Trends in
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Review

The role of timing in intraspecific trait ecology

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Intraspecific trait variation has tremendous importance for species interactions and community composition. A major source of intraspecific trait variation is an organism's developmental stage; however, timing is rarely considered in studies of the ecological effects of intraspecific variation. Here, we examine the role of time in the ecology of intraspecific trait variation, focusing on plants and their interactions with other organisms. Trait variation due to differences in developmental timing has unique features and dynamics, distinguishing it from variation due to genes or the environment. When time is considered in studies of intraspecific trait ecology, the degree of variability in timing within a population becomes a key factor structuring trait-mediated ecological interactions and community processes.

Highlights

Trait variation within species is important for shaping ecological interactions and communities.

Traits vary greatly through individual ontogenetic and phenological development, and individuals within populations vary in their developmental timing.

Timing therefore must be important for understanding intraspecific trait variation and its effects on ecology. However, this is rarely considered in the field.

A temporally explicit approach to the study of intraspecific trait variation in ecology is needed to fully understand population and community dynamics.

Timing variation as a cause of trait variation within species

Species' traits, including chemical composition, physical structures, and life history, have a major influence on ecological interactions and community patterns [1–4]. A surge of recent studies have shown that species-level trait averages explain only part of the effects of individual species on ecological communities; intraspecific variation in traits also plays a major role in shaping species interactions and community patterns [5,6]. In plants, intraspecific variation has been shown to influence multiple facets of ecology, including plant species coexistence and community assembly [7], the density and performance of insect herbivores [8–10], predator–prey interactions in plant-associated arthropod communities [11], and floral visitor communities [12,13]. Indeed, in many cases the effect size of intraspecific plant variation at the community level is comparable to the effect size of plant species diversity [14–16]. Intraspecific variation has been further linked to variation in ecosystem-level processes [17]. These discoveries have led to an increasing emphasis in community ecology on intraspecific variation [18,19].

One source of intraspecific trait variation that is receiving increasing attention is variation through plant development, which has two components: **ontogeny** (see Glossary) and **phenology** [20–22]. Plants may progress through ontogenetic stages over scales from months to centuries, depending on their lifespan. In annuals, variation in ontogeny is closely linked to variation in phenology, whereas in perennials phenological variation may be more independent of ontogenetic variation. Developmental timing can also vary among plant individuals in a population both within years (uneven age structure or phenological **asynchrony**) and across years (demographic or phenological shifts), as well as relative to interacting species (**phenological mismatch**). The timing of plant development can vary due to myriad interacting mechanisms that may be genetic or plastic, abiotic or biotic [23–25].

Trait variation associated with developmental timing is widespread. For example, chemical defenses in *Populus tremuloides* (quaking aspen) trees decline many fold as they age [26], and *Nicotiana attenuata* (coyote tobacco) plants can induce nicotine production in the rosette and bolting stages but not in the flowering stage [27]. Indeed, in the milkweed genus (*Asclepias*; Apocynaceae), there can be greater variation in defenses among conspecifics of different ages

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than among species on average, with impacts on herbivore success [28]. Developmental timing is also a major contributor to intraspecific variation in leaf morphology, physiology, and other functional traits [22,29]. Such differences among developmental stages suggest that even a single-genotype monoculture will contain substantial intraspecific trait variation if there is variability in developmental timing among individuals. Likewise, the degree of intraspecific trait variation within a population may change over time [29] due to differences in developmental trait trajectories among individuals [26,30].

Integrating time into the ecology of intraspecific trait variation

Considering evidence of both timing-based intraspecific trait variation and intraspecific variation in timing itself, it follows that a significant fraction of the variation in plant traits present within a population is due to timing. The ecological effects of such trait variation are thus also linked inherently to timing. Although these conclusions are the logical endpoint of previous research, direct evidence to support them is lacking. Timing is rarely considered in studies of the ecological effects of intraspecific variation; instead, most studies focus on isolating genetic or environmental components of variation. To date, most research surrounding the effects of population-level trait variation on species interactions has focused on the effects of instantaneous variation present within plant populations at single time points, often in experimental plots designed explicitly to minimize developmental variability. This snapshot approach to intraspecific trait ecology overlooks variation in developmental timing as a potential driver of intraspecific trait variability and its consequences.

