not necessarily break up correlations between different environmental drivers. Therefore, experimental manipulations should ideally be used in conjunction with observational approaches in a variety of field settings to ensure both that parameter combinations are relevant and that relationships are causal. Only 6 (4.4%) of the 136 studies in Table S1 combined examinations of effects of natural variation in an environmental driver with experimental manipulations of the same driver (Fröborg & Eriksson 2003; Ehrlén 2003; Dangremond, Pardini & Knight 2010; Dahlgren & Ehrlén 2011, Feldman & Morris 2011; Scanga 2014).

Differences in intraspecific density are rarely taken into account

The extent to which natural plant populations are strongly density-regulated, as opposed to being in an exponential growth phase following disturbance, is still unknown (Harper 1967; but see, e.g. Brook & Bradshaw 2006). Regardless, negative feedback effects of population density on population growth may occur even at low densities and are likely to be important in many systems (e.g. Watkinson 1980; Halpern & Underwood 2006; Dahlgren, Ostergard & Ehrlén 2014). It has been pointed out by several plant ecologists that density effects should be considered when determining environmental drivers of demography and that effects of environmental drivers need to be accounted for to correctly assess effects of intraspecific density (e.g. Hubbell, Condit & Foster 1990; Alvarez-Buylla 1994; Dahlgren, Ostergard & Ehrlén 2014; Diez *et al.* 2014). It is not only highly desirable, but also straightforward to incorporate the effects of density into structured demographic models (e.g. Caswell 2001). Yet, few demographic studies with plants have explored the simultaneous effects of environmental drivers and density (Crone *et al.* 2011). Only 19 (14.0%) of the reviewed studies considered intraspecific density (Fig. 2). In addition, density effects on vital rates or population growth rates were only tested using empirical data in 18 (10.6%) studies, and often only in terms of *post hoc* statistical tests of relationships between density and population growth rate, to justify assumptions that density effects are absent.

Effects of density may be obscured or biased if differences in relevant environmental factors are not considered. This is because population density should be correlated positively across space with carrying capacity, which in turn is correlated with environmental factors. As a consequence, estimates of density effects when not considering environmental factors may be incorrect if these correlations are strong. In contrast, we do not necessarily expect temporal variation in environmental drivers and intraspecific density to be correlated. Interdependence of density and environmental factors may indeed be a major reason for a lack of reports of correlations between density and population growth rates in studies based on spatial comparisons, and a consequent lack of inclusion of density-dependent effects in population models. Of the 18 studies in Table S1 that tested density effects on vital rates or population growth rate, 8 (5.9% of all reviewed studies) reported negative density dependence (Gustafsson & Ehrlén 2003; Rose, Louda & Rees 2005; Kauffman & Maron 2006; Dostal 2007; Feldman & Morris 2011; Adler, Dalgleish & Ellner 2012; Gornish 2013; Dahlgren, Ostergard & Ehrlén 2014). Feldman & Morris (2011) found that negative effects of density on survival were counteracted (but only partially) by positive effects on reproduction via increased pollination, and several other studies also found indications of positive density dependence for some vital rates (e.g. Kelly & Dyer 2002; Diez *et al.* 2014).

Moreover, not including differences in intraspecific density can bias fitted models of effects of environmental drivers on vital rates if environmental drivers and density are correlated. As stated above, such correlations are likely to occur in studies examining effects of spatially varying environmental drivers due to the interdependency of carrying capacity and environmental factors (Dahlgren, Ostergard & Ehrlén 2014). In addition, the effects of species interactions (Gustafsson & Ehrlén 2003; Feldman 2008), abiotic drivers (Dahlgren, Ostergard & Ehrlén 2014) and disturbance (Gornish 2013) have been shown to depend on density, requiring that such interactive effects are considered to correctly quantify effects of both drivers and density. In a recent study examining spatial variation in population growth rate of a forest herb, *Lathyrus vernus,* Dahlgren, Ostergard & Ehrlén (2014) showed that some effects of environmental factors (shade) on vital rates were not detectable in regression models unless density was taken into account by including it as a covariate and that an integral projection model based on these simultaneously estimated environmental and intraspecific density effects was needed to yield realistic predictions of population trajectories.

