New
Phytologist

Review

Research review

Niche construction through phenological plasticity: life history dynamics and ecological consequences

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Received: *7 September 2004*
Accepted: *19 December 2004*

Summary

Key words: dispersal, flowering time, germination, habitat selection, maternal effects, phenotypic plasticity.

The ability of an organism to alter the environment that it experiences has been termed 'niche construction'. Plants have several ways whereby they can determine the environment to which they are exposed at different life stages. This paper discusses three of these: plasticity in dispersal, flowering timing and germination timing. It reviews pathways through which niche construction alters evolutionary and ecological trajectories by altering the selective environment to which organisms are exposed, the phenotypic expression of plastic characters, and the expression of genetic variation. It provides examples whereby niche construction creates positive or negative feedbacks between phenotypes and environments, which in turn cause novel evolutionary constraints and novel life-history expression.

New Phytologist (2005) **166**: 83–92

doi: 10.1111/j.1469-8137.2005.01357.x

Introduction

An important feature of modern ecologies is the extreme mobility of species across a vast geography. How are species able to expand their ranges over heterogeneous landscapes? How are they, when introduced to new environments and even to new continents, able to take hold and expand? One option for such species is to evolve adaptive plasticity in response to the variable environments they encounter (Sultan, 1995, 2000). Another option is for them to take their environment with them – or at least to find suitable habitat wherever they may happen to be.

The ability of an organism to alter the environment it experiences has been termed 'niche construction' (Odling-Smee *et al.*, 1996, 2003; Laland *et al.*, 1999; Day *et al.*, 2003), and it can occur through direct habitat modification by the organism, through habitat choice or selection, or through resource use and depletion. While it is obvious how animals with complex behaviors can accomplish such feats, it is less obvious how plants can do a similarly good job of it.

Developmental plasticity and phenology can be extremely effective mechanisms of niche construction in plants. The ability of plants to sense and respond to the environment frequently gives them the ability to respond to it morphologically or phenologically in a manner that alters their exposure to specific environments. Potential mechanisms of habitat selection and niche construction in plants have been reviewed by Bazzaz (1991) and more recently by Donohue (2003). For example, plants can increase the light available to them through morphological responses, such as stem elongation, which enables them to overtop their neighbors (Smith *et al.*, 1990). Developmental responses in phenology, moreover, effectively determine the seasonal environment to which different life stages are exposed. This review gives some examples of niche construction in plants drawn from our own work and discusses how interactions among niche-constructing traits can alter ecological and evolutionary dynamics.

The first example is seed dispersal. Seeds are the most mobile life stage in most plants, excepting pollen, and their dispersal offers the opportunity to escape from adverse conditions such as pathogens, predators, or sibling competition at the maternal home site (reviewed in Howe & Smallwood, 1982; Willson, 2000). Perhaps the most predictable environmental consequence of seed dispersal is reduced conspecific density experienced by efficiently dispersed seeds in open habitats, and highly competitive conditions experienced by poorly dispersed seeds (Janzen, 1978; Baker & O'Dowd, 1982; Augspurger, 1983; Rees & Brown, 1991; Augspurger & Kitajima, 1992; Donohue, 1998). Therefore, dispersal ability frequently determines the competitive environment experienced by seeds, seedlings, and even adult plants.

The second example is flowering time. The season during which a plant flowers, matures and disperses seeds determines the seasonal environment that seeds experience during maturation and immediately after dispersal (Lacey, 1982; Galloway, 2002; Munir *et al.*, 2001). For example, plants that flower in the autumn mature seeds under cool, short days, and seeds experience winter conditions soon after dispersal. By contrast, plants that flower in the spring or summer mature seeds under warm, long days, and their seeds experience warm to hot conditions immediately after dispersal. Maternal environmental conditions that influence progeny environments and progeny attributes have been termed 'maternal effects', and maternal effects have recently attracted much attention from ecologists and evolutionary biologists because of their own interesting evolutionary dynamics (reviewed in Mousseau & Fox, 1998; for plants, see Gutterman, 1992; Donohue & Schmitt, 1998; Galloway, 2005, this issue).

The third example is germination timing. Germination responses to environmental factors can be exquisitely precise mechanisms of habitat choice in plants; certain environmental conditions must be present to break dormancy and additional environmental conditions must be present to enable germination after dormancy is broken (Simpson, 1990; Baskin & Baskin, 1998; Bewley, 1997). By having such specific environmental requirements for germination, seeds essentially ensure that the germinant experiences a specific set of environmental conditions (Evans & Cabin, 1995). Frequently, those environmental factors that elicit germination are reliable predictors of seasonal conditions likely to be experienced by germinants, seedlings and even adult plants (reviewed in Gutterman, 1992, 1994; Baskin & Baskin, 1998).

Using these examples, I will illustrate how the ability of plants to determine the environment they or their offspring experience can cause some interesting evolutionary and ecological dynamics. In particular, I emphasize how interactions among niche-constructing traits can result in novel life-history expression and plasticity-induced genetic constraints on evolution.