In community ecology, a focus on time and timing has been recently intensified by the increasing impacts of climate change on both organismal phenology [31–33] and temporally discrete extreme weather events [34]. Temporal ecology describes how the outcomes of species interactions are determined by the particular moment in time when the interaction occurs, including the stages and traits of the interacting organisms at that moment. The sequence of ecological interactions also matters and the effects of earlier events are propagated through time [35,36]. Studies that experimentally vary the timing of pairwise species interactions find that timing-based trait variation shapes outcomes both for the interacting species [28,37,38] and for ecosystem-level consequences of the interaction [39]. Natural variation in timing of flowering has also been linked to pollination success and plant reproductive outcomes [40–42]. To bridge the gap between intraspecific trait variation and community ecology, and to fully understand the effects of climate change, will require scaling up from pairwise interaction timing to consider the full contributions of variability in developmental timing to trait and community patterns.

We argue that fully understanding the ecological effects of intraspecific variation requires adopting a temporally explicit approach. This approach entails the specific examination of shorter intervals of time to better understand the dynamics of changing systems [36]. In the following sections we will highlight three major areas of current interest in ecology related to intraspecific trait variation and show how considering the role of timing reveals underappreciated mechanisms through which intraspecific trait variation influences ecological interactions.

Importance of intraspecific timing variation for species interactions in plant-associated communities

Intraspecific timing variation and community genetics

Community genetics aims to link host plant genes to species interactions and community dynamics [4,6]. To this end, single-age **common gardens** comprising replicated plant genotypes have been leveraged to quantify the genetic basis of associated community dynamics. Because genotypic effects are of primary interest, plants are often sampled at a single point in

Glossary

Asynchrony: variation in developmental timing among individuals within a population.
Common garden: an experimental approach wherein multiple genotypes are grown in a single environment, usually with the aim of quantifying genetic contributions to phenotypic variation.
Community genetics: a field of study linking intraspecific genetic variation to community and ecosystem processes.
Ontogeny: the process of development over an individual organism's lifetime, encompassing both continuous, age-based changes and discrete, stage-based changes.
Phenological mismatch: differences in developmental or life history timing relative to potentially interacting species or habitat conditions.
Phenology: the timing of organ development and life history events within a year or season.
Synchrony: consistency of developmental timing among individuals within a population.

time, providing a snapshot of the roles that genetically based intraspecific variation plays in biotic communities. Implied in a snapshot approach is that the magnitude of intraspecific variation is constant over time (Figure 1A). When traits vary with plant development (Figure 1B), spatiotemporal patterns of trait diversity, and thus of associated community composition, will inherently depend on the relative timing and trait trajectories of those different genotypes (Figure 1D). For example, we might predict that added genotype richness will have a greater effect on plant-associated community diversity if those additional genotypes are asynchronous in their development, rather than if they are all synchronous. In this way, variation in the timing of plant development can magnify intraspecific variation.

Although community genetics studies generally control for plant development in their sampling, phenological asynchrony has been implicated as a potential mechanism by which genetically diverse plant populations, which have a higher probability of containing plants with varying phenology, support higher arthropod species richness. For example, among-genotype asynchrony in flowering phenology has been linked to differences in floral visitor communities associated with *Solidago altissima* (tall goldenrod) [13]. Perhaps the clearest example of timing-related community genetics comes from studies on *Oenothera biennis* (evening primrose), where genotypic variation in flowering phenology leads to variation in arthropod communities (Box 1). When plant traits relevant to biotic interactions depend on host plant developmental stage, this additional axis of genotypic variation in timing contributes another pathway by which intraspecific variation may influence associated biotic communities.