Another important argument for considering density effects when studying environmental drivers is that they are necessary to reliably predict the long-term impact of environmental drivers. Disregarding density when projecting environment-dependent population growth means that predictions of environmental effects on population growth rate will only be reliable for a short time period, or rather, only for the population densities at the time when the data were gathered on which the model parameters are based. Moreover, including density dependence in projection models is important also when environmental effects are not quantified but when fluctuations in unknown environmental drivers are accounted for by the inclusion of stochastic environmental effects. Stochastic population growth rates are often calculated numerically by randomly drawing matrices describing annual transitions and iterating this process for a large number of time steps to finally calculate the geometric mean annual growth rate, which is the 'stochastic population growth rate' of Tuljapurkar (1990). In such calculations, environmental fluctuations are implicitly assumed to cause all yearly variation in vital rates. However, if some of this variation is caused by density dependence (or demographic stochasticity), the environmentally induced stochastic variation will be overestimated, which in turn will typically result in an underestimation of the mean growth rate in the short term. Indeed, such mean growth rates say little if anything about longer-term dynamics (e.g. Caswell 2001). Underestimation of stochastic population growth rates will result in overestimation of extinction risks of declining populations. On the other hand, not considering eventual density-dependent regulation when geometric mean growth rate is above 1 may lead to underestimation of extinction risks. More studies are needed to evaluate how often neglecting density dependence will lead to erroneous estimates of environmentally induced variation and resulting extinction risk in population viability analyses, which often utilize the above methods.

A final reason to include density effects when assessing vital rate/driver relationships is that density-dependent models will be required to predict how changes in drivers will affect the future equilibrium abundances of species (Ehrlén & Morris 2015).

Environmental factors may have both direct and indirect effects on vital rates

Many environmental factors influence vital rates both directly and through effects on other environmental factors. Indirect effects can be said to occur when one factor changes the level of another factor, which in turn influences one or several vital rates of the focal organism. Indirect effects differ from interactive effects, which occur when the effect of a given level of one factor changes with the level of another factor. To demonstrate an indirect effect, we need to show both that one factor influences an intermediate factor and that one or several vital rates respond to this intermediate factor. The overall effects of environmental drivers estimated using both natural correlations and experimental manipulations are likely to consist of a combination of direct and indirect effects. For example, precipitation (using natural variation or watering experiments) may influence plant vital rates both directly and through effects on nutrient availability. To both assess the overall effects of an environmental factor on vital rates and population growth rates and understand the mechanisms whereby this influence occurs, we therefore need to assess both the direct effects and indirect effects via different paths leading from a focal factor to vital rates. A simultaneous understanding of both direct and indirect effects is particularly important if we want to make predictions for future situations in which the levels of mediating factors change. For example, increased nitrogen input from exogenous sources may weaken an indirect effect of precipitation mediated by soil nutrient availability.

One important type of indirect effect in many systems is the effect of abiotic environmental factors on species interactions. For example, the abiotic environment may not only affect the vital rates of a focal species directly, but may also influence its interactions with other species, for example in terms of competition. Environmental factors have often been shown to have strong effects on biotic interactions, and thus, the effects of species interactions depend on both the abiotic (e.g. Adler, Dalgleish & Ellner 2012; Maron, Baer & Angert 2014) and the biotic (e.g. Strauss & Irwin 2004; Chamberlain, Bronstein & Rudgers 2014) environmental context. In many cases, there appears to be good reason to assume that the indirect effects can be important. For example, in cold to temperate regions, increased temperature is likely to have positive direct effects on many vital rates while indirect effects of increased abundance of competitors will be negative, and often stronger than the direct effect (e.g. Adler, Dalgleish & Ellner 2012; Sletvold *et al.* 2013). Conversely, increasing precipitation may indirectly create a situation in which the effect of neighbouring plants switches from competitive to facilitative as herbivore abundance increases, due to apparency

effects that are absent under more arid conditions when neighbours are less abundant (Louthan *et al.* 2014).