Feedbacks caused by niche construction

Niche construction occurs when an attribute of an organism determines the environment experienced by that organism. That 'constructed' environment, in turn, can influence either the same trait or a different trait through various plastic and evolutionary pathways that will be discussed in the following section (Fig. 1a). The second trait, moreover, may influence the first trait (or a third or fourth trait) either through a direct causal pathway (Fig. 1b) or because it, too, is a niche-constructing character that alters an environmental factor that influences the other trait or traits (Fig. 1c).

The point here is that, either through a very simple pathway involving only one niche-constructing trait, or through more complex pathways involving multiple traits, niche construction and plasticity to the resulting environment can cause positive or negative feedback pathways; phenotypic or evolutionary change in a niche-constructing trait can influence its own future phenotype or evolution, and it can influence those of other traits (Day *et al.*, 2003). Such feedback pathways have the potential to constrain or facilitate evolutionary responses to selection, and they can result in nonobvious patterns of life-history expression and demographic dynamics.

Evolutionary consequences of niche construction

The pathways through which niche construction can influence ecological and evolutionary trajectories are both plastic and evolutionary pathways (Day *et al.*, 2003; Donohue, 2003). According to the 'breeder's equation' of quantitative genetics, evolutionary responses to selection, R, are determined by: (1) the strength of selection acting on a trait, S; (2) the phenotype and phenotypic variance of the trait, V_p; and (3) the genetic variance of the trait, V_g (Fig. 2). The niche-constructing character determines the environment and the environment, in turn, influences each of the three components of evolutionary responses.

First, niche construction can determine the type of selection (S) and the selective agents to which an organism is exposed (Laland *et al.*, 1999; Day *et al.*, 2003; Donohue, 2003; Schwilk, 2003). Most theoretical treatments of niche construction have focused on this very important pathway. Perhaps the most interesting result of these analyses is that, when niche construction reduces the degree of environmental variation experienced by the population, the rate of specialization to the 'constructed' environment is faster (Whitlock, 1996), and the level of adaptation to that environment is higher (Levins, 1968; Holt, 1987; Rosenzweig, 1987; Brown, 1990). A reduction in environmental variation experienced by the organism, by extension, promotes specialization instead