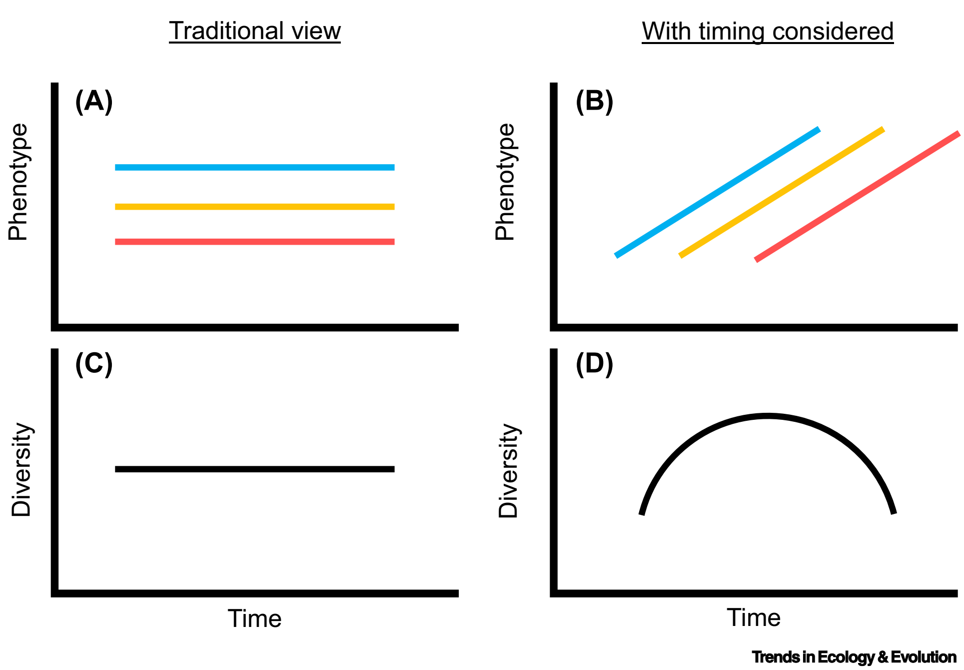

Figure 1. Role of timing in the diversity responsible for community genetics effects. Top panels show simplified trait values of three hypothetical plant genotypes (colors) over time. Bottom panels show diversity of phenotypes among the three genotypes over time, which is expected to correspond to diversity of associated communities. The traditional view of community genetics assumes that trait variation among genotypes is equal over time (A) and thus that trait and associated community diversity is constant (C). A more accurate, temporally explicit view shows that traits can vary with development and developmental timing can vary among genotypes (B). This leads to temporal dynamics of trait and associated community diversity (D).

Box 1. Empirical examples of the role of intraspecific temporal variability

Community genetics and intraspecific timing variation

Oenothera biennis genotypes support distinct communities of arthropods, with genotype explaining 41% of arthropod community diversity in individual plants [75]. Genetic variation in phenology has been invoked as a key mechanism underlying these unique ecological communities. For instance, genotypic variation in bolting and flowering phenology explained arthropod community metrics better than plant resistance traits [75]. When genotypes were combined into populations of varying levels of genotypic diversity, variation in flowering phenology was proposed as a potential mechanism underlying genotypic diversity effects on associated arthropods [76]. *O. biennis* genotypes can also exhibit variation in flowering strategy, where the proportion of annual and biennial individuals varies among genotypes [77]. Together, these studies highlight how genotypic variation in developmental timing can affect plant-associated communities at both the individual and population level.

