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Germination, Postgermination Adaptation, and Species Ecological Ranges

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Abstract

Germination behavior is one of the earliest phenotypes expressed by plants. This fact has several consequences for the evolution of postgermination traits, ecological niches, and geographic ranges. By determining the conditions that plants experience after they germinate, germination influences phenotypic expression of postgermination traits, natural selection on them, and their genetic basis. The breadth of germination niches may influence the ecological breadth and geographic ranges of species. Because germination is expressed early, it is frequently subjected to natural selection before other traits are expressed. We review evidence for natural selection on and adaptation of germination and discuss how the breadth of the germination niche is associated with the ecological niche and range of plant species. We review evidence for the coevolution of germination and postgermination traits and compare germination to postgermination niches. Finally, we discuss how germination responses to altered environments can influence species distribution and the evolution of postgermination traits after environmental change.

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1. INTRODUCTION: GERMINATION AS THE FIRST MAJOR DEVELOPMENTAL TRANSITION IN THE LIFE OF PLANTS

In Kingsley Amis's novel Lucky Jim, Jim Dixon makes a wee transgression early on, drinking a bit too much at a local pub. This inebriation caused him regrettably to fall asleep and burn the bedsheet of his boss's guestbed; in turn, this inspired him to mutilate the sheet with a razor, receive a fake phone call, quit the scene, impersonate a reporter. As one deceit builds upon another, the ramifying effects of early events propel the whole story.

The consequences of early actions can last a surprisingly long time. They shape not only the individuals that perpetrate them but the environment that surrounds them. This initial state influences what individuals do next, how successful they may be, and even where they are welcome. Every living thing that behaves and develops must deal with the consequences of its previous actions and responses. This makes early decisions and transitions of the utmost importance.

Among the earliest events that occur in the lifetimes plants is germination. The transition from seed to germinant is one of the most drastic developmental transitions that plants experience. They change from heterotroph to autotroph, from quiescent to active, from protected within a seed coat to exposed to all ambient elements. Many plants have elaborate checks on germination, which require very particular environmental conditions or even sequences of environmental factors to break dormancy and elicit germination. This review considers how this single developmental transition influences plant adaptation, ecological breadth, and geographic range.

Germination is especially important for plant adaptation because, being among the earliest life-stage transitions, it sets the context for subsequent development and natural selection. The environmental conditions that elicit germination are those that the new germinant must contend with, and in many cases those early conditions predict the environment experienced throughout the life of the plant. As such, the conditions under which a seed germinates will influence not only seedling survival but also the phenotypic expression of postgermination traits and environment-dependent selection on those traits. To the extent that genetically based germination behavior responds to natural selection, it influences the genetic context within which postgermination traits evolve. Thus, germination has the potential to influence the evolution of traits expressed throughout the life of plants.

The compounding effects of germination on the entire life cycle of plants imply that investigations of plant adaptation would benefit from explicitly considering the interactions between germination and postgermination traits. Given that germination determines aspects of the environment that is experienced, whenever natural selection on postgermination traits is environment-dependent, combinations of germination and postgermination traits might determine plant fitness more predictably than any trait singly. Germination cuing may also determine the environmental consistency—and therefore the consistency of natural selection—experienced by postgermination traits.

To address the consequences of such interactions between germination and postgermination traits, we first review evidence for natural selection on germination itself and how such selection defines a germination niche. We next review evidence for the coadaptation of germination and postgermination traits and evidence that germination influences the expression of and natural selection on postgermination traits. We discuss how species ecological ranges can be influenced by the germination niche and its relationship to postgermination niches. To conclude, we discuss how germination responses to altered environments can influence the evolution of postgermination traits after environmental change.

2. ADAPTATION IN DORMANCY AND GERMINATION PHENOLOGY

As one of the earliest traits that is expressed by plants, germination has the potential to be subject to strong natural selection: A plant needs to survive the seedling stage before it can express any adaptive traits later in life. Evidence that germination is subject to natural selection and contributes to local adaptation is reviewed below.

2.1. In or Out of the Seed Bank

Three main factors determine the adaptive value of germination behavior. Germination can be an escape from unfavorable conditions in the seed bank, dormancy can be a bet-hedging strategy in unpredictable environments above ground, or germination cuing can enable germination under optimal conditions for survival and/or growth.

Escape from the seed bank may increase survival if predators or pathogens attack seeds more than seedlings. Seed predation is frequently a major source of mortality (Wenny 2000), and if conditions are favorable for seedling growth then rapid germination could be advantageous (Xiao et al. 2007). Viability in the seed bank is required for dormancy to be adaptive, or seeds may die before they germinate, so the adaptive value of dormancy depends on the relative risk of mortality of the seeds in the soil versus mortality of the germinant. Intrinsic longevity in the soil also becomes an issue; if seeds are poorly provisioned or metabolically too active to withstand long periods before germination, then protracted dormancy would lead to seed mortality (Dalling et al. 1997).

Dormancy is favored as a bet-hedging strategy in temporally unpredictable environments (Venable & Brown 1988, Venable 2007, Venable & Lawlor 1980). Germination cuing may induce germination under favorable conditions, but those conditions may not persist long enough for survival and reproduction. The prevention of germination of some seeds even under presently favorable conditions can therefore reduce the risk of extinction if the conditions were to turn unfavorable. Moreover, some years may be more favorable than others, so dormancy of a proportion of seeds can increase the probability that some individuals will experience the best years. The greater the temporal variance in survival and reproductive success, the more favorable is dormancy as a bet-hedging strategy (Venable & Lawlor 1980). In some desert annuals, species with higher interannual variation in reproductive success had lower germination fractions, providing evidence for adaptive bet hedging via dormancy (Pake & Venable 1996). However, despite their bet hedging, the plants also germinated more during years in which they had high reproductive success, suggesting that the seeds also perceived particularly favorable conditions and germinated accordingly.

Accurate germination cuing—perceiving favorable conditions for growth and reproduction and germinating when those conditions are present—thus appears to be important even in species with large degrees of bet hedging. The optimal germination time is likely to depend on a number of opposing factors; depending on their balance within any given year, natural selection might favor early, intermediate, or late germination, and selection might be variable in both space and time (see below). Therefore, bet-hedging dormancy, in addition to germination cuing, is likely to be the most consistently favorable germination strategy.

2.2. Evidence for Natural Selection on Germination Phenology

Conflicting factors exert natural selection on germination phenology (**Table 1**). Although higher fecundity results from earlier germination, factors that induce mortality are frequently variable in space and time (**Figures 1** and **2**).