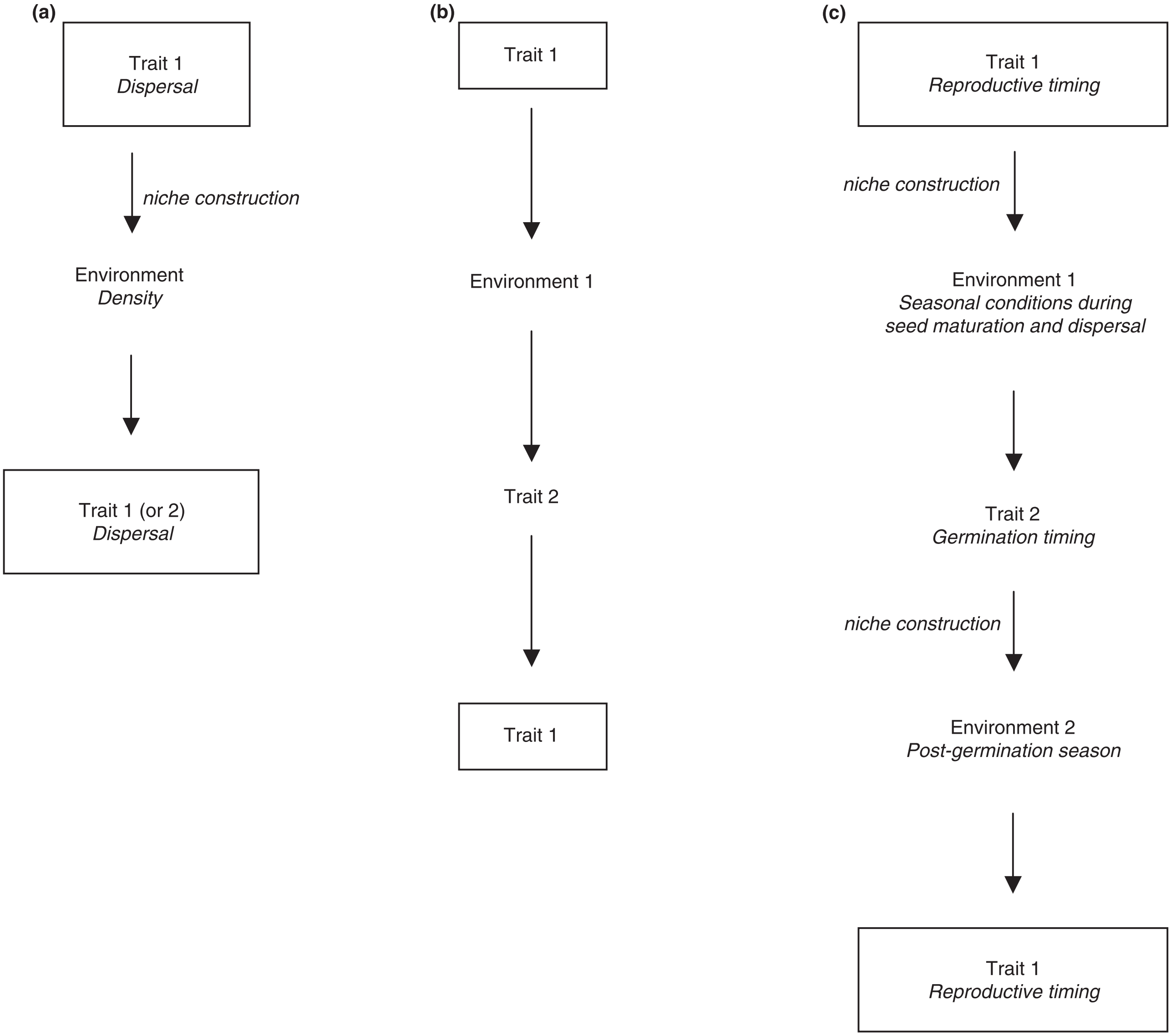

Fig. 1 Feedback pathways through niche construction. In the simple case (a), a niche-constructing trait influences the environment, which influences the same trait (or a different trait). In the second case (b), one niche-constructing character determines the environment, which influences a second trait. The second trait, in turn, influences the first trait directly. In the third case (c), one niche-constructing character determines the environment, which influences a second trait, which is also a niche-constructing trait. The environment constructed by the second trait influences the first trait. All cases present pathways whereby a trait influences itself through niche construction.

of phenotypic plasticity (Via & Lande, 1985; Schlichting, 1986; van Tienderen, 1991; Scheiner, 1993). Ironically, while we are used to thinking of plasticity and specialization as alternative mechanisms of adaptation, plasticity in a niche-constructing character can actually promote specialization in other traits when it decreases the environmental variation experienced by the organism.

The second pathway through which niche construction influences evolutionary and ecological dynamics operates when traits exhibit phenotypic plasticity to the 'constructed' environment, altering their phenotype and phenotypic variance (V_p). Analogous to the ability of niche construction to promote specialization, plasticity in niche-constructing characters can facilitate functional homeostasis (or reduce the variation) of other characters (Schlichting & Pigliucci, 1998) by producing a more constant environment. For example, the plasticity of underlying traits of generalist *Polygonum* species enabled more constant photosynthetic rates across a range of environments, potentially by maintaining a more constant light or water resource (Sultan *et al.*, 1998). More generally, plasticity can alter the opportunity for selection by altering both the mean phenotype of the population, and thereby determining how far from the optimum the population is, and by altering the phenotypic variance, which can influence the heritability of the trait.

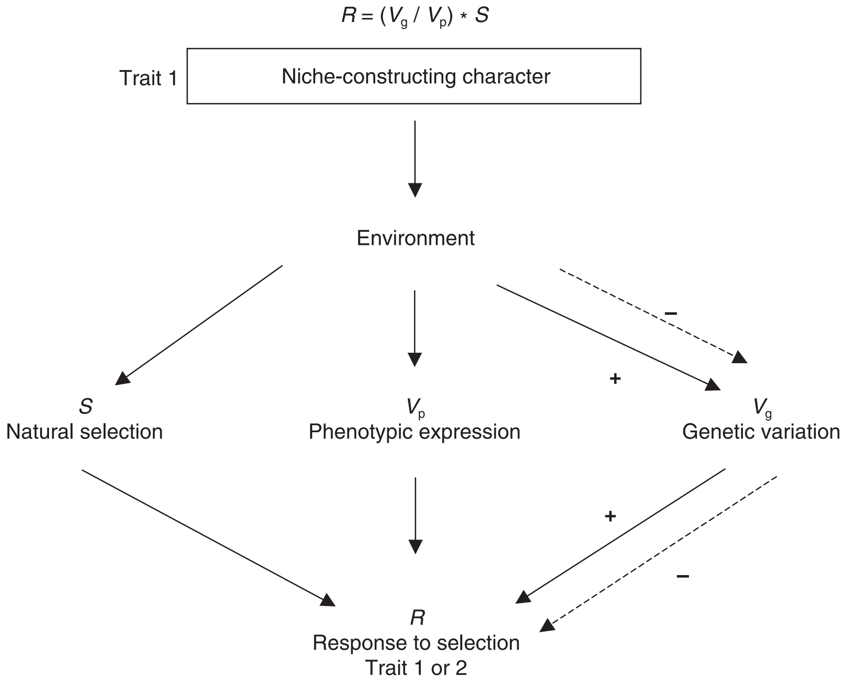

Fig. 2 The breeder's equation of quantitative genetics describes evolutionary responses to selection (*R*), or the change in phenotype from one generation to the next, as a function of the strength of selection (*S*), and the proportion of phenotypic variation (V_p) that results from genetic variation (V_g). Niche construction can alter the environment of natural selection, phenotypic expression and the expression of genetic variation for traits. When niche construction causes an increase in the expression of genetic variation (solid line), the response to selection is facilitated (+), but when it causes a decrease in the expression of genetic variation (dashed line), the response to selection is constrained (–). When niche construction influences the expression of genetic variation for the niche-constructing trait itself, it can facilitate or impede the response to selection of that trait. As it evolves, its ability to respond to selection can change.