Associational effects of neighboring plant phenology

Differences in timing can create substantial neighbor effects on plant susceptibility to herbivores. Floate *et al*. [56] found that the susceptibility of *Populus fremontii* (Fremont cottonwood) individuals to leaf beetle herbivory depended on whether they were neighbored by *P. fremontii* × *Populus angustifolia* (narrowleaf cottonwood) hybrids. Hybrid trees leafed out earlier, leading to high densities of a leaf-chewing beetle (*Chrysomela confluens*) that specializes on young leaves of both *Populus* species and their hybrids. As the season progressed, the beetles then shifted onto later-flushing *P. fremontii* trees adjacent to hybrids. This finding is an example of an associational effect on species interaction strength (in this case herbivore load) based on variation in developmental timing. Although this example describes associational effects between pure and hybrid trees, variation in timing among genotypes within a species is likely to produce similar outcomes.

Intraspecific priority effects from phenological variability

A key way that timing variation among host plants can shape community patterns is by allowing phenological stage specialists to reach high densities on individual plants early in the season. For example, Ekholm *et al*. [46] found that *Quercus robur* trees with early budburst timing received very high infestation of an early-season leaf mining caterpillar (*Acrocercops brongniardellus*). High miner infestation reduced arthropod richness and density of other miners and aphids later in the growing season. Crucially, the effect of plant phenology on arthropod patterns was far stronger than the nonphenological effects of plant genotype, suggesting that timing was the key phenotypic variation shaping community assembly. In a synchronous population, miners may have been more spread out among plants and not impacted later communities as severely.

Long-term, among-year developmental processes lend additional complexity to the study of timing-based intraspecific variation. Croy *et al*. [43] sampled arthropod communities over 8 years from a pair of *Artemisia californica* (California sagebrush) common gardens established in different years. This design allowed the effects of interannual abiotic variation and plant ontogeny to be disentangled. Across both common gardens, total arthropod abundance declined with plant age [43]. Interestingly, these effects were not driven by changes in plant productivity (i.e., growth rate) over time; arthropod abundance declined even after accounting for variation in plant size. Long-term ontogenetic variation is a key component of variation in communities associated with perennial species.

Intraspecific timing variation and associational effects

The attractiveness or susceptibility of a plant to potential interacting pollinators or herbivores is not a function only of the focal plant's identity and traits but also of the identity and traits of neighboring plants [44]; these spatial interactions are termed associational effects. Preliminary work indicates that neighbors' developmental stage relative to a focal plant is indeed a driver of associational susceptibility to herbivores [45]. Given these results, the degree of developmental asynchrony within a population is likely to contribute to spatial patterns of interspecific interaction strength.

In a developmentally synchronous plant population (Figure 2A), the distribution of an interacting species may be even across space, but with a single peak in abundance in time corresponding to the most attractive stage of plant development. In an asynchronous plant population