In spite of the potential importance of indirect effects of abiotic environmental factors via species interactions, only very few studies have simultaneously examined both the direct effects of an environmental driver, and the effects via changes in an intermediate factor. In our literature search, only 3 (2.2%) of studies examined both direct and indirect effects of environmental factors (Fig. 2; Table S1, Kolb, Leimu & Ehrlén 2007; Adler, Dalgleish & Ellner 2012; von Euler, Ågren & Ehrlén 2014). Adler, Dalgleish & Ellner (2012) examined both direct and indirect (via competitive interactions among plants) effects of climate change and found support for the hypothesis that indirect effects of climate change declined with the strength of stabilizing niche differences. von Euler, Ågren & Ehrlén (2014) showed how variation in abiotic factors among 24 populations of the perennial herb *Primula farinosa* influenced population growth rate, both directly and through effects on the intensity of antagonistic interactions with, and most likely abundance of, a moth seed predator. Given that a considerable part of the effects of environmental change is likely to occur through effects on species interactions, these examples illustrate how incorporating both direct and indirect effects can provide us with more comprehensive estimates of the overall effects of environmental drivers.

Interactive effects rarely taken into account

Often, the demographic effect of one environmental factor should depend on the level of another. An example is that the effect of precipitation on the availability of oxygen for plant roots will depend on soil properties affecting drainage. This interactive effect should also be expected to have effects on plant demographic rates. Such driver-driver interactions, however, have only rarely been incorporated in environmentally explicit plant demographic models. The majority of studies in Table S1 examined only one driver type, and only 21 of the 136 studies considered driver-driver interactions (Fig. 2). We expect the lack of assessments of interactive effects results from a lack of data and the fact that it is simply not possible to test statistically the effect of all potential ecological effects in any study, even if data on potentially important covariates are available. However, interactive effects between all types of environmental factors need to be much better explored.

The studies that did examine interactive effects among drivers illustrate the importance of considering interactions, even though the wide range of factors considered make generalisations difficult. Interactive effects were reported for all the different types of drivers examined. Eleven studies included interactions of climatic drivers with other climatic drivers or with other driver types. Studies that examined interactive effects of climate and other abiotic factors suggest that effects of climate will depend on local site characteristics, in agreement with expectations (Maschinski *et al.* 2006; Nicolè *et al.* 2011; Diez *et al.* 2014). For example, Nicolè *et al.* (2011) found that a higher frequency of droughts induced by climate

warming would have more severe effects on populations of the alpine species *Dracocephalum austriacum* that were located on steeper slopes due to a lower soil depth in these populations. Taken together, the results of these studies of interactive effects between climatic and other abiotic drivers show that projections of effects of climate change on local populations need to consider site-specific biotic and non-climate abiotic environmental conditions.

Relationships between vital rates and drivers may be nonlinear

Here, we refer to 'nonlinearity' as the situation when the relationship between environmental variables and vital rates or population growth rate cannot be described using a straight line even after transformations (i.e. we do not discuss nonlinearities in population models resulting from feedback effects, e.g. Caswell 2008). Neglecting to consider nonlinear relationships between environmental drivers, demographic rates and population growth rates may cause us to fail to identify important drivers, or to produce biased estimates of driver effects, particularly for extreme levels of the drivers. The existence of nonlinear effects is intuitively clear given that we know for a fact that plants will not grow if, for example, temperatures are either too low or too high. This should result in unimodal relationships between temperature and vital rates (cf. Doak & Morris 2010). Similarly, many plants can be expected to perform best when the soil is not too wet and not too dry. Such 'Goldilocks' relationships can be expected also for other abiotic environmental factors. Unimodal thermal performance curves have been well documented for animals, but this has been little examined for plants (Angilletta 2009; but see Angert, Sheth & Paul 2011). Many of the reviewed studies did not quantify drivers on a continuous scale, and many of the studies that did so only examined effects of three or fewer driver values, which would typically not be enough to reliably quantify nonlinear effects. As noted above, experimental studies were particularly likely to create just 2 or 3 levels of a driver without measuring the level of the driver in one or more of the treatments. Regarding the studies that did quantify continuous variation in the drivers, even though regression models that allow nonlinear relationships are often used when modelling species distributions (e.g. Elith *et al.* 2006), results of tests of nonlinear relationships between environmental factors and vital rates or population growth rates were reported in only five of the reviewed studies. These studies examined nonlinear effects of climatic factors and light availability (Doak & Morris 2010; Sletvold *et al.* 2013; Diez *et al.* 2014; Merow *et al.* 2014; Scanga 2014).