The influence of niche construction on phenotypic expression is also a potential pathway for what have come to be known as 'indirect genetic effects' whereby the evolution of the environment (through the evolution of the niche-constructing trait) can cause a phenotypic change in a second trait that responds plastically to the environment (Moore *et al.*, 1997; Wolf *et al.*, 1998, 1999). The evolution of the second trait is 'indirect' in the sense that there need not be any genetic change in the trait; all that is required is a genetic change in the niche-constructing trait and plasticity to the new environment created by niche construction. Therefore, with niche construction and plasticity, traits can evolve even if they themselves have no genetic variation.

Third, niche construction can influence evolutionary trajectories by influencing the expression of genetic variation, or evolutionary potential (V_g). Just as phenotypes respond plastically to environments, if different genotypes respond differently to the environment, then genetic variation for that trait can be environment dependent (Via & Lande, 1987). If the environment increases the expression of genetic variation, then evolutionary responses can be facilitated, but if the environment reduces the expression of genetic variation, then evolutionary responses will be constrained.

The following sections provide empirical examples whereby niche construction alters these three components of evolutionary responses to selection. The first example demonstrates how the niche-constructing character, seed dispersal, influences its own evolutionary potential (Fig. 1a). The second example shows how two interacting niche-constructing traits (Fig. 1c) – flowering time and germination time – influence selection, phenotypic expression and genetic variation, and how such dynamics result in novel life-history expression. Both examples are from *Arabidopsis thaliana*, a weedy, annual mustard (Brassicaceae).

Seed dispersal: a simple case of one niche-constructing character influencing itself

Arabidopsis thaliana has dehiscent siliquae and tiny seeds that are passively dispersed by wind and gravity, and secondarily by soil transport. In many species, efficient seed dispersal leads to lower sibling densities after dispersal and, more generally, lower conspecific density if plants do not grow in continuous stands (see Introduction). Because dispersal ability can determine conspecific density, it is important to know how density in turn influences dispersal ability and the expression of genetic variation for dispersal ability (Fig. 1a).

To investigate this, we conducted a quantitative genetic study using morphologically diverse inbred ecotypes, and we grew replicates of 12 ecotypes at high and low density (Wender *et al.*, 2005; Donohue *et al.*, 2005d). We measured seed dispersion patterns under controlled conditions and estimated population-level heritability of post-dispersal density at two spatial scales. The first spatial scale, 0.25 × 0.25 cm, is relevant for interactions among young germinants. The second spatial scale, 2.5 × 2.5 cm, is relevant for interactions among adult plants, and it approximated the scale of the density manipulation that we imposed on the maternal plants.

Significant genetic variation for post-dispersal density was detected at both spatial scales, but only when the maternal plants were grown at high density (Table 1). For the smaller spatial scale, high maternal density increased the genetic

Table 1 Ecotypic-level genetic and environmental variances of post-dispersal seed density when plants were grown in high and low density

	High density			Low density		
Post-dispersal density	V_{GH}	V_{EH}	H^2_H	V_{GL}	V_{EL}	H^2_L
Seeds/0.25 cm	0.0001	0.0005	0.17*	0.00	0.0037	0.00
Seeds/2.5 cm	4.93	28.31	0.15**	58.45	483.45	0.11

V_{GH}, Genetic variance at high density; V_{EH}, environmental variance at high density; V_{GL}, genetic variance at low density; V_{EL}, environmental variance at low density; H^2_H, ecotypic-level broad-sense heritability at high density; H^2_L, ecotypic-level broad-sense heritability at low density; Seeds/0.25 cm, mean crowding index (the number of neighbors a seed had within a unit area) at the small spatial scale (seeds/0.25 cm × 0.25 cm); Seeds/2.5 cm, mean crowding index at the larger spatial scale (seeds/2.5 cm × 2.5 cm). Significance levels of the heritability estimates are based on the significance of the ecotype main effects in a Kruskal–Wallis analysis for 'seeds/0.25 cm' and on ANOVA for 'seeds/2.5 cm'.
*,**$P < 0.05$ and $P < 0.01$, respectively; ns, not significant; $n = 236$. From Donohue *et al*. (2005d).

variance of post-dispersal density and also decreased the environmental variance, leading to higher heritability for plants grown in high density. For the larger spatial scale, the higher heritability of plants grown at high density was due entirely to a reduction of environmental variance at high density. Therefore, maternal density altered the evolutionary potential (V_g/V_p) for dispersal ability – specifically for post-dispersal density – by altering the expression of both environmental and genetic variation.

