

REVIEW

The ontogenetic dimension of plant functional ecology

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Abstract

1. Plant functional strategies change considerably as plants develop, driven by intraindividual variability in anatomical, morphological, physiological and architectural traits.
2. Developmental trait variation arises through the complex interplay among genetically regulated phase change (i.e. ontogeny), increases in plant age and size, and phenotypic plasticity to changing environmental conditions. Although spatial drivers of intraspecific trait variation have received extensive research attention, developmentally driven intraspecific trait variation is largely overlooked, despite widespread occurrence.
3. Ontogenetic trait variation is genetically regulated, leads to dramatic changes in plant phenotypes and evolves in response to predictable changes in environmental conditions as plants develop.
4. Evidence has accumulated to support a general shift from fast to slow relative growth rates and from shade to sun leaves as plants develop from the highly competitive but shady juvenile niche to the stressful adult niche in the systems studied to date.
5. Nonetheless, there are major gaps in our knowledge due to examination of only a few environmental factors selecting for the evolution of ontogenetic trajectories, variability in how ontogeny is assigned, biogeographic sampling biases on trees in temperate biomes, dependencies on a few broadly sampled leaf morphological traits and a lack of longitudinal studies that track ontogeny within individuals. Filling these gaps will enhance our understanding of plant functional ecology and provide a framework for predicting the effects of global change threats that target specific ontogenetic stages.

KEYWORDS

drought tolerance, ecophysiology, functional traits, heteroblasty, intraspecific trait variation, phase change, phenotypic plasticity

1 | INTRODUCTION

Plant functional traits have emerged as key drivers of biological processes. While the role of traits in mediating plant function and species interactions has long been recognized, it is increasingly apparent that traits also drive community assembly and ecosystem dynamics

(Adler et al., 2013; de Bello et al., 2021). Thus, the trait-based approach is now among the most commonly used and cited (Funk et al., 2017). In contrast to classical natural history and evolutionary ecology, which generally focus on the population or species scale, trait-based functional ecology often spans communities, landscapes and even attempts to characterize global patterns. To accommodate

such expansive species pools, trait-based ecology often assumes intraspecific trait variation plays a minor role compared with between-species variation, thereby justifying the characterization of traits as species means. However, the extent of intraspecific trait variation can be considerable, varying among species, biomes and traits (Albert et al., 2010; Siefert et al., 2015), and it is recognized that explicit incorporation of intraspecific trait variation can provide important insights into community and ecosystem dynamics (Albert et al., 2011; Violle et al., 2012; Westerland, Funk, et al., 2021). The spatial dimension to intraspecific trait variation is well documented, associated with population variation and environmental gradients (Kühn et al., 2021; Westerland, Knight, et al., 2021), leading to a clear predictive framework described by the spatial variance assumption hypothesis (Albert et al., 2011). In contrast, the temporal dimension to intraspecific trait variation remains underdeveloped (Cope et al., 2022) and so lacks a mechanistic framework.

Plant functional traits vary over time within individuals, populations and communities due to a combination of intrinsic and extrinsic processes. At the scale of communities, temporal trait variation reflects assembly processes and succession dynamics and can include changes in functional diversity over time (Spasojevic et al., 2014). Within individual plants, traits vary over time due to the simultaneous and interactive effects of developmental processes, epigenetics, and phenotypic plasticity. Specifically, four separate processes generally co-occur during plant development: (1) plants get older (age); (2) plants get larger (size); (3) plants move through phase change (ontogeny); and (4) plants become more complex (architecture). Traits also vary over time as an echo of parental environments via epigenetics, and the extent and duration of epigenetic variation in offspring generations are still largely unclear. Temporal intraspecific trait variation is also driven by phenotypic plasticity to changing environmental conditions as plants develop and grow, related to resource availability, uptake, and allocation, climate, and species interactions. Characterization of developmental (intraindividual) variation in functional traits is relatively under-represented in the intraspecific trait variation literature (Westerland, Funk, et al., 2021), though previous reviews have documented strong patterns of trait variation as plants grow and age (Meinzer et al., 2011). In contrast to the previous focus on age- and size-related change, general patterns and sources of heterogeneity in trait variation through plant ontogeny remain unclear. Thus, the aims of this review are to (i) clarify the role of ontogeny within a developmental framework for trait-based ecology; (ii) review evidence for the evolution of ontogenetic trajectories of plant functional traits; (iii) discuss the importance of integrating plant ontogeny within trait-based community and ecosystem ecology; and (iv) identify gaps in our knowledge for future research.