As with the omission of interactive effects of drivers, researchers typically know that the assumption of linearity is an oversimplification. However, this is an assumption often made in regression modelling (e.g. Harrell 2001). Often a lack of data points hinders more careful analyses, or indeed may result in, for example, polynomial terms not being statistically significant even though the relationship is in fact nonlinear. Moreover, it may be likely that relationships are fairly well described with linear models when individuals or populations that do not differ much in their environment are compared, and it is likely that nonlinear relationships have been ruled out in early stages of data analysis in many studies, which might not always be mentioned in the paper. However, when the entire environmental gradient a species experiences is accounted for, it should rarely be adequate to model demographic responses to this gradient as linear. Indeed, studies covering sufficiently large portions of environmental gradients show that nonlinear effects do occur (Doak & Morris 2010; Diez *et al.* 2014). If this is common, predictions of environmentally induced population changes that are based on linear relationships could be misleading, in particular if extrapolations are made to environmental conditions that were not observed. Flexible statistical techniques for quantifying nonlinear relationships and software based on these techniques are readily available to model such relationships and include them in demographic models (e.g. Dahlgren, García & Ehrlén 2011). The main challenge may lie in collecting data that span entire gradients of environmental drivers (e.g. Doak & Morris 2010).

Reciprocal biotic interactions are rarely considered

Plant populations are not only responding to the environment, but the density and structure of plant populations also influence the performance of other species and the abiotic environment. For biotic drivers, the interaction with a focal plant has consequences for the future abundance of the interacting species (herbivore, pathogen, competitor or mutualist) and thus for the future level of the driver of the focal plant's demography. Yet this reciprocal feedback between plants and their biotic drivers has very rarely been considered in population models (Fig. 2). Instead, most studies have measured the impact of the driver on plant vital rates but not the effect of the plant on the driver. The only exception in Table S1 is Adler, Dalgleish & Ellner 2012. Using data on survival, growth and recruitment of four plant species growing intermixed at one site over 22 years, they were able to quantify for each species how both climate and density of the other three species (as well as intraspecific density) impacted the vital rates. Moreover, they used the climate- and competition-dependent vital rates to parameterize a multispecies model that they then used to assess whether these four species would continue to coexist under an altered future climate. As long as plant demographic studies follow the tradition of quantifying the vital rates of a single species while ignoring the demography of interacting species in the same community, such comprehensive predictions accounting for reciprocal feedbacks will continue to be rare.

Studies of the impact of herbivores on plant vital rates make up a large portion of the studies in Table S1, but the reciprocal effects of the plants on herbivore vital rates, and thus future herbivore abundance, are rarely considered (and never in the studies we reviewed). This is particularly challenging when multiple plant vital rates can be affected by a

single biotic driver (e.g. a single herbivore species), and when multiple herbivore vital rates are affected by the plant. The few examples of models that have included reciprocal feedback between plants and herbivores have been unstructured models. For example, Schooler *et al.* (2011) modelled the biomass of the invasive aquatic plant *Salvinia molesta* and the abundance of its herbivore, a weevil. Similarly, Buckley *et al.* (2005) modelled abundance of an annual invasive weed in Australia and its herbivore (also a weevil). While they did include reciprocal feedback, these models included only one state variable for the plants and one for the herbivores and thus were much simpler than would be necessary to include feedbacks involving multiple vital rates in a structured population. The situation becomes even more complex if we take into account that most plant species interact with multiple herbivores and that many herbivore feed on multiple plant species. Then, we would also have to account for all interactions between herbivores and plants if we were to predict the future abundance of a herbivore as a demographic driver for the focal plant.

Perhaps the best-studied biotic feedback on plant performance is the interaction between plants and the soil microbial community, which may involve both soil pathogens and mutualists such as mycorrhizal fungi and rhizobial bacteria (Bever, Platt & Morton 2012). This is in sharp contrast to the total lack of demographic studies in Table S1 explicitly examining even the one-directional effects of soil microbes on natural plant populations.