Table 1 Natural selection on germination timing

	Early germination favored	Later germination favored	Stabilizing	Variable in space and/or time	None
Natural selection via postgermination survival	Seiwa 1998 Jones et al. 1997 Donohue 2002 Leger et al. 2009 Kelly & Levin 1997 Castro 2006 Kalisz 1986 Shimono & Kudo 2003	Kalisz 1986 Shimono & Kudo 2003 Blaire & Wolfe 2004	Fernandez-Quintanilla et al. 1986 Kalisz 1986 Donohue et al. 2005 Blaire & Wolfe 2004	Kalisz 1986 Shimono & Kudo 2003	
Natural selection via size or fecundity	Donohue 2002 Fernandez-Quintanilla et al. 1986 Kalisz 1986 Seiwa 2000 Simons & Johnston 2000 (could be a side effect of seed size) Gross & Smith 1991 Donohue et al. 2005				
Viability versus fecundity not determined	Bertin 2001 Boquet & Clawson 2009 Benard & Toft 2007 Stinchcombe & Schmitt 2006	Stratton 1992	Stratton 1992	Stratton 1992	Seiwa 2000

Early germination:
Increases fecundity via
larger size at reproduction and
longer reproductive duration

Mortality event

Later germination:
Increases survival
contingent on mortality event
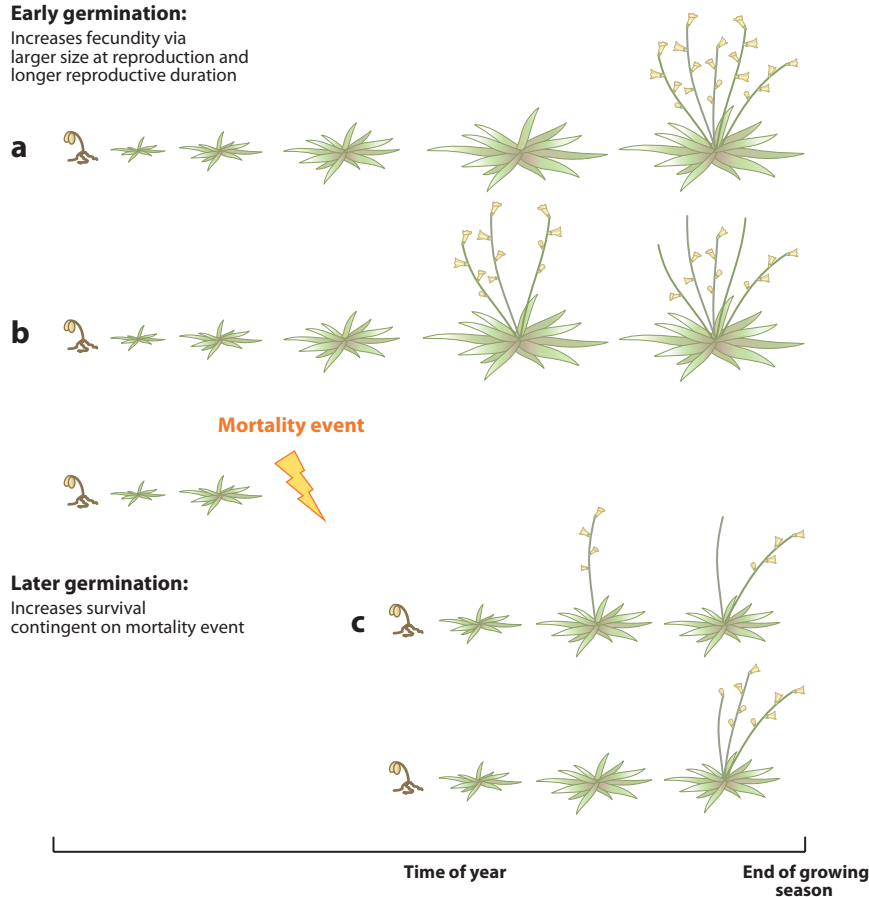
Time of year

**End of growing
season**

Figure 1

Natural selection on germination. Fecundity selection consistently favors early germination; (*a*) early
germination permits plants to attain larger sizes before reproduction or (*b*) lengthens the reproductive period.
(*c*) Mortality selection can favor late germination, contingent on the occurrence of the mortality event.

Selection for increased fecundity consistently favors early germination (**Table 1**). Early germi-
nation provides a competitive advantage, enables plants to reach a larger size before reproduction,
and/or provides a longer period during which reproduction occurs, all of which increase fecundity.

Mortality selection, in contrast, can favor either early or delayed germination, depending
on when the environmental factor that causes mortality occurs (**Table 1**). Various studies have
demonstrated mortality selection favoring early germination (Benard & Toft 2007, Castro 2006,
Donohue 2002, Jones et al. 1997, Seiwa 1998, Shimono & Kudo 2003, Stanton 1985) intermediate
germination time (Donohue et al. 2005, Fernandez-Quintanilla et al. 1986), and late germination
(Purrington & Schmitt 1998, Weekley et al. 2007). In at least one study, germination time had no
effect on survival (Seiwa 2000). Furthermore, selection on germination timing operating through
survival appears to be heterogeneous both in space and time within a given species. For instance,
in *Collinsia verna*, mortality selection varied between years and varied spatially within a given year
in (Kalisz 1986). Likewise in *Erigeron annuus*, the direction and mode (directional, stabilizing, or
disruptive) of selection on germination time exhibited spatial variation (Stratton 1992).
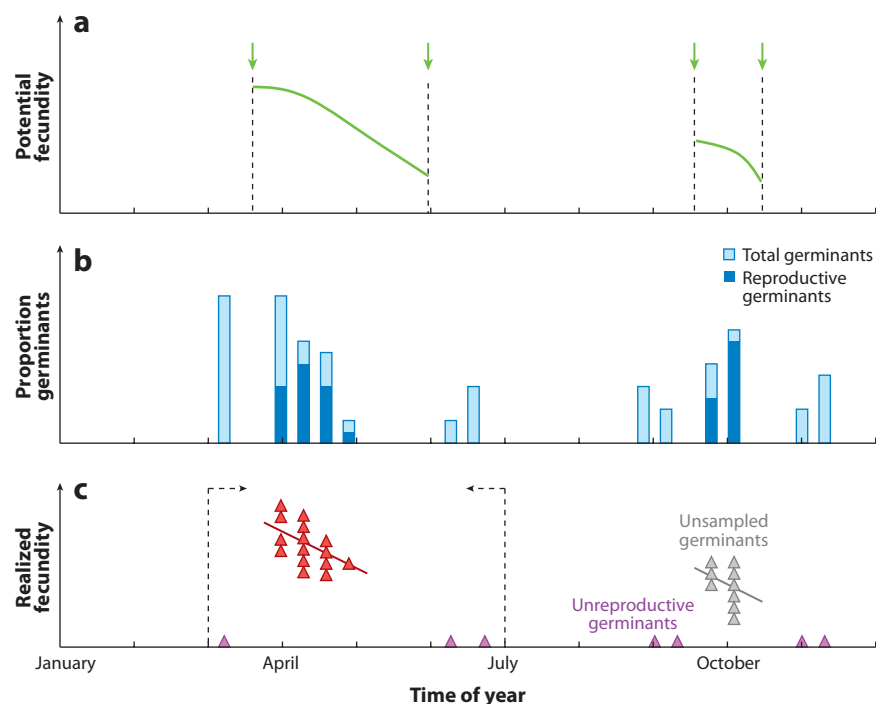
Figure 2

Effect of experimental sampling on estimates of selection on germination timing. (*a*) Fecundity of seeds that germinate at particular times of year. Green arrows indicate seasonal seedling mortality events whereby no fecundity can be measured because no seedlings survive to reproduce. (*b*) Natural germination timing of a hypothetical species. Bars show proportion of seedlings germinating over time. Dark blue portion of bars is the proportion of germinants that survive and can reproduce. (*c*) Fecundity of natural germinants, as in panel *a*. The time period sampled by the researcher is between the dashed lines. Because only one of the two germination periods was sampled (unsampled depicted by *gray triangles*), the fecundity of the fall germinants was not observed. In addition, seedlings that did not survive to reproduce (0 fecundity, *purple triangles*) are not included in the estimates of the relationship between germination time and fecundity.

