



Will among-population variation in seed traits improve the chance of species persistence under climate change?

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ABSTRACT

Aim Seed traits related to recruitment have direct relevance for plant fitness and persistence. Trait variation in time and among populations may increase species resilience and ultimately reduce the risk of extinction. However, patterns of among-population variation in critical recruitment traits remain poorly known and are often disregarded when considering extinction risk under future climates.

Location Global.

Methods In this paper we review and synthesize current knowledge about among-population variation in physiological and morphological traits related to plant recruitment. We outline the consequences of that variation for species persistence under climate change, and discuss the implications for conservation, management and restoration.

Results The evaluated studies provide compelling evidence that among-population variation in traits underpinning seedling emergence, growth and establishment is widespread. Contrary to expectations, environmental gradients do not appear to be reliable predictors of variation among populations and responses are often individualistic. Likewise, well-established cross-species patterns are not consistently reflected among populations within a species. As the pattern of this variation is unpredictable, we cannot make simple generalizations about how this variation is allocated across geographic ranges or the extent of environmental versus fixed genetic differences. Nor do these patterns clearly elucidate the potential for this variation to mitigate negative effects of climate change.

Main conclusions If we ignore among-population variation in seed traits, or assume it will follow simple environmental clines, we do so at our own peril. The consequences of such an approach are likely to include biased forecasts of future range dynamics, hindering identification of the genetic material most appropriate for conservation, restoration and management. Further research that integrates ecology and emerging evolutionary genetic techniques to identify the distribution of seed traits within foundation species and the mechanisms driving them is urgently required to guide the management and maintenance of systems in the face of rapidly changing climates.

Keywords

Adaptation, among-population variation, climate change, climate sensitivity, germination, intraspecific variation, plasticity, recruitment traits, seed banks, seed dormancy, seedlings, seeds.

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INTRODUCTION

Climate is a fundamental determinant of where plant species establish, grow and reproduce. A large body of evidence supports the existence of rapid human-induced climatic change (IPCC, 2013) and this is predicted to be a major threat to biodiversity (Parmesan & Yohe, 2003; Thomas *et al.*, 2004). The impacts of this forecast disruption to absolute fitness of organisms (i.e. a population's capacity to replace itself) are a growing concern for conservation, and correlative niche models suggest potentially severe geographic displacements and extinction for countless species (Parmesan & Yohe, 2003; Thomas *et al.*, 2004). Many such models focus on realized niches as indicated by the distribution of adult plants, but they say little about the demographics of species or the importance of the transitional stages of the life cycle in determining species ranges, and generally assume common among-population environmental similarities and tolerances across a species (Bolnick *et al.*, 2011). Although less common, process-based models aim to explicitly integrate the physiological responses of species to environmental change and provide an opportunity to incorporate the effects of local adaptation (Morin & Thuiller, 2009; Dormann *et al.*, 2012). These new models pave the way for reducing prediction uncertainty in species range shifts under climate change, although to date most work has focused on phenology-related traits (Chaine & Beaubien, 2001; Chaine, 2010).

Changing climatic conditions are expected to affect a range of plant life-history phases, including phenology; however, this impact will potentially be most severe on the early developmental stages in a plant's life cycle (Hedhly *et al.*, 2009; Walck *et al.*, 2011). Seed mass, seed dispersal, dormancy mechanisms and seed germination requirements are some of the physiological and morphological traits that underpin the ability of a seedling to emerge, grow and establish. Seed mass influences seedling survival (Moles & Westoby, 2004a; Metz *et al.*, 2010), seed dispersal is a mechanism for dealing with environmental variability and uncertainty (Venable & Brown, 1988), seed dormancy spreads the risk of temporal variance in germination success over multiple seasons (Venable & Brown, 1988) and germination timing influences the number of seeds that become seedlings and their subsequent survival (Simons, 2009). These key traits will play important roles in determining the ability of species to shift ranges or recover from disturbance and can be linked to local or global extinction probabilities (Fenner & Thompson, 2005; Walck *et al.*, 2011).

Selection pressures along environmental gradients can give rise to predictable variation in life-history traits and physiological tolerances (Vergeer & Kunin, 2011), with a major part of this overall variation captured at the species level (Westoby *et al.*, 2002; Kattge *et al.*, 2011). However, selection (including drift) often results in a suite of genetically variable individuals spaced in multiple populations located along a gradient, with populations operating as relatively disjunct entities. We refer to this variation within a species as 'among-population variation'. It is well established that flowering phenology can show clear geographic differentiation across a wide range of species, generally

correlated with climate at latitude or elevation (Rathcke & Lacey, 1985). Similarly, among-population variation in leaf traits is important in describing plant performance under different environmental conditions (Messier *et al.*, 2010). Such spatial variation may include differences in trait means as well as in sensitivity to environmental variables. As the climate changes, populations along environmental gradients will be disproportionately affected, with threats to different habitats and species expressed in different ways. Understanding the pattern of variation in vulnerability among populations and between developmental stages is critical for accurately predicting the impacts of climate change on species (Dawson *et al.*, 2011). Furthermore, the presence of among-population variation means that treating species phenology or leaf traits as homogeneous (i.e. a mean trait value) may be inadequate when predicting the effects of a changing climate (Visser, 2008; Bolnick *et al.*, 2011; Albert *et al.*, 2012).

A substantial literature now exists addressing among-population variation in trait-based ecology (Albert *et al.*, 2012), including its importance in the eco-evolutionary dynamics of populations and communities and their persistence under global climate change (Lavergne *et al.*, 2010). However, despite advances in our general understanding of trait-based ecology, the role of intraspecific variation in seed traits in determining the response of plants to climate change and the potential for this variation to act as a mechanism for coping with stress and adapting to new climates is still poorly understood and not yet synthesized.

Aims of the review

The aim of this paper is to review and synthesize current knowledge of among-population variation in seed traits in order to highlight the role that seed traits might play in buffering species against climate change, in addition to identifying gaps in our knowledge. We begin by exploring the relationship between seed traits and climate, discussing existing data on sensitivity, plasticity and genetic variation of seed traits in the context of vulnerability of a species to climate change. We then review studies that have considered among-population variation in seed traits along environmental gradients and quantify the frequency and direction of trait variation. We hypothesized that patterns of among-population variation in traits that underpin seedling emergence, growth and establishment would reflect those observed across species. For instance, on a global scale, seed mass commonly increases as temperature rises and rainfall and latitude decrease (Moles & Westoby, 2003; Kattge *et al.*, 2011; Liu *et al.*, 2013), with smaller seeds germinating faster than larger seeds (Norden *et al.*, 2009), seed longevity increasing with rising temperature and aridity (Probert *et al.*, 2009) and seed dormancy status being greater at higher elevations where temperature and rainfall are lower (Fernández-Pascual *et al.*, 2013). We expected to see similar among-population patterns in species with distributions along environmental gradients (i.e. latitude, elevation or aridity). If species with highly variable responses across their geographic range are more tolerant of

change and diversify more readily, identifying among-population variation in seed traits may assist with conservation and management actions that buffer against loss of diversity. We conclude this review by identifying key questions for future research.