The abundance of plant pathogens has most often been measured indirectly, by quantifying the density or frequency of infected individuals in the host population (Burdon 1993). Indeed, the dominant approach to modelling plant diseases compartmentalizes the host into classes based on disease status (e.g. the susceptible, infected and removed classes in the classical SIR model), and these models do not explicitly track the feedback from the plant to the size of the pathogen population (Gilligan & van den Bosch 2008; but see Cunniffe & Gilligan 2010 and Jeger, van den Bosch & Madden 2011). A classical result of SIR models is that an increase in host density can lead to an epidemic, but both increased transmission and increased pathogen abundance could contribute to disease outbreaks at high host density. Ultimately, accounting for pathogen abundance should allow us to do a better job of predicting how biotic feedbacks will influence future plant abundance.

The biotic feedback affecting plants about which we probably know the least at present is the effect of flowering plants on the abundance of their pollinators. Local pollinator abundance often increases in high-density plant patches (e.g. Feldman 2008), but this often represents a behaviour response of the pollinator rather than an increase in the size of the pollinator population. The radically different spatial scales on which plant and pollinator populations operate, as well as the fact that many pollinators are generalists, make biotic feedbacks between plants and pollinators challenging to quantify.

Although we have emphasized biotic feedbacks here, we must also recognize that feedbacks may operate through changes in abiotic drivers caused by responses of the focal species (e.g. changes in intraspecific nurse plant effects or in adult shading of seedlings). None of the demographic studies we reviewed examined such effects.

Evolutionary changes in traits influencing vital rate responses to driver are rarely examined

Our main aim in quantifying the relationship between environmental drivers and vital rates is to predict how future changes in the drivers will affect plant populations. Yet if we treat the driver/vital rate relationship as fixed, we are ignoring the possibility that evolutionary adaptation in traits that modulate the relationship may cause future population trajectories to deviate from predictions made under the assumption of a constant relationship.

Only two studies in our review addressed the possible population consequences of evolution in the relationship between vital rates and a driver (Fig. 2). Knight, Barfield & Holt (2008) showed that timing of flowering altered the probability that individuals of *Trillium grandiflorum* would be eaten by deer, an event that results in zero reproduction in the year a plant is eaten. Late-flowering plants are more likely to avoid deer herbivory than early-flowering plants. By exploring a range of values for the heritability of flowering time (which is not known for this plant), Knight *et al.* showed that evolution of later flowering time, and the resulting increase in fecundity, could cause the species to experience 'evolutionary rescue' and avoid extinction even with no change in deer abundance. Rose, Louda & Rees (2005) showed that an introduced weevil could – at least initially – select for a smaller size at flowering in a native semelparous thistle, but they did not assess whether evolution of size at flowering could rescue this plant from the predicted extirpation by the introduced herbivore.

Clearly, to incorporate potential evolutionary responses to environmental changes, we need to know much more than we do to measure the driver/vital rate relationship at one point in time. At a minimum, we need to know which traits alter that relationship, how variable those traits are among individuals, and how much of that variation is genetically determined. Given this plethora of additional information required, it is not surprising that eco-evolutionary models tailored to real populations are extremely rare. But if we are to predict population responses to environmental change over more than the moderate-term future, we need to begin to tackle the challenge of collecting the required information to make such models possible.

While future evolution may alter the responses of vital rates to drivers, past adaptation to local environmental conditions may also affect our ability to quantify vital rate/driver relationships. When data are combined across populations, we must be aware of the fact that the response of a vital rate to a driver may itself differ among populations, and these differences may reflect adaptation to local environmental conditions. Genetic differences among populations influencing the strength and direction of effects of environmental factors on vital rates could be included in a mixed model regression by allowing the slope of the relationship between the vital rate

and the driver to vary randomly among populations (perhaps in addition to random variation in the regression intercept). Similarly, among-population differences in the optimum and width of a unimodal relationship between a vital rate and a driver could be incorporated by allowing both the linear and quadratic coefficients in a second-order polynomial regression to vary randomly.