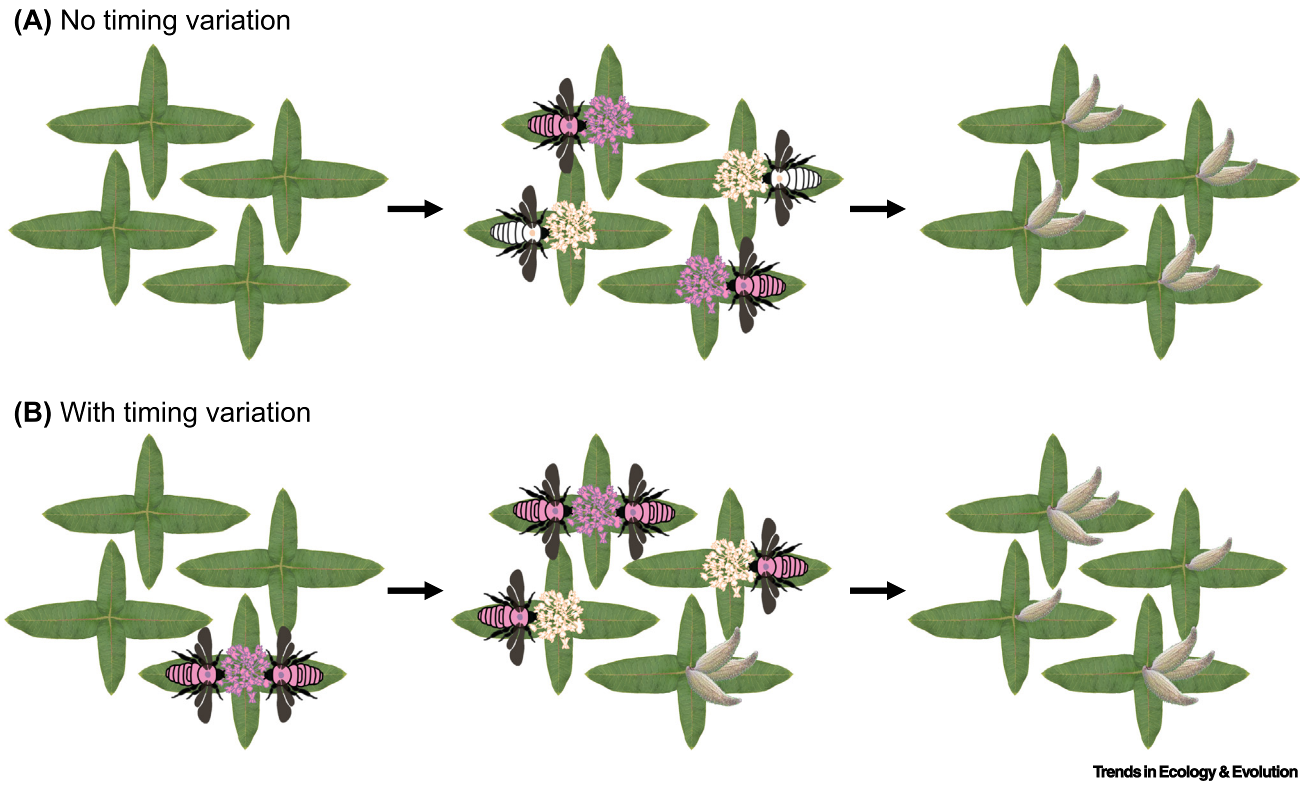

Figure 2. Role of timing in intraspecific associational and priority effects. (A) A generic plant population with two phenotypes and no timing variation. Pink and white phenotypes flower at the same time, drawing two pollinators specialized on those two phenotypes. Pollination success (fruit set) is even across phenotypes. (B) A generic plant population with timing variation. An individual of the pink phenotype flowers early and attracts pink-specialized pollinators. Pollinator community assembly comes to be dominated by pink-specialized pollinators (priority effects). Pollination success is lower for white-phenotype plants as a function of their early-flowering pink neighbor (associational effects).

(Figure 2B), the interacting species may have a more clumped distribution in space, with high abundance on the few attractive-stage plants, but be more evenly distributed in time, as individual plants come and go through the attractive stage for an extended period. Increased competition among plant-associated species is therefore a potential consequence of asynchrony in host plant populations due to the small number of appropriate plants available at a time. For example, in one study, the high density of leaf miners on *Quercus robur* (pedunculate oak) hosts that were at the most susceptible developmental stage led to an increase in intraspecific and interspecific competition among herbivores on those plant individuals [46]. Perhaps similarly, pollinators compete with each other for access when floral resources are limiting [47]. Thus, flowering **synchrony** within plant individuals [48] and within plant populations [49] is generally considered to be advantageous for pollinator attraction and pollination because it maximizes floral resources and minimizes competition. Exceptions include when plants are competing for limited pollinators [25,50] and in deceit-pollinated plants such as many orchids [51], where asynchronous flowering may be favored.