Combined effects of fecundity and survival can create stabilizing selection, favoring an intermediate germination time (Donohue et al. 2005, Fernandez-Quintanilla et al. 1986). Surprisingly, stabilizing selection is not as frequently observed as one might predict. One reason may be methodological; in situ observations might miss very early or very late germination events (**Figure 2**). In addition, natural selection itself may have eliminated extreme variants within a given location, preventing the detection of stabilizing selection. When germination phenology has been manipulated either phenotypically by forcing germination at different times (Boquet & Clawson 2009) or genetically by introducing a genetically variable sample that had not been previously exposed to selection (Donohue et al. 2005), strong stabilizing selection has been detected. Most studies that documented that early germination was favorable did not include cohorts that germinated soon after dispersal. As a consequence, when considering the full spectrum of possible germination times throughout the year, an intermediate optimum germination time is likely much more common than is documented, even though natural selection on extant variants is directional.

In summary, the balance between viability and fecundity selection is likely to vary, as is the precise optimal time for germination within any given year. Accurate

cuing combined with bet-hedging dormancy is likely to be advantageous under such conditions.

2.3. Indirect Evidence of Adaptation in Germination: Changes in Germination in New Habitats

Numerous studies have documented that variation in germination among and within taxa is associated with habitat (reviewed in Baskin & Baskin 1998). While a review of this literature is beyond the scope of the present review, such patterns suggest local adaptation in germination. Studies showing that germination behavior has changed when the species has changed its environment or range also provide evidence for adaptation in germination.

Comparisons of native and introduced populations of the same species have shown differences in germination. Sometimes, the introduced populations have a wider range of conditions in which its seeds can germinate or they germinate faster (Blair & Wolfe 2004, Cervera & Parra-Tabla 2009, Erfmeier & Bruelheide 2005, Lortie et al. 2009). Sometimes, introduced populations are more dormant (Hierro et al. 2009, Kudoh et al. 2007). In some such cases, the increased dormancy has been interpreted to be adaptive, for example, by preventing germination inappropriately in summer conditions (Hierro et al. 2009). In *Cardamine hirsuta*, native populations were more variable in their germination responses, whereas introduced populations comprised a subset of these germination phenotypes and exhibited stronger seed dormancy (Kudoh et al. 2007). Introduced populations may therefore differ from native populations due to adaptation or lineage sorting, or due to sampling alone.

Other studies document changes in germination that have accompanied alterations to the environment. In a review of adaptation to agricultural conditions, Clements et al. (2004) hypothesized that the increase in dormancy observed in some weeds that are associated with crops is an adaptation to tilling regimes. It has been suggested that native weeds tend to be fugitive species, which may consequently be selected for lower dormancy to take advantage of ephemeral habitats. When they colonize crops, delayed germination and seed banking is likely to offer escape from weed management practices.

Other anthropogenic alterations of the environment are associated with germination differences, suggesting that germination can evolve quickly. For example, weedy grasses in golf courses have different dormancy depending on the management regime within particular locations in the greens (Itoh et al. 1997). Populations of some species that inhabit areas of contamination are more able to germinate in contaminated areas than other populations (Ferasol et al. 1995, Rout et al. 2000), and populations that have expanded their range into human altered habitats, such as roadsides, also have increased abilities to germinate under such conditions (Greipsson et al. 1997). Populations that differ in herbicide resistance also can differ in germination (Ghersa et al. 1994, Gill et al. 1996).

Evidence is therefore consistent with rapid evolution of germination accompanying environmental change. However, observational reports require explicit experimental manipulations to document that the change in germination is actually adaptive in the new environment. In addition, it is possible that adaptive germination can result not from genetic evolution but from adaptive maternal effects on germination. Few of the studies mentioned above distinguished between genetic adaptation and maternal effects.

2.4. Evidence of Local Adaptation in Germination

The studies above provide evidence that natural selection on germination occurs and that natural variation in germination can be associated with habitat change. Demonstrating local adaptation,

however, requires reciprocal sowings of natural genotypes and estimations of their fitness. Surprisingly few studies have documented local adaptation in germination in this manner. *Silene ciliata* exhibited local adaptation in emergence and seedling survival at small spatial scales at high altitude, and such local adaptation was hypothesized to contribute to the persistence of the species at its range margins (Giménez-Benavides et al. 2007). In *Clarkia* species, germination ability did not exhibit local adaptation, but postgermination survival did, although it is not clear the extent to which variation in germination phenology contributed to those differences in survival (Geber & Eckhart 2005). In *Tragopogon pratensis*, seeds from roadside populations germinated faster and to higher percentages when grown in roadside locations than did those from nonroadside populations (Jorritsma-Wienk et al. 2007). *Bromus tectorum* showed local adaptation in germination, operating through seedling survival, in low-elevation sites but not high-elevation sites (Leger et al. 2009), and Szarek et al. (1998) reported local adaptation in germination in *Encelia farinose*. In a community of species associated with thyme, a number of species were able to germinate and grow better on the terpene of the thyme with which it co-occurred, exhibiting local adaptation to its associated thyme species (Grondahl & Ehlers 2008). Galloway & Fenster (2000) found in *Chamaecrista fasciculate* that germination proportion and overall fitness were higher for genotypes of local origin. In a comparative study using three common European grassland species (*Holcus lanatus*, *Lotus corniculatus* and *Plantago lanceolata*), Bischoff et al. (2006) found evidence of germination-mediated local adaptation in at least one of the three species (*P. lanceolata*).

Even reciprocal sowing studies provide ambiguous evidence for adaptation of germination cuing when germination percentage is the only germination characteristic that is measured. Neither the optimal fraction germination for a particular year or habitat is typically known, nor is the proportion of seeds that remain viable in the soil. Thus, although native sources may germinate to higher percentages in their home site, increased germination may not always be adaptive: exhibiting greater dormancy under the conditions of the experiment could possibly increase lifetime fitness.

Knowing only overall germination percentages also does not provide information on the fitness of individuals that germinated at different times: All seed sources in an experiment may germinate within the course of the experiment, but some may have germinated too early, some too late, and some just right. Testing for local adaptation in germination timing requires characterizing the fitness surface of germination timing, and then determining whether local seed sources are closer to the optimum fitness time.

Characterizing such fitness surfaces may require phenotypic or genetic manipulations in order to capture the extremes; because germination timing is sometimes under such strong selection (Donohue et al. 2005, Huang et al. 2010), these extremes may be eliminated rapidly in natural populations. This makes the detection of adaptation more difficult because of the lack of variance.

Finally, the vast majority of studies that investigate natural variation in germination are conducted with field-collected seeds. The environmental conditions during seed maturation in the field are likely to have strong effects on germination behavior (Donohue 2009). Demonstrating that native seeds have a fitness advantage in their home site does not, therefore, demonstrate local genetic adaptation, but may be the result of adaptive maternal effects instead.

The scarcity of explicit tests for local adaptation in germination precludes any generalizations except to say that more and more detailed studies are necessary. Although abundant anecdotal evidence exists for local adaptation in germination, in the form of correlations between germination and habitat, such observations do not demonstrate local adaptation. Considering the potential importance of adaptation in germination for defining species niches and ranges, explicit tests of local adaptation in germination phenology would contribute strongly to our understanding of these processes.

3. GERMINATION-POSTGERMINATION INTERACTIONS

So far, we have considered the effects on adaptation of germination alone. However, because germination occurs at one of the earliest life stages, it has the potential to have lasting effects on plants throughout their lives. This is because the timing and conditions of germination determine the ecological environment subsequently experienced by that plant, and that environment can influence phenotypic expression and natural selection on postgermination traits. Here we discuss evidence that germination influences postgermination trait expression, selection, and evolution.