This simple result has some interesting potential evolutionary consequences. Consider a population of plants growing at high density, but in which natural selection favors lower post-dispersal density, as it does in many species (Burdon & Chilvers, 1975; Augspurger & Kitajima, 1992; Donohue, 1997). Our results predict that an evolutionary response to such selection is possible, since genetic variation for dispersal ability is expressed at high density. However, once low post-dispersal density is achieved, genetic variation for dispersal will cease to be expressed. Such a negative feedback pathway would be a constraint on the further evolution of dispersal. Note that this genetic constraint is not caused by the elimination by natural selection of inappropriate genotypes, which would reduce genetic variation. Rather, this genetic constraint is caused by plasticity alone, causing less genetic variation to be expressed, even when the genotypes are identical. The evolution of the post-dispersal density environment and the density-dependent genetic expression for dispersal are, themselves, adequate to impose this constraint.

In this particular example, the dynamics operated so as to reduce the expression of genetic variation, but for other niche-constructing traits, they may increase the expression of genetic variation. In such cases, the evolution of the niche-constructing character could facilitate its further evolutionary responses to selection by enabling genetic variance to be expressed in the newly evolved environment. Thus, while natural selection may reduce genetic variation for a trait over time, the dynamics accompanying niche construction may act to provide additional genetic variation to enable more sustained responses to selection. Therefore the ability of organisms to determine the environment they experience, and the environment-dependent genetic variation for that ability, can cause unexpected evolutionary dynamics that can either constrain or facilitate the evolution of such characters. More generally, because environment-dependent genetic expression is so commonly observed (e.g. Mazer & Wolfe, 1992; Donohue *et al.*, 2000; Dorn *et al.*, 2000; Munir *et al.*, 2001), niche construction has the potential to alter the evolutionary potential of many traits whose genetic variation may depend on the 'constructed' environment.

Flowering and germination time: two interacting niche-constructing traits

Arabidopsis thaliana typically displays a winter annual life history, germinating in the autumn, overwintering as a rosette, and flowering, maturing seeds, and dispersing seeds in late spring and early summer (Ratcliffe, 1965; Effmertova, 1967; Evans & Ratcliffe, 1972; Nordborg & Bergelson, 1999). Some populations have a high frequency of spring annuals that germinate in the spring and flower, mature seeds, and disperse them all in late spring and early summer that same year. Some populations even have individuals that germinate, flower, and disperse seeds in a single autumn (Thompson, 1994; Griffith *et al.*, 2004). Thus, basic life histories vary greatly among natural populations.

Variation in the phenology of germination and flowering determines overall life-history expression in *A. thaliana.* In particular, the germination season determines the seasonal conditions experienced by seedlings and rosettes, with spring germinants experiencing long days and warm conditions while autumn germinants experience short days and cool conditions, and rosettes receive cold vernalization over the winter. It is well known in *A. thaliana* and many other species that these seasonal cues of photoperiod and temperature, and especially cold vernalization of rosettes, interact to determine flowering time (Koornneef *et al.*, 1991; Nordborg & Bergelson, 1999; Mouradov *et al.*, 2002; Simpson & Dean, 2002). In temperate climates, long days and cold vernalization usually accelerate flowering. We have seen another example in which the season of germination determines seasonal phenology and thereby life-history expression in *Campanula americana* in this volume (Galloway, 2005, this issue).

Likewise, the flowering season determines the seasonal conditions experienced by seeds during maturation and soon after dispersal. Plants that flower in spring mature and disperse seeds under long, warm days, and seeds experience warm after-ripening conditions soon after dispersal. These seeds do not experience a period of cold winter stratification. By contrast, plants that flower in autumn mature seeds under short, cool days, and seeds experience cool conditions and cold winter stratification soon after dispersal. These seasonal cues of maternal photoperiod and cold stratification of seeds influence germination in several species (reviewed in Baskin & Baskin, 1998). In *A. thaliana*, seeds matured under short days are induced to germinate at higher frequencies than seeds matured under long days when they experience cold temperatures (Munir *et al.*, 2001).

We wanted to determine how fruiting and dispersal phenology influenced germination schedules in the field, and how, in turn, germination timing influenced fruiting phenology (Fig. 1c). To this end, we crossed two natural ecotypes to create phenotypically and genetically diverse recombinant inbred lines that differed in the timing of flowering and germination. We then conducted a large field experiment that manipulated the photoperiod during seed maturation and the season of seed dispersal (Donohue *et al.*, 2005a,b,c). Specifically, we grew replicates of 110 of these recombinant inbred lines under controlled conditions at photoperiods of 14 h (similar to seeds maturing in late spring) and 10 h (similar to seeds maturing in autumn) and dispersed their seeds during late spring (June) and during autumn (November). We then monitored germination schedules of each genotype. We also monitored each germinant and determined how germination timing influenced subsequent flowering phenology. We found that the season of seed dispersal influenced the phenotypic expression of germination timing (V_p), natural selection on germination timing (S) and the genetic variation of germination timing (V_g).