Conclusions and recommendations for the future

Based on our review of studies linking environmental drivers to plant vital rates and population growth rates, we would like to particularly emphasize five points related to how we conduct demographic studies, how we analyse the data collected, and the questions we might address using structured population models.

First, to some extent, the papers in Table S1 present a misleading picture of the 'state of the art' of environmentally explicit plant demographic models, in that they include only the exemplary studies that had gathered data from enough years and or sites to identify important environmental drivers of demography. In a review of nearly 400 papers that presented projection matrix models for plants, Crone *et al.* (2011) found that half the studies used data from only one site, and those studies presented on average only 3.1 annual projection matrices. With such studies, limited year-to-year environmental variation and small sample size (i.e. few estimates of each vital rate) will make it difficult to discern the important environmental drivers of population dynamics even when information about putative drivers is available, which is indeed often not the case. Thus, our single most important recommendation of how we can improve our knowledge of the drivers of demography is that we routinely include measurements of potentially important environmental drivers in demographic studies and that we work to increase the number of long-term and/or multipopulation studies. We should strive to continue studies of intermediate duration to increase the chance of observing extremes of temporal variation at one site, but we should also recognize that with single-population studies, we might have a long wait until we have enough data to identify drivers, arguing for more multipopulation studies.

Secondly, we believe that the time is ripe for demographic analyses of environmental drivers of plants to move away from density-independent deterministic and stochastic models, and to incorporate density effects into the parameterization and analysis of the models. This step is necessary to correctly identify environmental drivers and quantify their effects on population dynamics. We therefore recommend that collection of demographic data and information about drivers is always accompanied by some assessment of population density.

Thirdly, studies and analyses should be designed to maximize the probability that drivers are correctly identified and effects correctly estimated. We recommend that experimental manipulations pushing drivers to extreme levels are considered as complements to observational studies and that studies are designed so that effects of drivers can be quantified at multiple levels of drivers (preferably over continuous ranges). Lastly, study designs and analyses should ideally consider also interactive, indirect and nonlinear effects. An obvious, but crucial consideration when designing such studies is that sample sizes must be much larger than in studies that do not include any of the complexities. Table S1 clearly suggest that the complexities we scored in our review have been included more frequently in more recent studies. Still, only one study in Table S1 (Adler, Dalgleish & Ellner 2012) included more than half of the complexities we scored in our review, and most studies included none of them. It is high time that we assess the importance of all of these complexities (and others) for at least a few 'model' species.

Fourthly, structured population models are increasingly used to assess how environmental conditions may influence populations with a given genetic composition (e.g. Knight, Barfield & Holt 2008). However, structured models have a great, but mostly unrealized, potential to address how both existing genetic differences among populations due to local adaptation and ongoing evolutionary changes within populations will influence plant population responses to environmental changes.

Fifth and finally, incorporating reciprocal feedbacks between plants and their biotic (and abiotic) drivers into structured models constitutes an important – and also largely unrealized – step towards linking plant demography with the dynamics of the communities in which those plants are embedded.

We believe studies of the relationships between plant vital rates and environmental drivers addressing the points above will be essential to understanding the drivers of population dynamics of individual species. Importantly, such understanding will allow us to predict consequences of expected changes in environmental drivers for abundances and distributions of species. Moreover, accumulating information about relationships between drivers and vital rates from a larger set of plants will enable us to assess how similar effect sizes of different types of drivers are among taxonomic groups and functionally similar taxa. Such general knowledge would inform us about the extent to which we can make feasible predictions for taxa that have not been monitored. While demographic studies are generally labour intensive, measuring environmental drivers is becoming less and less expensive (e.g. by using miniature data loggers of various abiotic factors), and the additional complexities that we have argued should be considered (e.g. density dependence) are not hard to measure. We thus believe it is realistic to expect future demographic studies to address most of the limitations of previous studies that we have discussed here, and start building a more general understanding of the environmentally explicit population dynamics of plants.

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Data accessibility

This paper does not use data.

Author's contribution

JE, WFM and JPD contributed equally to all aspects of this work. TvE contributed to the literature review.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Studies examining the relationship between environmental drivers and population growth rates in plants using structured population models, published during or after 1995.