3.1. The Integrated Organism: Associations between Germination and Postgermination Traits

If germination cuing is an effective mechanism of habitat selection, such that seeds germinate preferentially in environments in which they perform better (or which predict environments in which they perform better), germination responses are predicted to be associated with postgermination performance and with traits that determine that performance (**Figure 3**). Indeed, to the extent that natural selection on germination occurs through environment-dependent performance after germination, such correlations could be a byproduct of selection on germination and postgermination traits; seeds that germinate under particular conditions would not survive unless they also had the physiological properties to withstand and reproduce in that environment. Individual or genetic variation in germination cuing, accompanied by variation in environment-dependent fitness would create associations between germination and postgermination traits (**Figure 3a**).

However, associations between germination and postgermination traits are not always expected. First, if individual (or genotypic) germination niches are overlapping, or if environmental conditions are highly permissive and elicit germination of diverse individuals, such associations would not be expected even if selection after germination is environment-dependent (**Figure 3b**). This would occur when the environmental conditions that permit postgermination survival or reproduction are a subset of those that elicit germination.

In addition, postgermination niches affect the association between germination and postgermination trait (**Figure 3c**). Such associations would not be expected when individuals (or genotypes) have overlapping postgermination niches, if the environmental factor that exerts selection on postgermination traits is unrelated to the environmental factor that elicits germination or if postgermination performance is not environment dependent. Such would be the case if some postgermination traits were always advantageous regardless of the conditions in which a seed germinated.

In short, whether associations between germination and postgermination traits are expected depends on the degree of overlap among variants in their germination or postgermination niches, the range of environmental conditions they experience, and the degree to which the conditions that elicit germination also impose or predict natural selection on postgermination traits.

Admittedly, associations between germination and postgermination traits can only be assessed with the variance that remains in those traits, not variance that no longer exists. Thus, it may be that all individuals within a taxon germinate in autumn and are cold-resistant, with no variance in either germination or coldtolerance and, thus, no association between the two traits, even though cold tolerance evolved because germination occurred in increasingly cooler conditions. A positive association between germination and postgermination traits would be evidence of either correlational selection or pleiotropy between the traits; a lack of association cannot necessarily be interpreted as the independent past evolution of those traits.

Diverse taxa show associations between germination and postgermination traits, especially at the seedling stage (**Table 2**). Seeds germinate to higher percentages in environments in which
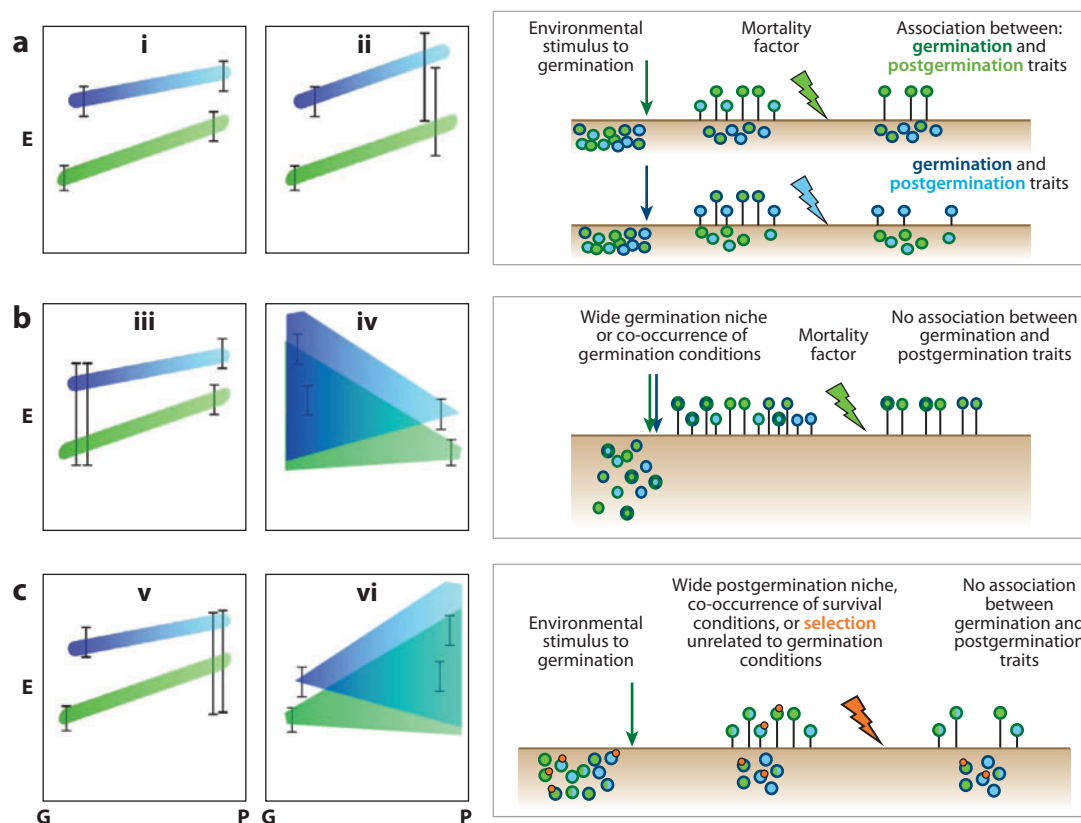
Figure 3

Co-adaptation of germination and postgermination traits. The germination niche is G, and the postgermination niche is P, as determined by the environmental scenario, E. Black vertical bars represent the range of environmental conditions (with respect to E) in which a single genotype can germinate (G), or survive and reproduce after germination (P). Colored bands represent different environmental scenarios to which the encompassed genotypes are exposed and in which they can successfully germinate and survive/reproduce. Left-hand panels: Effect of niche overlap of individual genotypes. When genotypes overlap in germination or postgermination niche, associations between germination and postgermination traits are expected to be weak. Center panels: Effect of the range of conditions permissible for germination and postgermination survival to which the variants are exposed. Right-hand panels: Individuals with combinations of germination (*outline color*) and postgermination (*central color*) phenotypes in existence in the soil (*left, below line*). Some germinate (*middle, above line*), and a subset of germinants survive (*right*). (*a*) Association between germination and postgermination traits is expected. In any given environmental scenario, only a subset of genotypes germinates and survives, and conditions of postgermination survival are associated with the conditions of germination; those that germinate under dark green conditions, for example, only survive under light green conditions, and likewise for blue conditions. Note that the environmental factor can change between germination and postgermination selection—that is, the slope of the line indicating the relationship between conditions of germination and postgermination survival is not necessarily zero—yet germination and postgermination conditions are nevertheless associated. Note also that associations can occur even if postgermination (or germination) niches are wide (*ii*), provided they do not overlap completely (compare to *i*). (*b*) No association between germination and postgermination traits is expected. All genotypes have equivalent germination because either all genotypes are capable of germinating in a large range of conditions (*iii*) or environmental conditions that are present encompass the full range of germination requirements for all genotypes (*iv*). (*c*) No association between germination and postgermination traits is expected. All genotypes have equivalent postgermination survival because either all genotypes are capable of surviving in a large range of conditions (*v*) or natural selection is weak or not highly environment dependent with respect to the environmental factor that elicits germination (*vi*).

seedlings grew or survived better, with respect to light, temperature, ion concentrations, terpene type, or simply geographic location. Moreover, germination niche breadth sometimes reflects seedling niche breadth; variants that were more capable of germinating in conditions of environmental stress, such as drought, high salinity, or heat stress, also had seedlings that were more resistant to those conditions. Likewise, seedlings that were not capable of surviving some conditions also did not germinate in those conditions.