Just as a given plant moves through developmental stages over time, its interacting species have their own parallel timing dynamics. Individuals of an interacting species typically become larger-bodied or more abundant as they interact with plants through time, until they reach their peak size or abundance. Late-developing plants will therefore experience a stronger interaction due to the presence of earlier-developing neighbors, who sustained the interactors when they were smaller or less abundant (Figure 2, note pollination success). For example, trees with later leaf-flush timing experience spillover of herbivores from their earlier-flushing neighbors (Box 1). This is an example of an associational effect that not only is temporally explicit (in the sense that the interacting species moves from one plant to another over time) but is based on variation in timing (in the sense that relative timing of plant development is the key neighbor trait). Relative ontogeny of competitors is often a critical factor in competitive outcomes within and among plant species [52–54]. Because of this, timing variation within a plant population is likely to influence selection dynamics [54], and timing variation relative to the surrounding plant community is likely to influence plant community assembly and species coexistence [55]. Few studies have directly addressed relative developmental timing as a contributor to associational effects [45,56] and more are needed to fully understand the extent of timing impacts on these interactions.

Intraspecific timing variation and priority effects on community assembly

In addition to shaping interactions between neighboring plants via associational effects, as discussed earlier, developmental asynchrony in plant populations will also influence associated community patterns via an intraspecific version of priority effects (Figure 2, note pollinator community), where the identity and traits of early colonizers (in this case early-developing plants) have outsized impacts on trajectories of community composition [57]. Early interactions with herbivores and pathogens are known to be important for later species interactions and plant-associated community composition [58,59]. If early-developing plant individuals are attractive to a particular interacting species, it could lead to priority effects on community assembly across the whole plant population and across time.

Priority effects of early-developing plants on associated community dynamics may have a variety of mechanisms. For oaks, spring phenology influences the success of early-season outbreaking insects, which reach high densities when trees of the right phenological stages are present and can subsequently shape arthropod community patterns (Box 1). Priority effects can also link aboveground interactors to belowground interactors when the former cause changes in host plant traits and soil characteristics that eventually affect the latter [60]. One likely mechanism of timing-driven priority effects on plant-associated community assembly is induced plant responses to herbivores. Many plants are more inducible at younger developmental stages, and induced plant trait responses to herbivory strongly impact the subsequent composition and spatial distribution of arthropod communities [38,61]. Therefore, the distribution of developmental stages at the time of herbivore attack could impact both trait distributions at the population level and subsequent community-level interactions.

Effects of plant asynchrony on interacting species may differ between stage specialists (those that are narrowly adapted to a particular plant stage) and stage generalists (those that use multiple plant stages). Among herbivores, gall formers are an extreme example of stage specialists because they require a specific, newly-formed tissue to induce a gall [62]. While many browsing mammals have preferences among developmental stages, they are often able to feed on multiple stages and tissue types and, as such, could be considered stage generalists [21]. In addition, herbivores adapted to feed on longer-duration plant stages, such as summer foliage, may be less sensitive to timing variation than those adapted to short-lived stages, such as new spring foliage [63]. However, even groups that feed only on a single broad developmental stage can differ in their level of fine-scale specialization. For example, flower traits vary over the course of floral development, so there may be degrees of stage specialization even among pollinators and florivores. Flowers of some plant species change color, stop producing nectar, and/or emit altered fragrances once they have been pollinated, giving pollinators signals that allow them to specialize on pre-pollination flowers [64,65]. In other species, color change in flowers is age-dependent (not pollination-dependent), allowing pollinators to detect and specialize on younger or older flowers [66,67]. Floral traits can also change between male- and female-phase flowers in protandrous plant species [68], which could influence the attraction of pollinators specializing on either nectar or pollen foraging. On the other hand, being able to chew through both open and closed flowers could allow nectar robbers to be more generalist in the stages of flower development on which they feed [69].