CLIMATE HAS DRIVEN THE EVOLUTION OF SEED TRAITS

Seed traits related to recruitment have direct relevance to plant fitness under current and future environments. Seeds link plant generations and are the means by which many plants endure in the landscape (i.e. as seeds in the soil seed bank) or migrate across it during dispersal events. The interaction between plant and environment begins with seed germination, the first major life-history transition, often a serious population bottleneck and one of the most dramatic events in a plant's life cycle (Donohue *et al.*, 2010). Germination timing is especially important: in fire-prone Mediterranean-climate ecosystems timing germination to coincide with winter enables adequate seedling growth prior to the onset of summer drought (Moles & Westoby, 2004b), as later season drought stress is a common cause of seedling mortality. In contrast, seedling mortality in cold-climate ecosystems can occur as a result of low temperatures and a short growing season. Germination timing shows a degree of phenotypic plasticity (Simons, 2011), but is also under strong natural selection (Donohue *et al.*, 2010) with environmental cues that influence where and when seeds germinate being evolved to optimize seedling establishment (Donohue, 2005).

The strong correlation between climate and recruitment has resulted in the development of specific germination strategies for many species (Baskin & Baskin, 2001; Fenner & Thompson, 2005). Non-dormant, imbibed seeds of most species germinate over a range of temperature conditions with an optimum above and below which germination can be depressed, delayed or, in some cases, prevented (Baskin & Baskin, 2001). The breadth of the optimal range can change as the seed matures and ages, and as dormancy is imposed or alleviated (Alvarado & Bradford, 2002; Steadman *et al.*, 2004; Simons, 2011).

Physiological dormancy is the ability of seeds to postpone germination despite optimal environmental conditions, a trait that is particularly important in unpredictable and unreliable environments. By producing seeds with varying dormancy status, a plant can spread the risk of temporal variance in success over multiple seasons (i.e. hedge its bets), thereby increasing mean fitness through increasing the likelihood that some seedlings will survive regardless of environmental conditions (Venable & Brown, 1988; Starrfelt & Kokko, 2012). Like germination, the alleviation of dormancy is strongly influenced by patterns of temperature and moisture. The ability of seeds of many species to persist in the soil until dormancy is alleviated or germination requirements met is an adaptive strategy that can buffer against the negative effects of environmental heterogeneity (Cohen, 1966; Ooi, 2012). Maintenance of dormant seeds in the seed banks stored in the soil plays an important role in

community dynamics and regeneration (Venable, 2007), and is strongly influenced by climate (Fenner & Thompson, 2005).

Seed mass has recently been identified as a key fitness-related trait (Adler *et al.*, 2014) which links germination with seedling growth and survival, and is related to life-history strategies, dispersal distances and regeneration (Leishman *et al.*, 2000). Larger seeds confer advantages to the plant during early seedling establishment (Rodríguez-Pérez & Traveset, 2007; Metz *et al.*, 2010), producing larger seedlings that appear to be more drought resistant (McWilliams *et al.*, 1968; Keeley, 1991; Milberg *et al.*, 1998; Leishman *et al.*, 2000). Large seeds, however, may reflect a trade-off between short-term reductions in reproductive success (e.g. reducing seed production) in favour of longer-term risk reduction (Venable, 2007). In some cases, production of dimorphic or heteromorphic seeds by a single plant allows plants to decrease temporal variance in offspring success, e.g. bet-hedging (Venable *et al.*, 1987).

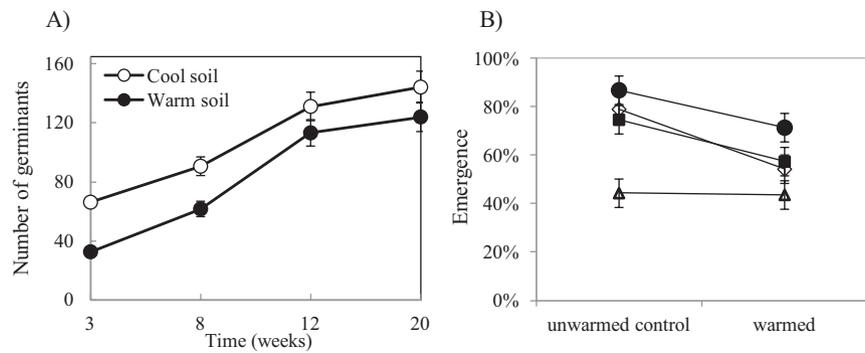
Finally, seed dispersal strategy may also be an effective bet-hedging mechanism for dealing with spatial variation in environmental conditions, with the rate, timing and distance of dispersal critical for colonization success and population persistence (Venable & Brown, 1988; Nathan & Muller-Landau, 2000; although see Siewert & Tielborger (2010)). Dispersal mode (e.g. wind, water, gravity and/or animal assisted) determines seed placement in the environment, and the differential placement of seeds in 'safe' microsites influences germination and establishment success. When long-distance dispersal mechanisms are absent, other traits become increasingly important means for coping with environmental variation and facilitating persistence.

The potential impacts of climate change on germination strategies

Rapid environmental change is expected to affect seed strategies and lead to significant changes in seed responses. For example, soil warming resulted in reduced seedling emergence from the Australian alpine soil seed bank (Hoyle *et al.*, 2013) (Fig. 1a) and reduced seedling emergence of species from the mediterranean-climate ecosystem of south-western Australia (Cochrane *et al.*, 2014) (Fig. 1b). Likewise, long exposure to high soil temperatures approximating those predicted for the Australian arid zone under future climates caused changes in dormancy and viability of seed from native annual and short-lived perennial species, resulting in the depletion of the soil seed bank (Ooi *et al.*, 2009).

While the individual effects of temperature and moisture on seed germination and seedling establishment are reasonably well understood, the interactive effects of novel changes in either or both climate parameters will be difficult to predict *a priori*. We know that soil water potential can modify the temperatures over which germination occurs, and vice versa, affecting both rate and percentage of germination (Alvarado & Bradford, 2002). However, interactions between climate parameters have often led to contrasting responses. Soil warming in a temperate grassland altered recruitment of perennial species as a result of changes in soil water potential (Hovenden *et al.*, 2008).

Figure 1 (a) The total number of seedlings from the alpine soil seed bank (predicted mean \pm standard error) was lower at warm day/night soil temperatures (c. 23/16 °C), compared with cool (c. 19/12 °C) temperatures. Taken from Hoyle *et al.* (2013) with permission. (b) The final percentage emergence for four *Banksia* species from south-western Australia was greater in unwarmed plots than warmed plots: ■, *B. baxteri*; △, *B. coccinea*; ●, *B. media*; ◇, *B. quercifolia*. Taken from Cochrane *et al.* (2014) with permission.



Drought, but not warming, was responsible for reduced seedling emergence in a Mediterranean shrubland (Lloret *et al.*, 2005). Warmer first rains are predicted to lower the germination of three rare annual species in California (Levine *et al.*, 2008), and warming and drying in the Sonoran Desert over a 25-year period has led to an increase in cool temperature germination, attributed to the timing of germination-triggered rainfall events rather than temperature *per se* (Kimball *et al.*, 2010).