In other cases, differences in germination responses to particular environmental factors did not predict differences in postgermination performance. Germination of some Korean species was stimulated by the presence of polycyclic aromatic hydrocarbon contaminants, but seedling growth of all species was comparably depressed (Hong et al. 2009). In *Centaurea*, burnt soil inhibited germination, even though the nutrient release from burning increased seedling growth; however, seedlings also grew better in shade, which would be eliminated by fire (Riba et al. 2002). In other examples, germination showed some evidence of adaptation in terms of germination percentages, but seedling performance did not (Jorritsma-Wienk et al. 2007). In some cases, seeds tended to germinate in environments that were actually less favorable for seedling survival. In *Erythronium grandiflorum*, for example, seeds preferentially germinated in locations that increased the risk of seedling predation (Thomson et al. 1996).

In these examples in which associations were observed, it is not known whether the association was due to pleiotropy or linkage disequilibrium caused by correlational selection. It is easy to imagine that physiological tolerances or optima might be shared by seeds and seedlings because of shared genetic and physiological pathways. In *Brassica oleracea* (Bettey et al. 2000), germination and seedling growth were shown to be genetically distinct, but other studies have documented pleiotropy between germination and flowering time (Burgess et al. 2007, Chiang et al. 2009) or other vegetative traits such as leaf length (Van Hinsberg 1998).

Evidence is therefore mixed concerning the coadaptation of germination and early postgermination traits. In examples in which associations have been documented, it is not known whether the association is due to pleiotropy or linkage disequilibrium. In short, we know very little about how accurately germination cuing achieves habitat selection, that is, accurately matching the conditions of germination with conditions for subsequent growth and survival of a particular genotype. It does appear, however, that an increase in the range of physiological tolerances of germination sometimes corresponds to a wider range of tolerances for seedling growth and survival. Thus, increases in the range of germination conditions could provide the opportunity for adaptation of postgermination traits to a wider range of conditions—these are opportunities that would not occur if germination were not possible under those conditions. Even so, pleiotropy itself could account for such associations.

Distinguishing between these possibilities requires genetic studies that disrupt potential linkage disequilibrium between germination and postgermination traits, as well as selection studies that explicitly test the adaptive value of particular combinations of germination strategies and postgermination phenotypes. Phenotypic or genetic manipulations of germination timing and postgermination traits could enable measurements of correlational selection. Studies that impose selection on germination or postgermination traits could test for correlated responses to such selection.

3.2. Effects of Germination Timing on Postgermination Traits: Phenotypic Expression, Natural Selection, and Genetic Basis

The environmental conditions under which germination proceeds determine the environmental conditions experienced after germination (Donohue 2003, Donohue et al. 2005). Due to phenotypic plasticity, the expression of postgermination traits can differ depending on when the

Table 2   Evidence of associations between germination and postgermination traits

Species	Germination cue	Seedling trait	Matching of optima/increase in range	Association and interpretation	Reference
Gossypium hirsutum (cultivated cotton)	High temperature (40°C)	High temperature tolerance	Increase in range	Lines that could germinate at high temperature could also survive at high temperature	Ashraf et al. (1994)
Tillandsia flexuosa and *T. fasciculata*	Water availability, drought	Drought tolerance	Increase in range	*T. flexuosa* was able to germinate and grow better in drier habitats than *T. fasciculata*	Bader et al. (2004)
Spartina alterniflora	Sowing depth and habitat	Emergence from various burial depths	Matching	Germination was highest at soil depths where seedling survival was highest	Deng et al. (2009)
Vaccinium myrtillus, *V. oxycocos* and *V. vitis-idae*	Germination in the site of preponderance	Seedling-juvenile growth in the site of preponderance	*V. oxycocos*: matching *V. vitis-idea* and *V. myrtillus*: lack of matching	*V. oxycocos*: germination was highest in sites where adults persisted, although adults persisted in a subset of those sites *V. vitis-idea* and *V. myrtillus*: germination was not higher in sites of greater juvenile and adult juvenile persistence	Eriksson (2002)
Four *Eucalyptus* species	Darkness and water potential	Growth under leaf litter versus barren soil	Matching	Germination predominantly occurred under conditions favorable for seedlings	Facelli & Ladd (1996)
Pinus cembra and *Pinus sylvestris*	Germination in lowland, alpine, and arctic sites	Seedling survival at the diverse sites	Matching	Germination was highest at sites where seedling survival was highest	Hattenschwiler & Korner (1995)
55 Korean Species	Polycyclic aromatic hydrocarbons (PAHs)	Seedling growth in the presence of PAHs	No clear pattern	Some species were stimulated to germinate, others inhibited, but no species was capable of growing with a high level of PAHs	Hong et al. (2009)

Species	Environmental factor	Response measured	Type	Description	Reference
Six tropical species (*Aspidosperma cruenta*, *Ceiba pentandra*, *Cordia alliodora*, *Gustavia superba*, *Luehea seemannii*, *Ochroma pyrimidale*)	Shade versus full light	Growth in shade	Matching	Shade-adapted species (*A. cruenta* and *G. superba*) germinated better in shade	Molofsky & Augspurger (1992)
Lasthenia californica and *L. gracilis*	High ion content (Na^+, K^+, Mg^{2+}, Ca^{2+})	Survivorship and growth in specific soil types	Increase in range	Species that were more capable of germinating in high ion concentrations were also more capable of growing there	Rajakaruna et al. (2003)
Suaeda splendens	Salinity levels	Survival and growth under high salinity	Increase in range	Seed morphs that were more capable of germinating at high salinity were more capable of growing there	Redondo-Gomez et al. (2008)
Echinochloa colona	Chromium and nickel	Growth in mining sites	Increase in range	Genotypes that were more capable of germinating in contaminated sites also were more capable of growing there	Rout et al. (2000)
33 diverse species	Habitat patches with higher germination%	Seedling survival in patches with higher germination	Some matching	Survival was better in locations of high germination in 61% of the species	Schupp (1995)
Suaeda salsa	Salinity levels	Abundance of adults at high salinity	Increase in range	Plants that grew at high salinity had seeds that could germinate at high salinity	Song et al. (2008)
Hordeum spontaneum	Sites that differed in soil moisture and frost	Establishment in different sites	Matching	Germination was higher in home sites where survival was higher	Volis et al. (2002)
Agathis australis	Gaps	Establishment success	Matching	Germination and seedling survivorship were both higher in the forest gaps	Ogden et al. 1987
Plantago lanceolata	Low red:far red	Seedling growth	Matching	Germination was inhibited at low red:far red, where seedlings grew smaller	Van Hinsberg 1998

seeds germinated. In *Arabidopsis thaliana*, for example, rosettes are larger and reproduction occurs at a larger size when seeds germinate in autumn than when seeds germinate in spring (Donohue 2002, Donohue et al. 2005, Korves et al. 2007). The timing of germination also influences the timing of flowering. In *Campanula(strum) americanum*, seeds that germinate in autumn flower the following spring, whereas seeds that germinate in spring do not flower until the following spring (Galloway 2001, 2002) because they do not receive a winter vernalization period to stimulate flowering that first year. Thus, germination timing determines whether an annual or biennial life cycle is expressed.

Such effects of germination timing clearly operate through its effect on the seasonal environmental conditions experienced after germination. In the case of *C. americanum*, the critical seasonal environmental factor was winter vernalization. In *Arabidopsis thaliana*, Wilczek et al. (2009) modeled and measured flowering time as a function of the rate of accumulation of photothermal units throughout the season. Seeds that germinated early in autumn accumulated enough units to flower in autumn, whereas seeds that germinated only two weeks later did not, and they postponed flowering until the following spring. In a more extreme example (Donohue 2002), also in *A. thaliana*, seeds that germinated in the spring produced rosettes that never received the environmental conditions required for reproduction and so died before reproducing.