The season of seed dispersal strongly influenced germination schedules (Fig. 3), with seeds dispersed in June germinating over a much longer period of time and with many seeds exhibiting pronounced primary dormancy (Donohue *et al.*, 2005a). By contrast, most seeds dispersed in November did not exhibit any dormancy, germinating almost immediately. The effects of maternal photoperiod were very subtle (affecting only seeds with primary dormancy), and were quite weak compared with the effects of the post-dispersal seasonal conditions. Therefore, flowering phenology is likely to influence germination schedules more strongly by determining post-dispersal seasonal conditions rather than by determining the photoperiod during seed maturation.

The season of seed dispersal also strongly influenced natural selection on germination timing (Fig. 3; Donohue *et al.*, 2005c). Seeds dispersed in June experienced strong stabilizing selection, favoring intermediate germination timing in mid-October. By contrast, seeds dispersed in November experienced very weak directional selection, favoring early germination. The striking contrast here is that, for seeds dispersed in November, nondormant seeds had the greatest fitness, but for seeds dispersed in June, nondormant seeds had zero fitness.

The evolutionary potential of germination timing also strongly depended on the season of seed dispersal (Fig. 4; Donohue *et al.*, 2005a). First, the heritability of germination timing was much higher for seeds dispersed in June than for seeds dispersed in November. The low heritability of germination in November-dispersed seeds was caused by the extreme synchrony of germination of these seeds. In addition, the degree of transgressive segregation for germination also varied with the season of seed dispersal. Specifically, the number of recombinant progeny that exhibited novel germination phenotypes beyond those of either parent was higher when seeds were dispersed in November. Most of the transgression for November-dispersed seeds led to earlier germination than either parent, which was adaptive. Therefore, in addition to influencing the heritability of life-history traits, niche construction (through dispersal phenology) can also influence the degree of transgressive segregation, which can create novel adaptive phenotypes (Rieseberg *et al.*, 2003a,b). This genetic consequence of niche construction is likely to be important for highly inbred species such as *A. thaliana* (Abbott & Gomes, 1989) that experience periodic outcrossing events and that are dispersed into novel environments (Sharbel *et al.*, 2000; Hoffman, 2002).

In summary, niche construction through reproductive phenology, and particularly through the timing of seed dispersal, strongly influenced phenotypic expression, natural selection and evolutionary potential of germination timing. By altering all three of these components of evolutionary responses, niche construction through reproductive timing is expected to strongly influence the evolutionary dynamics of germination timing.

Germination timing, in turn, influenced reproductive phenology by determining the seasonal environment experienced by young rosettes (Donohue *et al.*, 2005b). In particular, seeds that germinated in the spring reproduced much earlier in development and at a smaller size than seeds that germinated in the autumn (Fig. 5).

This mutual interaction between the two niche-constructing traits of flowering time and germination time leads to some interesting consequences for life-history expression. First, variation in germination timing accounts for the difference between the winter annual and spring annual life history, with winter annuals germinating in the autumn and spring annuals germinating in the spring. However, spring germination alone