The disruption of current germination strategies as a consequence of changes in frequency and seasonality of precipitation and temperature associated with predicted climate change are likely to result in alteration of demographic rates and potentially a mismatch in the timing and placement of germination for many species (Walck *et al.*, 2011; Fordham *et al.*, 2012; Ooi *et al.*, 2012), similar to that which is apparent for other biotic interactions (Parmesan & Yohe, 2003; Walther, 2010). These consequences include implications for the survival of individual species (Donohue, 2002; Quintana *et al.*, 2004; Hovenden *et al.*, 2007), for competitive interactions (Levine & Hillerislambers, 2009) and for community composition (Suttle *et al.*, 2007; Kimball *et al.*, 2010; Suggitt *et al.*, 2011). Indeed, models of recruitment under future climates predict reductions in population viability and declines in population size as a response to specific climate events (e.g. drought) (Maschinski *et al.*, 2006; Yates *et al.*, 2007). In cold-adapted floras the predicted reduction in snow cover, earlier snow melt, increased summer temperatures and length of the growing season, in conjunction with higher evapotranspiration, are expected to disrupt recruitment strategies (Mondoni *et al.*, 2012) and are likely to affect the location and timing of germination (Milbau *et al.*, 2009; Shevtsova *et al.*, 2009). This potential uncoupling of environmental cues and germination response may lead to lower fitness via higher seed or seedling mortality, if the diversified strategies that currently spread risk across seasons are disrupted (Childs *et al.*, 2010).

ECOLOGICALLY SIGNIFICANT SEED TRAITS VARY ACROSS SPECIES RANGES

Many ecological studies have taken a species approach to assessing seed traits (Moles *et al.*, 2007; Kimball *et al.*, 2010; Saatkamp *et al.*, 2011), and indeed it is generally assumed that the species

level captures a major part of trait variation (Kazakou *et al.*, 2014). However, species occur on gradients of temperature, moisture and soil nutrients (as discussed in McGill *et al.*, 2006), and the extreme sensitivity of traits to environmental variation can act to diversify the responses of plants to environmental cues (Simons & Johnston, 2006), with different individuals and populations potentially expressing different phenotypes and tolerances. The relative fitness of populations may vary due to spatially variable environments, particularly when such variation satisfies the requirement for differing responses (Chesson, 2000; Donohue *et al.*, 2010; Simons, 2011).

Among-population variation does not consistently reflect patterns at the cross-species level

We performed a search on ISI Web of Science for published studies based on criteria related to seed (i.e. seed germination, seed dormancy, seed longevity, seed mass, seed shape or seedling), including parameters associated with among-population variation (population*, within species, within-species, intraspecific or intra-specific) and environmental gradients (latitude, elevation, altitude, rainfall gradient or aridity). We restricted the output to ecology and environmental science, as we were interested in wild species rather than horticultural, forestry or agronomic studies. From the resulting 212 papers, we excluded articles that were only peripherally related to seed traits, or for which multiple populations were not considered. We also included additional articles known to the authors or uncovered in the process of reading the above collection. The resulting compilation of 54 papers represents our current understanding of among-population variation in seed traits and implications for species responses to environmental change. These papers illustrate a mix of observational studies *in situ* and empirical studies under controlled conditions, often reporting on multiple traits (Appendix S1 in Supporting Information). Study sites were generally limited to a narrow range of habitats and the majority of studies that examined among-population variation focused on annual, short-lived herbaceous perennials, including invasive species. Few detailed studies dealt with woody species (although see Meyer & Mosen, 1991; Cochrane *et al.*, 2014).

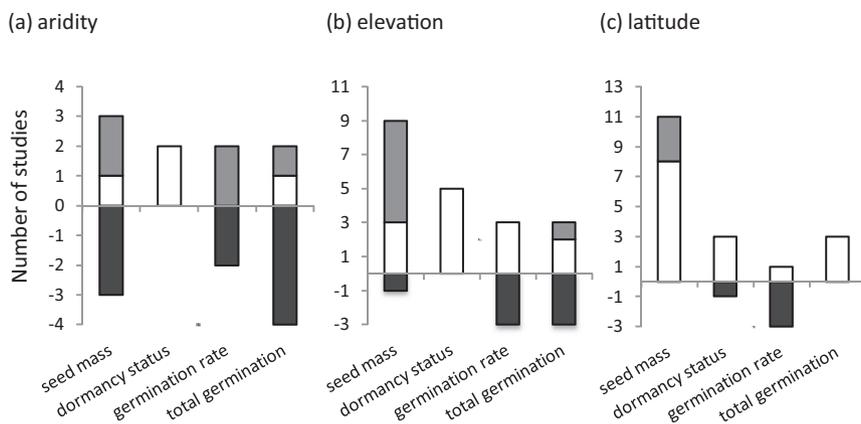


Figure 2 Number of among-population studies that reported a change in mean trait value of seed mass, dormancy status, germination rate and/or total germination along environmental gradients of aridity (a), elevation (b), and/or latitude (c). An increase (above line), decrease (below line) and no clinal change (above line) are represented as white, black and grey, respectively. Across the studies, dormancy status consistently increased with elevation and aridity, seed mass increased with latitude but the response was mixed along an aridity gradient, and the germination rate showed no consistent pattern along the climatic gradients.

In many cases (61 examples within 49 studies), clinal trends were evident where among-population differences in seed traits correlated with latitude, elevation or soil moisture. However, contrary to our working hypothesis, patterns of among-population variation did not consistently follow the patterns expected from cross-species analyses. Rather, trait responses often diverged with a somewhat even spread of studies reporting an increase, decrease or no change (19 cases in 11 studies) in a given seed trait along a climatic gradient (Fig. 2). The search demonstrates that differentiation of seed mass in response to environmental gradients is well documented among populations within species (e.g. Völler *et al.*, 2012), albeit not universal (e.g. Zhao *et al.*, 2013). We also note the possibility that studies without clear geographic correlates may be more common than this analysis shows, but also more difficult to publish.

For some important seed traits it is not possible to assess general trends simply because there are not enough published studies. For example, geographic patterning was reported for soil seed bank persistence in one study – seeds from cooler environments had a greater response to dormancy-breaking treatment than did seeds from warmer environments (Ooi *et al.*, 2012) – but such studies are rare. Likewise, in one of very few studies of among-population variation in seedling emergence patterns, emergence of four congeneric species from southwestern Australia did not vary predictably along the longitudinal rainfall gradient from which the seed was sourced (Cochrane *et al.*, 2014). Comparing germination, dormancy and seed mass along clinal gradients is relatively simple, and many examples exist. However, there are fewer examples that document soil-stored seed bank size and longevity and actual emergence or survival for a single species, let alone whole communities. This is a challenging task, and consequently this issue warrants further research.

Does the breadth of climate gradient or species range correlate with the extent of among-population variation?