Germination timing also influences natural selection on postgermination traits. In *A. thaliana*, the timing of germination influenced the strength, direction, and mode of selection on reproductive timing and size (Donohue 2002, Donohue et al. 2005). In *Abutilon theophrasti* (Weinig 2000), selection on shade-avoidance responses depended on germination time, with elongation being favored in early germinants but not in later germinants. These studies illustrate the influence of germination timing on estimates of natural selection on postgermination traits. Thus, studies that measure natural selection on experimental transplants should take note that the timing of the transplants may influence their estimates of selection.

Germination timing also can influence the genetic basis of postgermination traits. In *A. thaliana* genetic variation in germination timing sometimes augmented the expression of genetic variation in postgermination traits such as branching and the age and size of reproduction, whereas in other cases plasticity in response to postgermination seasonal conditions caused genotypes to be more similar to each other, diminishing the expression of genetic variation in those traits (Donohue et al. 2005). Wilczek et al. (2009) compared differences in reproductive timing between two well-characterized genotypes of *A. thaliana* when they germinated (were planted) at different times during the year. Although the genotypes differ greatly in flowering time under standard laboratory conditions, no differences were expressed when seedlings were planted at certain times of year. Thus, plasticity of those genotypes in response to postgermnation seasonal conditions affected the expression of differences between those genotypes.

In principle, germination time could also influence which genetic loci themselves are involved in postgermination trait expression. For example, in *A. thaliana*, autumn germinants are induced to flower by low temperatures via the vernalization pathway (Ausin et al. 2005, Baurle & Dean 2006, Dennis & Peacock 2007, Simpson & Dean 2002). In contrast, spring germinants are induced to flower in part by long photoperiods, through the photoperiod pathway. It is possible that different pathways are more important elicitors of flowering depending on the season of germination, so the evolutionary importance of variation in genes in these pathways may depend on germination time.

The timing of a phenological transition of one life stage, such as germination, can influence subsequent traits simply by determining the seasonal conditions experienced after that transition. Although this example, and this review, concerns the phenological transition of seed to germinant, these dynamics apply to any developmental transition that occurs within a seasonal context, which is most of development in the wild.

3.3. Constraints of Ontogeny: Adaptation of Early and Late Life Stages

Within a given generation, selection on germination behavior occurs before selection on postgermination traits. As such, selection on postgermination traits occurs against the background of the environment—both genetic and ecological—that is determined by successful germinants.

Because allele frequencies at loci associated with germination can increase in frequency extremely quickly within a single generation (Huang et al. 2010), selection on germination has the potential to alter the genetic background against which subsequent selection occurs. With genetic epistasis for fitness—correlational selection across loci such that the adaptive value of one locus depends on alleles at other loci—trajectories for adaptive evolution can be limited and can depend on the temporal sequence of fixation at particular loci (Poelwijk et al. 2007, Weinreich et al. 2005). Thus, rapid fixation at germination loci, early in development or early in the colonization process, may influence the adaptive value of loci throughout the genome when epistasis is present.

Similarly, genetic correlations between traits expressed early and late in development influence the evolution of ontogenetic trajectories (Atchley 1987, Gomulkiewicz & Kingsolver 2007, Rice 2008). If traits are genetically correlated, a response to selection of one stage can cause correlated responses in other stages. Most ontogenetic models do not explicitly incorporate the phenomenon whereby the environment of selection on later traits depends on the phenotype expressed earlier in ontogeny. However, such dynamics could be incorporated in part by inclusion of correlational selection matrices (Lande & Arnold 1983) between early and late ontogenetic stages.

One omission of such quantitative-genetic treatments is that they do not include consequences of the selective elimination of alleles at early life stages and the consequent changes in genetic variances and covariances and natural selection that result from that depletion. Just as most quantitative-genetic models do not include changes in genetic variances and covariances during the course of evolution, so models of the evolution of ontogenetic trajectories include neither genetic changes that occur as a result of selection early in ontogeny and nor the influence of these genetic changes on the genetic expression and selection on later ontogenetic stages. How important such omissions are is not known: It depends on how effectively selection on one stage alters allele frequencies, and how changes in those allele frequencies early in life influence selection and genetic variation at later stages. The topics reviewed thus far suggest they may be relevant.

Ontogeny may affect successful colonization of novel environments in particular. Colonizing life stages are frequently early life stages, such as seeds. As such, early life stages are likely to be the first that are exposed to selection in novel environments, and successful establishment in new locations requires surviving the earliest episodes of selection. Organisms may therefore be expected to exhibit local adaptation in colonizing life stages before they adapt in later expressed traits, all else being equal.

How general is the faster adaptation of early traits compared to later traits is not well known. In an experimental population of *A. thaliana* that contained abundant genetic variation in many life-history traits, the QTLs associated with germination phenology were the ones that colocated with loci for fitness—not QTLs for later life stages (Huang et al. 2010). Moreover, some of these QTLs attained allele frequencies approaching fixation within a single generation even though they started at below 50%. Thus, germination evolved quickly within a single generation and faster than did traits expressed later in ontogeny (Huang et al. 2010). In other studies, selection was shown to be stronger during early life stages rather than later life stages (Latta & McCaub 2009), and some studies show local adaptation in seed and seedling stages but not later stages (Jorritsma-Wienk et al. 2007, Volis 2009).

Such patterns depend on the degree of specialization in the germination niche of a particular taxon; a generalist germination strategy may not exhibit local adaptation in germination, so local

adaptation in later life stages may be more prevalent. It would be interesting to compare the degree of local adaptation of different life stages in taxa with different colonization strategies and with different breadths of germination niches.

4. CONTRIBUTIONS OF GERMINATION TO ECOLOGICAL BREADTH AND SPECIES RANGES

The studies discussed above provide evidence that adaptation in germination contributes to local adaptation. Geographically variable local adaptation within a species, in turn, can enable a species to inhabit a larger ecological breadth and range. Alternatively, a wide germination niche at the level of species could be achieved by very broad germination requirements of all members of that species. Furthermore, interactions between germination behavior and postgermination adaptation also can influence the range of environmental conditions that species inhabit. Here we discuss evidence regarding how the width of the germination niche—at the individual or species level—predicts the breadth of species niches or geographic ranges.

4.1. Associations between Germination Niche Breadth, Ecological Niche Breadth, and Range: Comparative Studies

The evidence from comparative studies that the germination requirements of species are associated with their geographic range is inconsistent. In a sample of British flora, Thompson et al. (1999) showed that species' geographic ranges are significantly associated with the range of temperature in which the species can germinate, but the proportion of variance in geographic range that was explained by germination was low (2–4%). Baskin & Baskin (1988) likewise noted that widely distributed and narrowly endemic temperate species do not differ consistently in germination characteristics. In contrast, in a sample of weedy species, Brandle et al. (2003) found that species with a wider range of germination temperature had larger geographic ranges, as did Grime et al. (1981) in a sample of 403 species from England. In parasitic broom rape, Fernandez-Aparicio et al. (2009) found that more generalist species were stimulated to germinate by a greater range of root exudates than were specialist species. Other researchers have found similar associations between the width of the germination niche and the species ecological or geographic range when comparing closely related wild and cultivated (e.g., Baruah et al. 2009, Berger et al. 2005) or invasive and noninvasive taxa (e.g., Cervera & Parra-Tabla 2009; Hierro et al. 2009, Radford & Cousens 2000). Therefore, in some cases, a wider germination niche does correspond to a wider ecological niche or range, but it is not clear how prevalent this pattern is.