Population asynchrony and large trait changes over development may favor colonization by stage generalists, because those species are able to move easily between plant stages with different phenotypes. Alternatively, plant asynchrony could favor stage specialists instead due to an increased likelihood at any given time of finding an individual plant at the appropriate stage and thus of avoiding phenological mismatch. Synchrony and/or weak developmental trait trajectories could likewise favor either stage generalists or stage specialists in different scenarios. Synchrony within plant populations could favor stage generalists if they are able to avoid competition by switching to a different host species at another developmental stage. Or, synchrony could favor stage specialists that have more reliable cueing strategies to find appropriate hosts. Both phenological asynchrony and priority effects among colonizing species tend to be greater with higher temperature [70], so intraspecific priority effects based on variation in developmental timing may be even more important under climate change.

Concluding remarks

Given the inherent role of developmental timing in trait variation, the age or stage structure of plant populations is likely to have extended consequences beyond population growth or demography. Although inferences can be made from current research, questions remain (see Outstanding questions) and direct studies of timing-based plant trait variation are needed. Of particular interest is the relationship between genetic and developmental variation, between phenological and ontogenetic variation, and between asynchrony and other types of diversity. Ecologists studying intraspecific variability should consider variation due to timing explicitly, rather than lumping it in with genetic variation or other types of individual-level variation.

Studies partitioning variation between genotype, environment, and developmental stage will help quantify how much of the observed variation in plant traits and species interactions in nature is driven by relative timing. To date, experiments manipulating developmental variability are rare in trait-based ecology and those manipulating genotypic and developmental variability separately are nonexistent. Artificial warming may be one way to experimentally induce phenological variation in particular [63,71]. Manipulating timing variation will help disentangle the effects of timing variation itself from those of timing-related trait variation. For example, pollinator preferences are known to influence natural selection on flowering time [25,54]; future studies should investigate the selection effects of species interactions on other aspects of developmental timing and consider the contribution of timing-related trait variation to these selective pressures. In perennials, it will be especially important to consider developmental timing on multiple scales and to determine the interactions between within-year phenological variation (e.g., 1-week-old leaves versus 2-week-old leaves) and among-year ontogenetic variation (e.g., 1-year-old trees versus 2-year-old trees). Establishing common gardens of varying ages also allows researchers to separate these developmental effects from those of interannual variation [43]. Combining such gardens with longitudinal surveys of associated communities within and among years could further elucidate how different aspects of plant developmental timing (phenology, ontogeny) contribute to the assembly of associated biotic communities.

Additional research is particularly needed to determine how timing-based trait variation within populations scales up to higher-level processes. Plant trait diversity in general is an important

Outstanding questions

What is the relationship between phenological and ontogenetic trait variability in perennial species?

What are the effects of timing-based intraspecific trait variation on community and ecosystem processes?

How do the consequences of timing variation due to genes versus due to environment differ?

How much does timing contribute to observed effects of genetic diversity?

How do associational effects differ between earlier- and later-developing neighbors?

How does the degree of phenological synchrony in a plant population differentially affect specialist and generalist interactors?

Do early-developing individuals have priority effects on plant-associated community assembly?

component of biodiversity conferring ecosystem resilience to species loss and other anthropogenic stressors [72]. Developmental timing is critical to understanding the temporal distribution of this trait diversity within species (Figure 1). In addition, recent studies suggest that climate change is increasing the intraspecific variability in developmental timing at any one time in some systems, mainly by extending the length of the growing season [71,73]. And although this has yet to be tested in plants, timing asynchrony has been shown to buffer against the functional impacts of species loss in a predatory insect community [74]. Future studies that address the relationship between plant timing variation, community composition, and ecosystem functioning would lead to major advances in our understanding of ecological resilience.

The mean or absolute timing of organismal development is not all that matters for ecology: intraspecific variation in timing is itself a key factor structuring ecological interactions. Timing variation therefore offers a new axis of intraspecific biodiversity to be considered in ecological research and applications. Such a temporally explicit framework will paint a more dynamic and, potentially, a more predictable picture of ecological interactions.

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Declaration of interests

No interests are declared.

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