Given that patterns of differentiation in seed traits among populations do not appear to reflect those across populations one

must consider other potential drivers of differentiation within species. For example, the breadth of the climate gradient across which a species is distributed or range size could explain among-population differences. Theory predicts that species which can exist under a wide variety of environmental conditions, and make use of a wide range of resources (i.e. a larger fundamental niche), must be generalists and so are likely to cope better with climate variation because their populations already encounter broad climatic conditions across their range (Thuiller *et al.*, 2005; Luna *et al.*, 2012; Sides *et al.*, 2014). Among-population variation in seed traits is thus predicted to increase with increasing range size and heterogeneity. The species studied thus far differ dramatically in range size and in the steepness of the climatic gradients and environmental heterogeneity experienced across their ranges; however, there are insufficient studies to attempt to analyse the importance of these factors in explaining among-population variation in seed traits.

We suggest that among-population variation in seed traits corresponds to a combination of environmentally induced and genetically fixed differences among populations of a species and may be a sign of local adaptation or genetic drift leading to differentiation in trait means and plasticities across populations. Below we consider the relative contribution of fixed genetic and environmentally induced plastic or maternal effects to this variation.

Does among-population variation reflect environmentally induced phenotypic plasticity, fixed genetic differentiation in trait means or both?

The spatial variation we see in morphological and physiological traits *in situ* may reflect genetic differentiation (Linhart & Grant, 1996), including adaptation to local climate (Davis *et al.*, 2005), but may also reflect environmentally induced phenotypic plasticity (Nicolson *et al.*, 2010). Genetic differentiation across a species' range reflects a combination of random processes (e.g. drift) and selective processes (e.g. evolution), leading to ecotypic differentiation which may confer local adaptation. Early life stages are likely to be the first to be exposed to new

environments, and as such are anticipated to exhibit local adaptation (Donohue *et al.*, 2010). Plasticity may improve performance, and has been theorized to be an important mechanism for generating phenotypic variation under novel conditions upon which selection can act, thus directly facilitating adaptive evolution (Ghalambor *et al.*, 2007; Chevin *et al.*, 2010). Although it is often difficult to separate trait variation from environmental variation, much of the variation among plant populations appears to reflect direct effects of the environment (i.e. phenotypic plasticity; Ackerly *et al.*, 2000).

For more than a quarter of the studies in Fig. 2 we cannot evaluate whether the variation was due to plastic or genetic effects. Sixteen studies directly assessed genetic variation in plasticity across populations by using reciprocal transplant or common garden experiments (e.g. Etterson, 2004). Kalisz & Wardle (1994) used a transplant experiment to assess differentiation in seed mass and days to emergence among five populations of *Campanula americana* (Campanulaceae) distributed along a latitudinal gradient. They documented both plasticity and differences reflecting broad-sense genetic variation for the traits measured. Likewise, Meyer & Kitchen (1994) assessed differences among populations of *Linum perenne* (Linaceae) in seed germination patterns in a common garden experiment and found evidence of genetic differentiation as well as changes in phenotypic expression not related to genetic shift. Studies of species introductions beyond their natural distribution have provided some convincing evidence that local adaptation to novel conditions can occur in seed traits (Kudoh *et al.*, 2007), but can also be facilitated by phenotypic plasticity (Zhao *et al.*, 2013). These examples make it clear that the extent of local differentiation or patterns of plasticity can complicate interpretation of many experiments, as genetic and plastic effects are not alternatives.

What is not possible, based on currently available data, is quantification of the patterns of among-population differentiation in plasticity of seed traits along climatic gradients. In addition to changes in trait means, there may be ecologically important differences in the plasticity of those traits. Another concern is that plasticity may lead to a mismatch between environmental cue and germination response. Instead of responses increasing resilience (e.g. diversified strategies that aim to avoid risk), seeds may become 'less discerning' about when and where they germinate (Hoyle *et al.*, 2008b), and plastic responses to the novel environment may reduce fitness. Reduced viability in the soil seed bank (Ooi *et al.*, 2009) and reduced and delayed seedling emergence (Cochrane *et al.*, 2014) with exposure to warmer soils are clear examples of non-adaptive responses.

To what extent do trans-generational maternal effects complicate interpretation of the results to date?

An important factor that can further complicate assessment of fixed genetic and plastic sources of variation among populations is trans-generational maternal effects (Donohue, 2009). Many of the studies to date have used seed collected in the wild, and thus

cannot exclude the role of such maternal effects on trait means and plasticities. It is well known that resource availability during seed maturation affects seed provisioning (Baskin & Baskin, 2001), with the plant's ability to anticipate the environment that the seed will experience determining the level of variation in provisioning. We see this in the significant differences detected in seed mass between maternal plants of *Rhamnus alpinus* (Rhamnaceae), both before and after pollination manipulation (Bañuelos & Obeso, 2003). More subtle temperature and moisture conditions during seed development can also leave a lasting impression on seed dormancy status and germination requirements (Fenner & Thompson, 2005; Hoyle *et al.*, 2008a; Donohue, 2009; Barua *et al.*, 2012): as the maternal environment changes, seed characteristics and seeds' ability to decipher environmental cues can also change. This was clearly demonstrated by Steadman *et al.* (2004) in the invasive weed *Lolium rigidum* (Poaceae), with high maternal day/night temperatures during seed production reducing dormancy of the progeny. Environmental maternal effects may evolve as a source of adaptive plasticity between generations, enhancing offspring fitness in the environment that they are likely to experience (Galloway, 2005). Again, there are insufficient studies to allow assessment of how such maternal effects may vary among populations, or for that matter of how important such effects will be for determining recruitment patterns under novel climates.

What generalizations can we reach about among-population variation?

The available studies provide evidence that among-population variation exists, and that variation is often associated with climatic gradients. In the case of seed mass we can see that patterns across species are reflected in among-population differentiation, but otherwise the direction of shifts among populations along climate gradients are highly variable. There are simply too few studies that explain within-species variability in seed traits or show what leads to these differences. In addition to the factors mentioned above, life-form, phylogenetic association and/or habitat might also be important explanatory factors. We cannot as yet generalize as to whether, or which, maternal or plastic and/or fixed genetic differences in seed traits will buffer against environmental variation and thus be sufficient to guarantee that seeds will respond appropriately to the environment to enable persistence under novel climatic conditions.