That some researchers have failed to detect an association between germination conditions and species ranges is not surprising, given that many comparative studies use germination data that were collected from one or a small number of populations within a taxon. If local adaptation in germination is prevalent in that species, then the germination conditions of the samples used may not represent the full range of germination conditions expressed by the species. Indeed, ecotypic differentiation in germination itself may contribute to the geographic range of diverse species (Dunbabin & Cocks 1999). For example, Meyer et al. (1995) report that more widely distributed *Penstemon* species exhibit more variable germination patterns across their range.

Too few data exist on the geographic distribution of genetic variation in germination to make any generalizations. To test whether local adaptation in germination enhances species ranges, it is necessary first to distinguish between genetic variation in germination versus maternal effects; second, we must test whether variation in germination is locally adapted, as discussed above; and third, we must compare the ecological breadths and geographic ranges of species with different

degrees of genetic variation and local adaptation in germination. Associations between germination and geographic ranges could also be tested for at the level of ecotypes or genotypes that differ in germination rather than at the level of entire species.

4.2. Germination as a Limiting Stage: Evidence that the Absence of Germination Requirements Limits the Ecological Niche

For a species to inhabit a particular habitat, it first must be able to germinate in that habitat. If a seed has very specific germination requirements, the mere absence of that requirement alone could prevent its establishment.

Some evidence exists that the absence of environmental conditions for establishment limits the presence or abundance of species in particular habitats. Some species are inhibited from germinating until they have received a specialized cue such as fire, host, symbiont, or light signal (Baskin & Baskin 1998), and the permanent absence of that cue could preclude the species from inhabiting a particular location. Studies have documented that the prevalence of environments that enable germination and seedling establishment also limit the presence or abundance of a species. For example, the abundance of establishment microhabitats in roadside ditches predicted the abundance of ditch specialists, even when ditches themselves were not limiting (Blomqvist et al. 2006). Pearson et al. (2002) suggested that the distribution of tropical trees within a patch of forest is mostly determined by their seeds' germination requirements, and Hobbie & Chapin (1998) found that germination and recruitment limitation determined the latitudinal range of five tree species. Swagel et al. (1997) argued that certain strangler figs are limited in their distribution because of their inability to germinate in conditions of low water availability; in more xeric sites, they occur only in palm crowns, which have adequate moisture for germination and establishment. The endemic *Gillia tricolor* is apparently limited in its distribution by its inability to germinate outside of its occupied patches (Baack et al. 2006). Anderson et al. (2009) report that the distribution of the understory shrub, *Itea virginica*, in floodplains is determined by the microsites that are optimal for seedling recruitment rather than by those that are optimal for adult growth. Mondoni et al. (2009) compared two closely related *Anemone* species, and found that the species restricted to woodlands was not able to germinate under alternating temperature conditions, as would occur in open sites. Thus, plant distributional patterns can be affected by the distribution of conditions necessary for seedling emergence and establishment.

In these examples, germination and establishment were not always distinguished. Whether the absence of a species was due to the absence of a germination cue alone or whether conditions would not permit establishment or seedling survival even if the seed had germinated, is rarely known. To implicate germination restrictions alone as the limit to species distributions requires experimental manipulations of germination. Forcing germination throughout the growing season would determine whether seedlings could survive in a given location if they were able to germinate at an appropriate time of year. Such studies, similar to dispersal limitation studies, are necessary to determine whether germination limitation alone restricts species ranges. In short, studies need to decouple effects of environmental factors that elicit germination from those that permit seedling establishment.

4.3. Germination as a Limiting Stage: Evidence that Inappropriate Germination Cuing Limits Establishment in Novel Habitats

For a species to be present in a particular location, it not only needs to be able to germinate in that location, but it needs to germinate in an appropriate manner that permits its survival and

reproduction there. Appropriate germination cuing within a habitat therefore could be a severe prerequisite for persistence within a given location and habitat.

Studies have documented establishment limitation, but it is less clear whether that limitation was due to inappropriate germination cuing within that habitat or the absence of appropriate establishment conditions anywhere within that habitat. In pine and spruce populations along an elevational gradient, seeds could germinate below their altitudinal limit, but the seedlings could not survive (Barton 1993). It is not known whether those seeds could have survived had they germinated at a different time within that low-elevation habitat, and this could only be determined with experimental manipulations of germination timing. Studies that demonstrate local adaptation in germination, however, suggest that inappropriate germination behavior does influence the performance of a species (or population) outside of its native habitat.

To determine the extent to which germination requirements and appropriate germination cuing limit species ranges, it would be beneficial to conduct studies that assess and manipulate germination across and beyond the range of a species. Observations of germination of different genetic seed sources when planted throughout and beyond the range of a species would be able to determine whether the species can germinate under novel conditions and whether the geographic source of the seeds influences that ability. Phenotypic manipulations of germination throughout and beyond the range of a species would determine whether the species could persist had it been able to germinate. Phenotypic and genetic manipulations of germination throughout and beyond ranges could characterize the fitness surface of germination phenology more thoroughly than would be possible with native seed sources and could possibly identify viable germination behaviors even if they are not naturally expressed by the species.

4.4. Constraints of Ontogeny Revisited: Comparing the Germination Niche and Postgermination Niche

The relationship between germination and postgermination niches can influence species ranges. Evidence reviewed above indicates that an increase in the germination niche breadth is sometimes associated with an increase in the postgermination niche (**Table 2**), suggesting that broader germination niches provide the opportunity for postgermination adaptation to a greater range of conditions. How germination niches influence the ecological and geographic range of species depends on whether germination niches are broader than postgermination niches, whether they are qualitatively different and shift across ontogeny or whether they are appropriately matched.

Wider germination niches are less constraining to species ecological ranges but engender the risk of germination under suboptimal conditions. In situations of spatial rather than temporal environmental variation, when delayed germination cannot improve the probability of experiencing a more favorable environment, broader germination niches would be more favorable because they would increase germination percentages without affecting postgermination fitness. Evidence exists for broader germination niches than postgermination niches. In *Vaccinium oxycoccos*, adult niches comprised a subset of conditions present in niches of juveniles, which were determined by germination preferences (Eriksson 2002). Niche contraction from germination through ontogeny has been documented in other taxa as well (e.g., Barton 1993, Hattenschwiler & Korner 1995, Quero et al. 2008).

The germination or establishment niche can limit the distribution of later life stages. In *Itea virginica*, seedlings could not establish in locations subjected to flooding, and adult distributions were limited primarily to locations that were not flooded (Anderson et al. 2009). However, adults tended to be found in more flood-prone locations, suggesting that after establishment, flooded

areas might actually be more favorable for adults. In this case, the niche not only contracted but actually appeared to shift across life stages.

Such ontogenetic niche shifts have been documented in other taxa (e.g., Dalling et al. 2001, Miriti 2006, Molofsky & Augspurger 1992, Parrish & Bazzaz 1985, Redondo-Gomez et al. 2008, Song et al. 2008, Thomson et al. 1996). Such niche shifts can potentially restrict the conditions under which a taxon can persist; conditions that permit survival of both stages must be present within a given location, and this is a situation that is likely to be less common than the occurrence of conditions that permit the survival of only one stage. If traits under selection are correlated across ontogeny, moreover, adaptation at early stages to early environments may cause maladaptation to environments experienced subsequently when ontogenetic niche shifts occur.