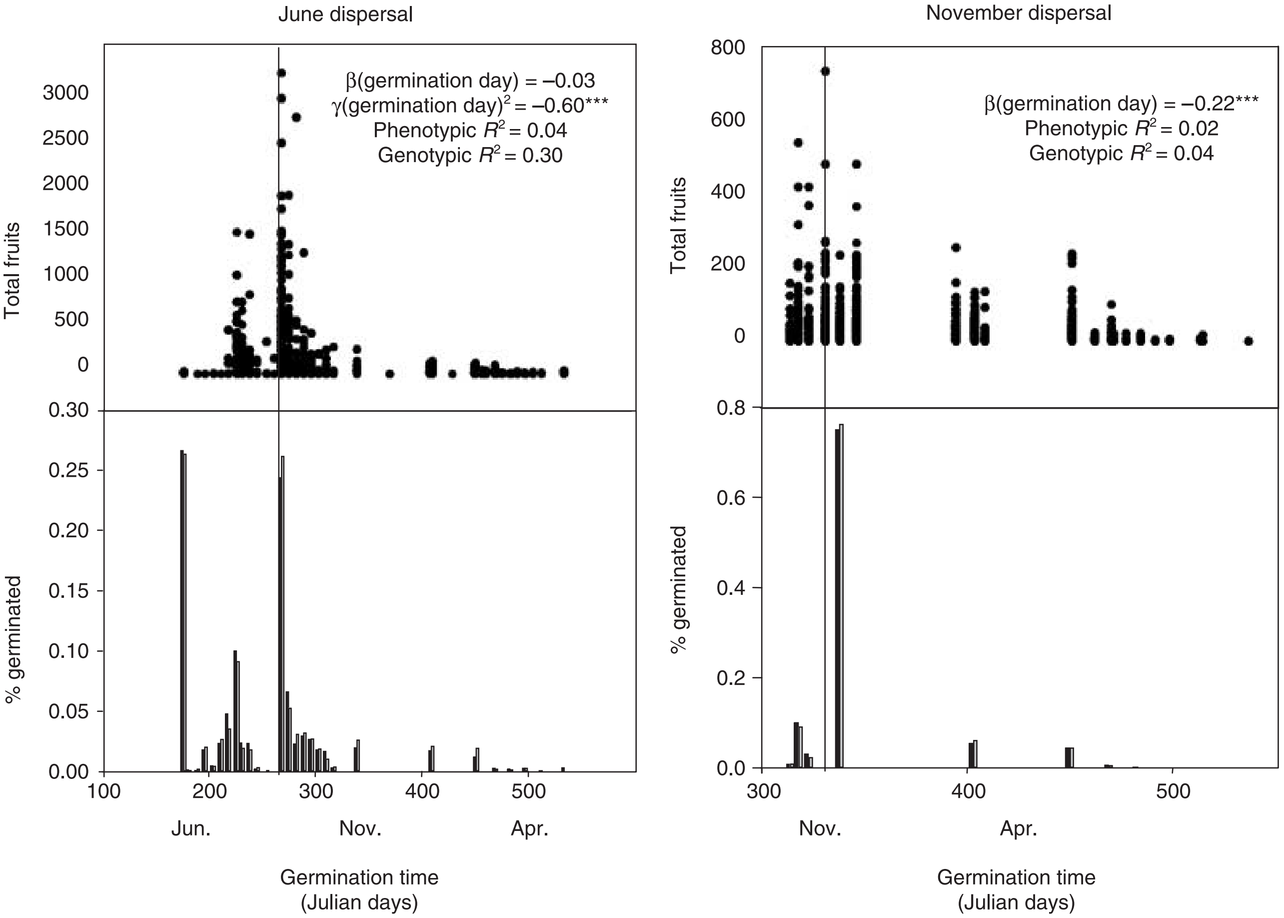

Fig. 3 Germination schedules of seeds dispersed in June (left), and November (right) are shown in the lower panel as the proportion of all seeds that germinated (y-axis) over time (x-axis). Days are in Julian days, with January 1, 2001 being the first day. Closed bars represent seeds matured under long days, and tinted bars represent seeds matured under short days. A scatter-plot of germination timing (x-axis) vs the total number of fruits produced (y-axis) is shown in the upper panel. Each point represents the value for a given plant. The vertical line indicates the date on which fruit production was highest; β, standardized directional selection gradient (regression coefficient) indicating the strength of selection on germination timing, based on a phenotypic selection analysis; γ, standardized quadratic selection coefficient indicating the strength of stabilizing selection on germination timing (Lande & Arnold, 1983, Arnold & Wade, 1984). Nonsignificant stabilizing selection coefficient is not shown. 'Phenotypic R^2' and 'Genotypic R^2' indicate the proportion of the variation in fitness (fruit production) among individuals or genotypes, respectively, that is explained by variation among individuals or genotypes in germination timing. Adapted from Donohue *et al*. (2005a,c).

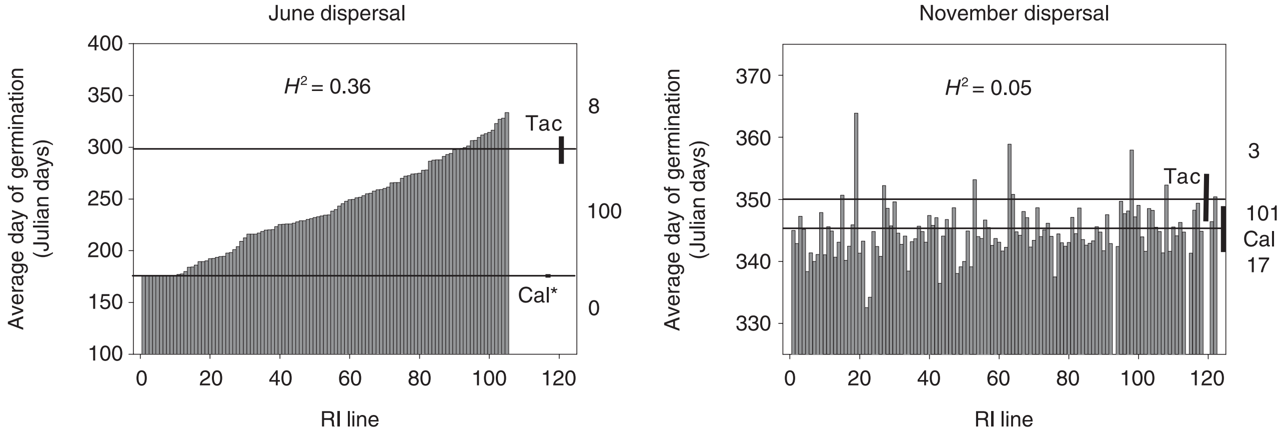

Fig. 4 Average day of germination of seeds dispersed in June and November. Each bar represents the mean phenotype of a separate recombinant inbred line. The order of the genotypes is the same in both graphs. Horizontal lines indicate the mean germination day of the parental lines (Cal and Tac); closed bars, the standard errors for the parental lines; numbers to the right indicate the number of genotypes with germination later (above), between, or earlier (below) than those of the parental lines; H^2, broad-sense heritability of germination date. Adapted from Donohue *et al*. (2005a).