AMONG-POPULATION VARIABILITY IN SEED TRAITS IN THE CONTEXT OF PREDICTING SPECIES RESPONSE AND MANAGEMENT FOR CONSERVATION UNDER CLIMATE CHANGE

Understanding mechanisms and adaptations that will permit species to persist and coexist in temporally variable environments is essential for predicting responses to future climate change (Childs *et al.*, 2010). In spatially varying environments, and under rapid climate change, the strength of buffering will be affected by life-history attributes and among-population

variation. For seeds, theory predicts that there will be high variation in germination strategies within populations and among individuals, with plants having very complicated strategies for provisioning offspring for uncertain futures (Clauss & Venable, 2000). For some species, gains will be made through changes to mechanisms such as dormancy, for others it might be seed dispersal, occurring via temporal and spatial storage effects *sensu* Chesson (2000). Bet-hedging as a mechanism for seed persistence under variable environments is reasonably well documented (Cohen, 1966; Clauss & Venable, 2000; Simons & Johnston, 2006; Gremer *et al.*, 2012; Tielbörger *et al.*, 2012). Seed heteromorphism is a good illustration of bet-hedging. Some plants are able to provision seeds in a variety of different ways to maximize success in the environment. In *Heterosperma pinnatum* (Asteraceae), three seed morphs are produced, but the proportion of each morph varies within the progeny of a single individual, with individuals and populations varying in the proportion of progeny that exhibit each type of morph (Venable *et al.*, 1987). Bet-hedging may also be fine-tuned by plasticity, evidenced by the production of aerial and subterranean achenes in *Emex spinosa* (Polygonaceae), each with variable dormancy and dispersal mechanisms (Sadeh *et al.*, 2009). The allocation to each type of achene changes according to nutrient availability, and each phenotype is successful only when the particular situation to which it is adapted occurs. These kinds of mechanisms provide species with potential pathways for effecting appropriate population responses to changing environments, minimizing the risk of recruitment failure, with the success of the strategy being averaged over multiple seed types.

Rapid adaptation in some traits may be possible across several generations, particularly in genetically diverse species with short life cycles (Hoffmann & Sgro, 2011; Sgrò *et al.*, 2011). The capacity to undergo rapid evolutionary change may increase the invasive potential of newly introduced populations (Daws *et al.*, 2007; Konarzewski *et al.*, 2012), but for many species it is unlikely that natural selection of tolerant genotypes will keep pace with the rate of predicted climate change (Jump & Peñuelas, 2005).

Adapting to novel conditions is expected to be a common response (Bellard *et al.*, 2012); however, environmentally induced shifts in phenotype will also be critical for plant performance, persistence and range expansion under global change (Anderson *et al.*, 2012). If population responses relate directly to the reproductive and functional success of plants then responses have both ecological and evolutionary significance that can provide some resistance to climate change (Hoffmann & Sgro, 2011; Barua *et al.*, 2012). Strategies may be risky for individuals, but if populations are large, then risk behaviour can be spread widely and trade-offs can still provide benefits for species survival and persistence.

Incorporating among-population variability – a challenge for predicting species responses?

High levels of plastic and/or genetic variation among populations present complications for forecasting species response to

climate change. So too does the likely difference in predicted climate across species distributions, particularly if the climate gradient is large. In turn, population response will differ depending on local climate and the level of seed trait variation present within a population. Furthermore, trait interactions may result in potential trade-offs between mean fitness and variance (Rees, 1996; Metz *et al.*, 2010). Further confounding our ability to forecast response to environmental change is the fact that, in some cases, plants may have larger climatic optima than previously recognized. This disparity between the realized and fundamental niche was demonstrated by Rehfeldt *et al.* (2002) for *Pinus sylvestris* (Pinaceae): populations tended to inhabit climates colder than their optima, with the difference between the optimal and inhabited climates becoming greater as the climate became more severe.

However, to effectively assess the demographic responses of a species to climate change an understanding of both current levels of adaptation within a species and future adaptive potential is required (Davis *et al.*, 2005). Given the considerable among-population variation in seed traits discussed above, moving from models that assume that a species has a single static environmental tolerance function (Pearson & Dawson, 2003), to models that incorporate variance in species response will increase the predictive power of existing climate models to forecast the vulnerability of species to decline or extinction (Keith *et al.*, 2008; Ooi *et al.*, 2009; Chevin *et al.*, 2010; Yates *et al.*, 2010). Understanding the degree to which populations are sensitive to their prevailing environment, and to the climatic variables that are likely to change in the future, will increase our ability to predict vulnerability (Dawson *et al.*, 2011).

How is among-population variation in seed traits important for conservation and management for assisted migration?

The regeneration niche is important for the maintenance of plant communities (Grubb, 1977), and a major concern for conservation is the impact that climate change will have on species persistence and its potential for dispersal and range shifts. Natural resource managers need to anticipate, mitigate or adapt to the challenges of climate change, with the identification of among-population differences in responses critical for developing adaptive management strategies that can facilitate restoration, help build ecosystem resilience and, most importantly, identify the most appropriate populations for restoration. However, many restoration programmes currently aim to minimize asynchrony and seed trait variability in order to optimize restoration success (Turner *et al.*, 2013). We would argue that increased synchrony in traits may result in a reduction in variation, in turn leading to a decline in resistance to the negative impacts of environmental heterogeneity. Where populations show little ability to adapt to climate change *in situ*, gene flow from populations more tolerant of novel conditions will be critical. However, habitat fragmentation poses a major problem for gene flow and assisting migration of propagules in fragmented habitats will be crucial for persistence. Failure to

consider population responses in important early life-history traits may over- or under-estimate species plasticity and their capacity for adaptation. Restoring entire species ranges may be untenable, but shifting genotypes from populations more amenable to novel climates might be feasible and less controversial (Vitt *et al.*, 2010; Weeks *et al.*, 2011). Knowing which populations to concentrate on for seed collection and use in restoration may prove crucial for species persistence.

FUTURE DIRECTIONS AND CONCLUDING REMARKS

The ability of seeds to germinate and to weather time has fascinated scientists for many hundreds of years, but the spatial distribution of seed traits within species and their likely response to changing environments remain poorly understood. The available evidence indicates that plants are flexible in their early life-history stages, and that certain seed traits allow plants to cope with unreliable environmental conditions, thereby increasing fitness. However, the evidence is limited and does not permit us to generalize easily on how this variation is allocated across geographic ranges, the extent of environmental and fixed genetic differences, or the potential for this variation to mitigate the negative effects of climate change. Under a rapidly changing climate, the reliability of environmental cues for development, dispersal and colonization will alter, the magnitude of disrup-

tions will be species and habitat specific, and the impact will be uneven across a species' distribution. Among-population variation is likely to be important for mitigating the negative impacts of climate change, especially in the context of natural and assisted range shifts. Comparing variation in seed traits, and plasticity therein, among populations provides a means to understand the roles played by those traits in enhancing the adaptability of species.

Contrary to expectations, within-species patterns of variation are not consistently comparable with those at the cross-species level, and responses to changing climatic conditions are often inconsistent. Clearly, understanding the mechanisms that drive this variation is critical for predicting and managing for climate change (see Box 1). The underlying reasons why people collect data on the traits we have examined in this review are quite distinct, with few studies actually designed around collecting data to help understand species responses in the context of climate change. We advocate the integration of ecology and emerging evolutionary genetic techniques to identify the distribution of seed traits within foundation species as the best approach to managing systems in the face of rapidly changing climates. We emphasize the need to understand the link between vulnerability and among-population variation in traits across a climate gradient, considering climate sensitivity and adaptive capacity at the population level (Dawson *et al.*, 2011). In all cases, studies should focus on regions where traits may be most

Box 1

Future directions

Finding answers to the following outstanding questions would advance our understanding of how variation in seed traits will drive responses to climate change.