Ontogenetic niche shifts need not be disadvantageous, however, provided that the environment itself changes over the course of ontogeny. Seasonal or successional changes in vegetation cover, competitive environment, or abiotic factors such as water or nutrient availability often change over the course of the lifespan of individuals, as does the organisms' exposure to particular environmental factors over the course of development (Bazzaz 1991). When the environment itself changes during ontogeny in a manner that matches the niche, ontogenetic niche shifts could actually be advantageous (Anderson et al. 2009, Redondo-Gomez et al. 2008).

In contrast to niche contraction or niche shifts across ontogeny, germination may act as habitat selection, such that germination and postgermination niches are associated (**Table 2**). With such germination cuing of conditions appropriate for postgermination stages, species may be able to track favorable environments across a broader geographic range, thus effectively selecting appropriate conditions within a temporally variable landscape or altering seasonal phenology to match appropriate conditions even in locations with different seasonality. Evidence for germination as habitat selection is mixed, as reviewed above, but its occurrence has the potential to influence species ranges at present and in the future.

5. GERMINATION AND CLIMATE CHANGE

Climate change has contributed to major shifts in the timing of important seasonal events such as the onset of spring and summer drought. Species have responded to these changes by tracking the environment to which they are best suited by either migrating or altering their phenology (Menzel et al. 2006, Parmesan & Yohe 2003, Walther et al. 2002). In plants, changes in reproductive and leafout phenology are common (Bertin 2008, Fitter & Fitter 2002, Menzel 2000, Miller-Rushing & Primack 2008), and the inability of certain species to adjust phenologically to climate change has been linked to declines in abundance (Willis et al. 2008). It is probable that changes in germination phenology are comparably important, but there are as yet few data to test that hypothesis. Here, we discuss what determines the likelihood of phenological tracking through germination, and how changes in germination phenology can influence postgermination traits.

5.1. Cues and Cue Combinations: the Potential for Seasonal Tracking

The ability of germination cuing to track appropriate seasonal conditions for germination depends on what cues and combinations of cues are required for germination, and how consistently those cues are associated after environmental change.

Seeds with broad germination niches are likely to be able to germinate under altered conditions, although they are less likely to be able to track optimal conditions for growth and reproduction. Seeds with narrower germination niches may be better able to track changing conditions, but they may be more vulnerable to extinction if the combinations of cues required for germination no

longer co-occur. For example, a species that currently germinates in response only to the onset of rains could germinate at various times of year and in diverse temperature conditions depending on when the rains start; as a consequence, this species may have to adapt to novel temperature conditions. In contrast, if the species also has narrow temperature requirements, it may germinate at the temperature to which it is adapted. Alternatively, it could be prevented from germinating altogether if the rain no longer occurs at the required temperature.

To predict how plants will adjust their germination phenology to environmental change, it is necessary to investigate germination responses to multiple cues in concert. Altered geographic distributions of combinations of those environmental factors, not single factors, will determine the geographic limits of germination (e.g., MacDonald 2010). Analysis of predicted associations of environmental cues could likewise identify novel prevalent combinations of environmental factors, and the capacity to germinate under these new combinations could be necessary to maintain viable germination niches within species ranges (Parmesan 2006).

5.2. The Correlated Evolution of Germination and Postgermination Traits under Environmental Change

Wide germination niches are likely to expose postgermination stages to novel environments after environmental change. Some degree of germination cuing may maintain exposure to environmental factors that elicit germination, but alter exposure to others that formerly covaried with that cue but no longer do. To the extent that the cue that elicited germination is the most important factor determining the fitness of germinants, continued germination in response to this cue would remain an adaptive strategy, and the postgermination traits may still be highly adapted to the postgermination environment. If this cue becomes only a weak predictor of the environmental factors that exert selection, however, germinants will be exposed to novel environmental factors to which they will have to adapt.

Studies have not yet explicitly documented novel selection following shifts in germination within a given species. However, one study using a 25-year-old data set of a Sonoran Desert plant community (Kimball et al. 2010) showed that changes in the timing of seasonal rains have caused seeds to germinate at lower temperatures than they did previously. Consequently, plants develop under colder conditions, leading to an increase in the abundance of cold-tolerant species. Thus, the germination cue (precipitation) remained unchanged, but the postgermination conditions changed, resulting in altered selection on postgermination traits. A similar shift of selection could conceivably occur within a species as well.

Another likely outcome of environmental change that cannot be overlooked is the alteration of germination due to maternal environmental effects. If environmental conditions during seed maturation are altered, it is likely that germination behavior will also be altered. Moreover, as reproductive phenology evolves in response to climate change, as it is predicted to do, such evolutionary change is likely to cause changes in germination because of maternal environmental effects. To our knowledge, no studies of climate change have investigated the potential consequences of maternal effects on germination.

SUMMARY POINTS

1. Fecundity selection favors early germination, but viability selection is variable in space and time. Germination cuing plus some bet-hedging dormancy is likely frequently optimal.

2. Direct evidence for local adaptation in germination timing is limited, although evidence for local adaptation via increased germination proportion is more common.

3. Germination and postgermination traits are commonly, but not always, associated. Expansion of germination tolerances can co-occur with expansions of seedling tolerances.

4. Germination timing can influence phenotypic expression, genetic expression, and natural selection on postgermination traits.

5. Germination can adapt quickly when genetic variation is present, but the relative rates of adaptation of early versus late life stages, as well as the constraints of ontogeny to adaptation to novel environments, are still poorly characterized.

6. Some association between germination niche breadth and ecological niche breadth or geographic range exists in some systems, but it is not clear how general this association is. Ecotypic variation in germination may obscure such broad associations.

7. Germination niches are commonly broader than postgermination niches, and niches sometimes shift across life stages. Germination as habitat selection may enhance postgermination performance, but may also constrain adaptation to other environments in later life stages.

8. To predict changes in germination phenology with climate change, predicting changes in combinations of environmental factors is necessary. The decoupling of environmental cues can influence germination patterns as well as the evolution of postgermination traits.

FUTURE ISSUES

1. The adaptive value of germination cuing: Phenotypic and/or genetic manipulations of germination timing are required to accurately assess fitness functions of germination timing.

2. Ecotypic differentiation and local adaptation in germination: Studies need to use seed sources raised in a common environment in order to control for maternal effects on germination. Manipulations of maternal environments could explicitly test for contributions of maternal effects to adaptive differences in germination.

3. Germination and postgermination coadaptation: Explicit comparisons of the optimal conditions for germination versus postgermination performance are necessary. Experimental manipulations of germination, which disrupt associations between germination and postgermination traits, could test for correlational selection.

4. Distinguishing linkage disequilibrium from pleiotropy across life stages: Genetic studies and artificial selection studies are necessary to determine whether associations between germination and postgermination traits are due to linkage disequilibrium or pleiotropy.

5. Ontogeny and adaptation in colonizing species: Comparisons of rates of adaptation of early versus late life stages would be of interest, as would assessment of genetic variances and covariances across life stages. Estimating rates of depletion of genetic variance, or rates of allele changes, at particular life stages under novel selection regimes would be especially informative.

6. Germination niche and ecological niche: Explicit tests that germination requirements alone limit species distributions require manipulations of germination within and beyond the range of species.

7. Conflicts of adaptation across life stages: Characterizing ecological niches across life stages and experimental extensions of the germination niche could test how strongly germination cuing enhances or constrains postgermination performance in native and novel environments.

8. Germination and climate change: How germination phenology is predicted to change with climate change is unknown. Predicting changes in combinations of environmental factors that influence germination would identify conditions that prevent germination in altered environments and could identify changes in predicted relationships between germination and postgermination environments.

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