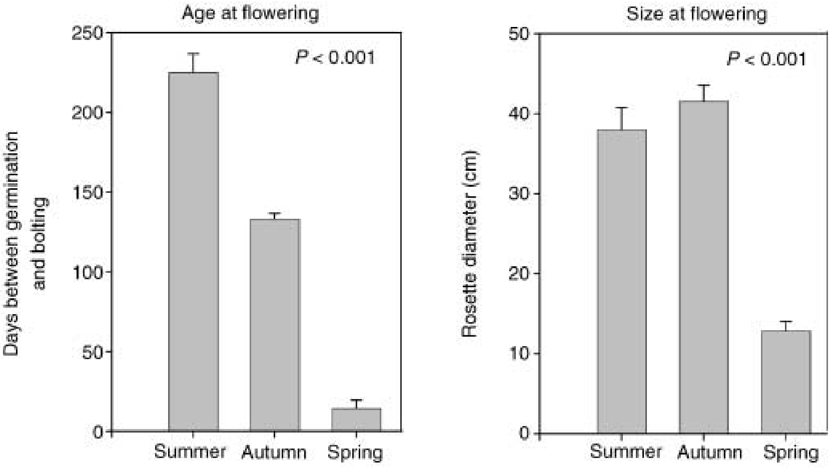

Fig. 5 Flowering traits of plants from seeds that germinated in summer, autumn and spring. Means and untransformed standard errors are indicated. *P*-values indicate significant differences among germination seasons. Adapted from Donohue *et al.* (2005b).

would not lead to a successful spring annual; plants also need to respond plastically to the season of germination by accelerating their reproduction. Therefore, niche construction through germination timing, and plasticity to the constructed environment, can account for variation between spring and winter annual life histories.

Variation in reproductive phenology also contributes to interesting life history variation. Some genotypes (both within these recombinant inbred lines and in natural populations) are able to flower and disperse seeds in the autumn instead of waiting until the following spring. When such variation in reproductive phenology is present, a bivoltine life-history is possible. In particular, dispersal in autumn accelerated germination, so seeds could germinate in spring (or even late winter) instead of waiting until the following autumn to germinate with the spring-dispersed cohort. As before, these spring germinants are capable of responding to germination timing by accelerating reproduction and reproducing during the same season. Thus autumn flowering conditions enabled spring germination, and spring germination conditions enabled spring flowering. These interactions can actually enable two generations to be completed within a single year instead of the typical one generation. We are currently in the process of documenting this bivoltine life-history in natural genotypes from New England, USA (see also Thompson, 1994) and assessing its demographic consequences.

This novel bivoltine life history is the outcome of one niche-constructing character influencing the seasonal environment experienced by a second niche-constructing character, and vice versa. Niche construction, and the resulting feedback pathways, can therefore have important life-history and demographic consequences. In this case, the feedback caused the generation time to be reduced dramatically, which could increase rates of population growth. Such a halving of generation timing as observed here is, indeed, an impressive demographic innovation for a weedy, introduced plant.

Conclusions

In plants, niche construction frequently occurs through plasticity in developmental phenologies. We have seen a simple case of a niche-constructing character influencing itself, and a more complex case of two niche-constructing characters influencing each other. In the case of seed dispersal, niche construction can potentially cause a novel, plasticity-induced genetic constraint on the evolution of dispersal. As dispersal evolves, the environment created by dispersal is expected to change so as to reduce the expression of genetic variation and thereby impede further evolutionary responses to selection. In the case of flowering and germination timing, the mutual interaction between these niche-constructing traits led to a novel bivoltine life history in which generation time was halved.

For mobile species such as *A. thaliana*, niche construction is a very important component of its ecology. It has the potential to influence the evolution of dispersal, and it can influence something as fundamental as generation time. Both of these characters are extremely important determinants of the ability of mobile species to persist, grow in population size, and expand their range. By considering the evolution of the environments that organisms experience as well as the evolution of traits themselves, we can gain insight into evolutionary and ecological dynamics that determine the success of species in modern ecological contexts.

Acknowledgements

The author thanks Chandra Polisetty and Naomi Wender for their collaboration on the studies of seed dispersal. I also thank Johanna Schmitt, Lisa Dorn, Converse Griffith, Eunsuk Kim, Chandra Polisetty and Anna Aguilera for their collaborations on the studies of germination cited here. Wei Qui Weng, Andrew Wheeler, Suzen Huang, Shaun Takao, Kevin Kump, Jessica Selby and Jeremy Cesarec provided valuable technical assistance. This work was funded by USDA grant CREES-#2001-35311-09845, NSF grant #DEB-0079489, a Bullard Fellowship from the Harvard Forest, and by the Harvard Forest NSF REU summer program.

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