Are some traits more sensitive to environmental change? Implementation of large global-scale screening of within-species variation in simple traits like seed mass, germination characteristics and dormancy status could provide a solution to this question. Established seed banks around the world hold high-quality, often multi-provenance, collections of a large range of native species (Smith *et al.*, 2011). Enlisting the expertise of these seed banks for a global study makes sense: manipulating environmental variables beyond historical/present ranges, and relating environmental changes to phenotypic responses, will give us a better understanding of how fitness consequences are determined, particularly in the critical stages of recruitment. Furthermore, determining a seed's ability to survive, germinate and establish under challenging conditions can provide us with critical threshold values. Such investigations may be field or laboratory based.

Are these traits associated with particular lineages, range size, habitat, growth form, longevity or regeneration strategies? If we correlate the above data with evolutionary and ecological strategies then we can answer this latter question and potentially reach generalizations across species.

Are some traits more important for persistence in some ecosystems than others? Answering this question may prove more difficult than the preceding ones. We know that the ability to postpone germination (via dormancy) and the presence of soil-stored seed banks are critical for species persistence, particularly in times of environmental perturbation. However, traits studied in isolation often provide an incomplete view of the relevance of variation for adaptation. Studying patterns of trait covariation (and trade-offs) along environmental gradients may allow us to understand which traits are most important for persistence, and help us to understand the adaptive evolution of trait pairs.

Are some effects (fixed genetic and/or environmental plastic effects) more important for persistence? Finally, we must use common garden and reciprocal transplant studies to answer this last question. Studying populations distributed along clear environmental gradients can elucidate phenotypic effects of natural selection and reveal adaptive plant strategies. However, understanding how parent plants can alter specific developmental traits in their progeny to enhance the success of their offspring under stressful conditions necessitates large empirical studies with replicate plants grown in contrasting conditions and offspring subsequently raised under similar conditions to evaluate adaptive adjustments in seed traits.

vulnerable, for example in disturbance-prone or more climatically variable regions such as Mediterranean-climate regions, high-elevation ecosystems and coastal areas. Although data are beginning to accumulate, in particular for seed size, many questions remain unanswered, and the degree to which these traits vary among populations is mostly unknown. The difficulty in measuring some traits and the different approaches used often make comparisons problematic. Standardized methods for collecting and describing data related to seed studies will go a long way towards rectifying these problems.

A multifaceted and cross-disciplinary approach to research would recognize that species may be able to adjust to changes in climate by adapting via innate phenotypic plasticity (Parmesan, 2006) or evolutionary processes (Hoffmann & Sgro, 2011). As our data on within-species trait variation along environmental gradients grow we may be better able to apply quantitative methods to their analysis and identify general patterns with predictive power for assessing the role of among-population variation in seed traits in determining species response to climate change. Finally, we need to consider the consequences for community ecology of potentially large among-population variation in seed traits. Traditionally, between-species variation has been the broad concern of ecological theory; however, more recently emphasis has been placed on the importance of intraspecific trait variation for species coexistence and the dynamics of communities (Bolnick *et al.*, 2011; Violle *et al.*, 2012). As species rarely exist in isolation, the responses of individual populations to climate can be overshadowed by the lag effects of altered community-level interactions (Suttle *et al.*, 2007). Hence, future research will not only need to consider the direct impacts of climate change on among-population trait variation, but also the indirect effects arising from species interactions and their impact on community dynamics.

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REFERENCES

- Ackerly, D.D., Dudley, S.A., Sultan, S.E., Schmitt, J., Coleman, J.S., Linder, C.R., Sandquist, D.R., Geber, M.A., Evans, A.S., Dawson, T.E. & Lechowicz, M.J. (2000) The evolution of plant ecophysiological traits: recent advances and future directions. *BioScience*, **50**, 979–995.
- Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M. (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences USA*, **111**, 740–745.
- Albert, C.H., De Bello, F., Boulangeat, I., Pellet, G., Lavorel, S. & Thuiller, W. (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, **121**, 116–126.
- Alvarado, V. & Bradford, K.J. (2002) A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant, Cell and Environment*, **25**, 1061–1069.
- Anderson, J.T., Panetta, A.M. & Mitchell-Olds, T. (2012) Evolutionary and ecological responses to anthropogenic climate change. *Plant Physiology*, **160**, 1728–1740.
- Bañuelos, M.J. & Obeso, J.R. (2003) Maternal provisioning, sibling rivalry and seed mass variability in the dioecious shrub *Rhamnus alpinus*. *Evolutionary Ecology*, **17**, 19–31.
- Barua, D., Butler, C., Tisdale, T.E. & Donohue, K. (2012) Natural variation in germination responses of *Arabidopsis* to seasonal cues and their associated physiological mechanisms. *Annals of Botany*, **109**, 209–226.
- Baskin, C.C. & Baskin, J.M. (2001) *Seeds: ecology, biogeography, and evolution of dormancy and germination*, 2nd edn. Academic Press, San Diego, CA.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, **26**, 183–192.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review Ecology and Systematics*, **31**, 343–366.
- Chevin, L.-M., Lande, R. & Mace, G.M. (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLOS Biology*, **8**, e1000357.
- Childs, D.Z., Metcalf, C.J.E. & Rees, M. (2010) Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3055–3064.
- Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3149–3160.
- Chuine, I. & Beaubien, E.G. (2001) Phenology is a major determinant of tree species range. *Ecology Letters*, **4**, 500–510.
- Clausen, M.J. & Venable, D.L. (2000) Seed germination in desert annuals: an empirical test of adaptive bet hedging. *The American Naturalist*, **155**, 168–186.
- Cochrane, A., Hoyle, G., Yates, C., Wood, J. & Nicotra, A. (2014) Climate warming delays and decreases seedling emergence in a Mediterranean ecosystem. *Oikos*, DOI:10.1111/oik.01359.
- Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, **12**, 119–129.
- Davis, M.B., Shaw, R.G. & Etterson, J.R. (2005) Evolutionary responses to changing climate. *Ecology*, **86**, 1704–1714.
- Daws, M.I., Hall, J., Flynn, S. & Pritchard, H.W. (2007) Do invasive species have bigger seeds? Evidence from intra- and inter-specific comparisons. *South African Journal of Botany*, **73**, 138–143.

- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53–58.
- Donohue, K. (2002) Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. *Ecology*, **83**, 1006–1016.
- Donohue, K. (2005) Seeds and seasons: interpreting germination timing in the field. *Seed Science Research*, **15**, 175–187.
- Donohue, K. (2009) Completing the cycle: maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1059–1074.
- Donohue, K., Rubio De Casas, R., Burghardt, L., Kovach, K. & Willis, C. (2010) Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 293–319.
- Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B. & Singer, A. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–2131.
- Etterson, J.R. (2004) Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. 1. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution*, **58**, 1446–1456.
- Fenner, M. & Thompson, K. (2005) *The ecology of seeds*, 2nd edn. Cambridge University Press, Cambridge.
- Fernández-Pascual, E., Jiménez-Alfaro, B., Caujapé-Castells, J., Jaén-Molina, R. & Díaz, T. (2013) A local dormancy cline is related to the seed maturation environment, population genetic composition and climate. *Annals of Botany*, **112**, 937–945.
- Fordham, D.A., Resit Akçakaya, H., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C. & Brook, B. (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.
- Galloway, L.F. (2005) Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phytologist*, **166**, 93–100.
- Ghalambor, C.K., McKay, J.K., Carroll, S.P. & Reznick, D.N. (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, **21**, 394–407.
- Gremer, J.R., Crone, E.E. & Lesica, P. (2012) Are dormant plants hedging their bets? Demographic consequences of prolonged dormancy in variable environments. *The American Naturalist*, **179**, 315–327.
- Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Hedhly, A., Hormaza, J.I. & Herrero, M. (2009) Global warming and sexual plant reproduction. *Trends in Plant Science*, **14**, 30–36.
- Hoffmann, A.A. & Sgro, C.M. (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.
- Hovenden, M.J., Wills, K.E., Schoor, J.K.V., Chaplin, R.E., Williams, A.L., Nolan, M.J. & Newton, P.C.D. (2007) Flowering, seed production and seed mass in a species-rich temperate grassland exposed to FACE and warming. *Australian Journal of Botany*, **55**, 780–794.
- Hovenden, M.J., Newton, P.C.D., Wills, K.E., Janes, J.K., Williams, A.L., Vander Schoor, J.K. & Nolan, M.J. (2008) Influence of warming on soil water potential controls seedling mortality in perennial but not annual species in a temperate grassland. *New Phytologist*, **180**, 143–152.
- Hoyle, G.L., Daws, M.I., Steadman, K.J. & Adkin, S.W. (2008a) Pre- and post-harvest influences on physiological dormancy alleviation of an Australian Asteraceae species: *Actinobole uliginosum* (A. Gray) H. Eichler. *Seed Science Research*, **18**, 191–199.
- Hoyle, G.L., Steadman, K.J., Daws, M.I. & Adkins, S.W. (2008b) Pre- and post-harvest influences on seed dormancy status of an Australian Goodeniaceae species, *Goodenia fascicularis*. *Annals of Botany*, **102**, 93–101.
- Hoyle, G.L., Venn, S.E., Steadman, K.J., Good, R.B., McAuliffe, E.J., Williams, E.R. & Nicotra, A.B. (2013) Soil warming increases plant species richness but decreases germination from the alpine soil seed bank. *Global Change Biology*, **19**, 1549–1561.
- IPPC (2013) *Climate change 2013: the physical science basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY.
- Jump, A.S. & Peñuelas, J. (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.
- Kalisz, S. & Wardle, G.M. (1994) Life history variation in *Campanula americana* (Campanulaceae): population differentiation. *American Journal of Botany*, **81**, 521–527.
- Kattge, J., Diaz, S., Lavorel, S. *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.
- Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J. & Garnier, E. (2014) Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*, **25**, 235–247.
- Keeley, J.E. (1991) Seed germination and life history syndromes in the California chaparral. *Botanical Review*, **57**, 81–116.
- Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B. & Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.
- Kimball, S., Angert, A.L., Huxman, T.E. & Venable, D.L. (2010) Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Global Change Biology*, **16**, 1555–1565.
- Konarzowski, T.K., Murray, B.R. & Godfree, R.C. (2012) Rapid development of adaptive, climate-driven clinal variation in seed mass in the invasive annual forb *Echium plantagineum* L. *PLoS*, **7**, e49000.

- Kudoh, H., Nakayama, M., Lihova, J. & Marhold, K. (2007) Does invasion involve alternation of germination requirements? A comparative study between native and introduced strains of an annual Brassicaceae, *Cardamine hirsuta*. *Ecological Research*, **22**, 869–875.
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 321–350.
- Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds: ecology of regeneration in plant communities* (ed. by M. Fenner), pp. 31–57. CAB International, Wallingford.
- Levine, J.M. & Hillerislambers, J. (2009) The importance of niches for the maintenance of species diversity. *Nature*, **461**, 254–257.
- Levine, J.M., McEachern, A.K. & Cowan, C. (2008) Rainfall effects on rare annual plants. *Journal of Ecology*, **96**, 795–806.
- Linhart, Y.B. & Grant, M.C. (1996) Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics*, **27**, 237–277.
- Liu, J., Bai, Y., Lamb, E.G., Simpson, D., Liu, G., Wei, Y., Wang, D., McKenney, D.W. & Papadopol, P. (2013) Patterns of cross-continental variation in tree seed mass in the Canadian boreal forest. *PLoS ONE*, **8**, e61060.
- Lloret, F., Peñuelas, J. & Estiarte, M. (2005) Effects of vegetation canopy and climate on seedling establishment in Mediterranean shrubland. *Journal of Vegetation Science*, **16**, 67–76.
- Luna, B., Pérez, B., Torres, I. & Moreno, J. (2012) Effects of incubation temperature on seed germination of Mediterranean plants with different geographical distribution ranges. *Folia Geobotanica*, **47**, 17–27.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- McWilliams, E.L., Landers, R.Q. & Mahlstede, J.P. (1968) Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. *Ecology*, **49**, 290–296.
- Maschinski, J., Baggs, J., Quintana-Ascencio, P. & Menges, E. (2006) Using population viability analysis to predict the effects of climate change on the extinction risk of an endangered limestone endemic shrub, Arizona cliffrose. *Conservation Biology*, **20**, 218–228.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.
- Metz, J., Liancourt, P., Kigel, J., Harel, D., Sternberg, M. & Tielborger, K. (2010) Plant survival in relation to seed size along environmental gradients: a long-term study from semi-arid and Mediterranean annual plant communities. *Journal of Ecology*, **98**, 697–704.
- Meyer, S.E. & Kitchen, S.G. (1994) Life history variation in blue flax (*Linum perenne*: Linaceae): seed germination phenology. *American Journal of Botany*, **81**, 528–535.
- Meyer, S.E. & Monsen, S.B. (1991) Habitat-correlated variation in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seed germination patterns. *Ecology*, **72**, 739–742.
- Milbau, A., Graae, B.J., Shevtsova, A. & Nijs, I. (2009) Effects of a warmer climate on seed germination in the subarctic. *Annals of Botany*, **104**, 287–296.
- Milberg, P., Pérez-Fernández, M.A. & Lamont, B.B. (1998) Seedling growth response to added nutrients depends on seed size in three woody genera. *Journal of Ecology*, **86**, 624–632.
- Moles, A.T. & Westoby, M. (2003) Latitude, seed predation and seed mass. *Journal of Biogeography*, **30**, 105–128.
- Moles, A.T. & Westoby, M. (2004a) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, **92**, 372–383.
- Moles, A.T. & Westoby, M. (2004b) What do seedlings die from and what are the implications for evolution of seed size? *Oikos*, **106**, 193–199.
- Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A., Wood, J.T. & Westoby, M. (2007) Global patterns in seed size. *Global Ecology and Biogeography*, **16**, 109–116.
- Mondoni, A., Rossi, G., Orsenigo, S. & Probert, R.J. (2012) Climate warming could shift the timing of seed germination in alpine plants. *Annals of Botany*, **110**, 155–164.
- Morin, X. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **9**, 1301–1313.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F. & Van Kleunen, M. (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, **15**, 684–692.
- Norden, N., Daws, M.I., Antoine, C., Gonzalez, M.A., Garwood, N.C. & Chave, J. (2009) The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. *Functional Ecology*, **23**, 203–210.
- Ooi, M., Auld, T. & Denham, A. (2012) Projected soil temperature increase and seed dormancy response along an altitudinal gradient: implications for seed bank persistence under climate change. *Plant and Soil*, **353**, 289–303.
- Ooi, M.K.J. (2012) Seed bank persistence and climate change. *Seed Science Research*, **22**, S53–S60.
- Ooi, M.K.J., Auld, T.D. & Denham, A.J. (2009) Climate change and bet-hedging: interactions between increased soil temperatures and seed bank persistence. *Global Change Biology*, **15**, 2375–2386.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimatic

- envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Probert, R.J., Daws, M.I. & Hay, F.R. (2009) Ecological correlates of ex situ seed longevity: a comparative study on 195 species. *Annals of Botany*, **104**, 57–69.
- Quintana, J.R., Cruz, A., Fernández-González, F. & Moreno, J.M. (2004) Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of central Spain. *Journal of Biogeography*, **31**, 241–249.
- Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, **16**, 179–214.
- Rees, M. (1996) Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351**, 1299–1308.
- Rehfeldt, G.E., Tchekakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. & Milyutin, L.I. (2002) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology*, **8**, 912–929.
- Rodríguez-Pérez, J. & Traveset, A. (2007) A multi-scale approach in the study of plant regeneration: finding bottlenecks is not enough. *Perspectives in Plant Ecology and Evolution*, **9**, 1–13.
- Saatkamp, A., Affre, L., Dutoit, T. & Poschod, P. (2011) Germination traits explain soil seed persistence across species: the case of Mediterranean annual plants in cereal fields. *Annals of Botany*, **107**, 415–426.
- Sadeh, A., Guterman, H., Gersani, M. & Ovadia, O. (2009) Plastic bet-hedging in an amphicarpic annual: an integrated strategy under variable conditions. *Evolutionary Ecology*, **23**, 373–388.
- Sgrò, C.M., Lowe, A.J. & Hoffmann, A.A. (2011) Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, **4**, 326–337.
- Shevtsova, A., Graae Bente, J., Jochum, T., Milba, A., Kockelbergh, F., Beyens, L. & Nijs, I. (2009) Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology*, **15**, 2662–2680.
- Sides, C.B., Enquist, B.J., Ebersole, J.J., Smith, M.N., Henderson, A.N. & Sloat, L.L. (2014) Revisiting Darwin's hypothesis: does greater intraspecific variability increase species' ecological breadth? *American Journal of Botany*, **101**, 56–62.
- Siewert, W. & Tielborger, K. (2010) Dispersal–dormancy relationships in annual plants: putting model predictions to the test. *The American Naturalist*, **176**, 490–500.
- Simons, A.M. (2009) Fluctuating natural selection accounts for the evolution of diversification bet hedging. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1987–1992.
- Simons, A.M. (2011) Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1601–1609.
- Simons, A.M. & Johnston, M.O. (2006) Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging. *Evolution*, **60**, 2280–2292.
- Smith, P., Dickie, J., Linington, S., Probert, R. & Way, M. (2011) Making the case for plant diversity. *Seed Science Research*, **21**, 1–4.
- Starrfelt, J. & Kokko, H. (2012) Bet-hedging – a triple trade-off between means, variances and correlations. *Biological Reviews*, **87**, 742–755.
- Steadman, K.J., Ellery, A.J., Chapman, R., Moore, A. & Turner, N.C. (2004) Maturation temperature and rainfall influence seed dormancy characteristics of annual ryegrass (*Lolium rigidum*). *Australian Journal of Agricultural Research*, **55**, 1047–1057.
- Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. & Thomas, C.D. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, **120**, 1–8.
- Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.
- Tielbörger, K., Petrů, M. & Lampei, C. (2012) Bet-hedging germination in annual plants: a sound empirical test of the theoretical foundations. *Oikos*, **121**, 1860–1868.
- Turner, S.R., Steadman, K.J., Vlahos, S., Koch, J.M. & Dixon, K.W. (2013) Seed treatment optimizes benefits of seed bank storage for restoration-ready seeds: the feasibility of pre-storage dormancy alleviation for mine-site revegetation. *Restoration Ecology*, **21**, 186–192.
- Venable, D. (2007) Bet hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.
- Venable, D.L. & Brown, J.S. (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist*, **131**, 360–384.
- Venable, D.L., Búrquez, A., Corral, G., Morales, E. & Espinosa, F. (1987) The ecology of seed heteromorphism in *Heterosperma pinnatum* in central Mexico. *Ecology*, **68**, 65–76.
- Vergeer, P. & Kunin, W.E. (2011) Life history variation in *Arabidopsis lyrata* across its range: effects of climate, population size and herbivory. *Oikos*, **120**, 979–990.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution*, **27**, 244–252.
- Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 649–659.

- Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D. & Yates, E. (2010) Assisted migration of plants: changes in latitudes, changes in attitudes. *Biological Conservation*, **143**, 18–27.
- Völler, E., Auge, H., Prati, D., Fischer, M., Hemp, A. & Bossdorf, O. (2012) Geographical and land-use effects on seed-mass variation in common grassland plants. *Basic and Applied Ecology*, **13**, 395–404.
- Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K.E.N. & Poschlod, P. (2011) Climate change and plant regeneration from seed. *Global Change Biology*, **17**, 2145–2161.
- Walther, G.-R. (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2019–2024.
- Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K.A., Byrne, M., Coates, D.J., Eldridge, M.D.B., Sunnucks, P., Breed, M.F., James, E.A. & Hoffmann, A.A. (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications*, **4**, 709–725.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review Ecology and Systematics*, **33**, 125–129.
- Yates, C.J., Ladd, P.G., Coates, D.J. & McArthur, S. (2007) Hierarchies of cause: understanding rarity in an endemic shrub *Verticordia staminosa* (Myrtaceae) with a highly restricted distribution. *Australian Journal of Botany*, **55**, 194–205.
- Yates, C.J., Elith, J., Latimer, A.M., Maitre, D.L., Midgley, G.F., Schurr, F.M. & West, A.G. (2010) Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: opportunities and challenges. *Austral Ecology*, **35**, 374–391.
- Zhao, X., Liu, W. & Zhou, M. (2013) Lack of local adaptation of invasive crofton weed (*Ageratina adenophora*) in different climatic areas of Yunnan Province, China. *Journal of Plant Ecology*, **6**, 316–322.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Summary of 54 key studies assessing among-population variation in seed traits and their findings. Additional references to data sources can be found at the end of Appendix S1.

BIOSKETCH

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