The focus of this review is on resource-use functional traits and their ontogenetic patterns through the seedling–juvenile and juvenile–adult phase changes. These functional traits feature prominently in trait-based ecology, forming the basis of global patterns of plant form and function and driving higher order processes at the population, community and ecosystem scales (Díaz et al., 2016; Reich, 2014; Wright et al., 2004). Traits mediating biotic interactions are not

reviewed here because those involved in pollination and seed dispersal relate only to the reproductive adult phase and because those involved in defences against herbivores have been reviewed extensively already (Barton & Boege, 2017; Barton & Koricheva, 2010; Boege & Marquis, 2005; Koricheva & Barton, 2012; Quintero et al., 2013). While there is interesting overlap between functional traits mediating abiotic and biotic dynamics due to trait multifunctionality and covariance (Agrawal, 2020; Armani et al., 2020), ontogenetic patterns in multivariate traits are discussed here largely in the context of resource use. The role of ontogeny underlying simultaneous shifts in traits driving biotic and abiotic interactions remains an understudied but interesting future research direction (Mason & Donovan, 2015).

2 | ONTOGENY DEFINED

Ontogeny is the genetically regulated transition of plants through a series of developmental stages, including the seed, germinant/seedling, juvenile, vegetative adult, reproductive adult, and senescent stages (Jones, 1999). Classification of plants into ontogenetic stages is highly inconsistent across studies, obscuring general ontogenetic patterns. The seedling/germinant stage can be defined as the earliest stage following germination when the plant depends on maternal resources (Hanley et al., 2004). In practice, plants are often called seedlings well into the juvenile stage when it would be more accurate to classify these plants as juveniles (or saplings). It is similarly difficult to identify phase change from the juvenile to adult stage unless it coincides with reproduction (Day & Greenwood, 2011; Jones, 1999), and so plants are typically assumed to be juvenile until the onset of reproduction. However, vegetative phase change and the onset of reproduction are genetically regulated separately, and so these developmental shifts are usually decoupled, leading to occasional examples of flowering plants in juvenile–vegetative stage and long-lived adult vegetative states without flowering (Poethig, 2013).

The magnitude of trait changes across ontogeny ranges from subtle, gradual changes that are easy to overlook ('homoblasty') to dramatic, abrupt changes in leaves or architecture, which can lead to plants at different stages being mistaken for different species ('heteroblasty'; Goebel, 1889). While it has been suggested that homoblasty and heteroblasty are separate functional strategies (Jameson & Clemens, 2019; Zotz et al., 2011), it is more likely that all plants express some degree of trait variation across ontogeny, with homoblasty and heteroblasty representing extremes along a single continuum. Moreover, although heteroblasty has historically been defined as abrupt developmental changes in leaf morphology (Goebel, 1889; Ray, 1990; Zotz et al., 2011), leaf function depends on the co-expression and intrinsic linkages among morphological, physiological and anatomical traits, and so defining leaf heteroblasty with respect to morphology alone is overly simplistic (Jones, 2001). Thus, heteroblasty is included here with other examples of ontogenetic trait variation.

Plants generally increase in size as they age and pass through ontogeny, and it is often assumed that age and size are good proxies for ontogeny. However, age, size and ontogeny are not synonymous

(Figure 1), and while shifts in functional traits have been described across both plant age and size (Meinzer et al., 2011), these are not necessarily consistent with ontogenetic patterns (Damián et al., 2018; Moriuchi & Winn, 2005). Age-dependent patterns reflect initial dependence on maternal reserves in seed plants, declines in meristem integrity over time, and eventually, senescence in older stages (Thomas, 2011). Size-dependent patterns are not only driven by resource acquisition throughout ontogeny (e.g. larger plants tend to have access to deeper sources of water, greater soil volumes of nutrients and more light) but also reflect architectural and mechanical processes, particularly to support large woody plants, as size increases (McConnaughay & Coleman, 1998; Steppe et al., 2011). While ontogeny and size apply to the whole-plant scale, age is variable within an individual plant due to modularity and indeterminate

growth. Organs also undergo developmental trait shifts (Barton et al., 2019; Turgeon, 1989), leading to developmental mosaics within canopies due to the simultaneous presence of leaves/branches/stems of variable ages (Hackett, 1985; Kearsley & Whitham, 1989).

Imprecise language when reporting patterns of plant functional traits across age, size or ontogeny has led to inconsistent characterizations across studies of developmental trajectories that likely obscures general patterns. Future studies should carefully define which metric of development is under consideration and should avoid extrapolating trait patterns across plant size or age to ontogeny. Studies that simultaneously consider multiple developmental axes may reveal the extent to which each contributes to trait variation through development and potential interactive effects. For example, it is likely that size and age contribute to trait variation within

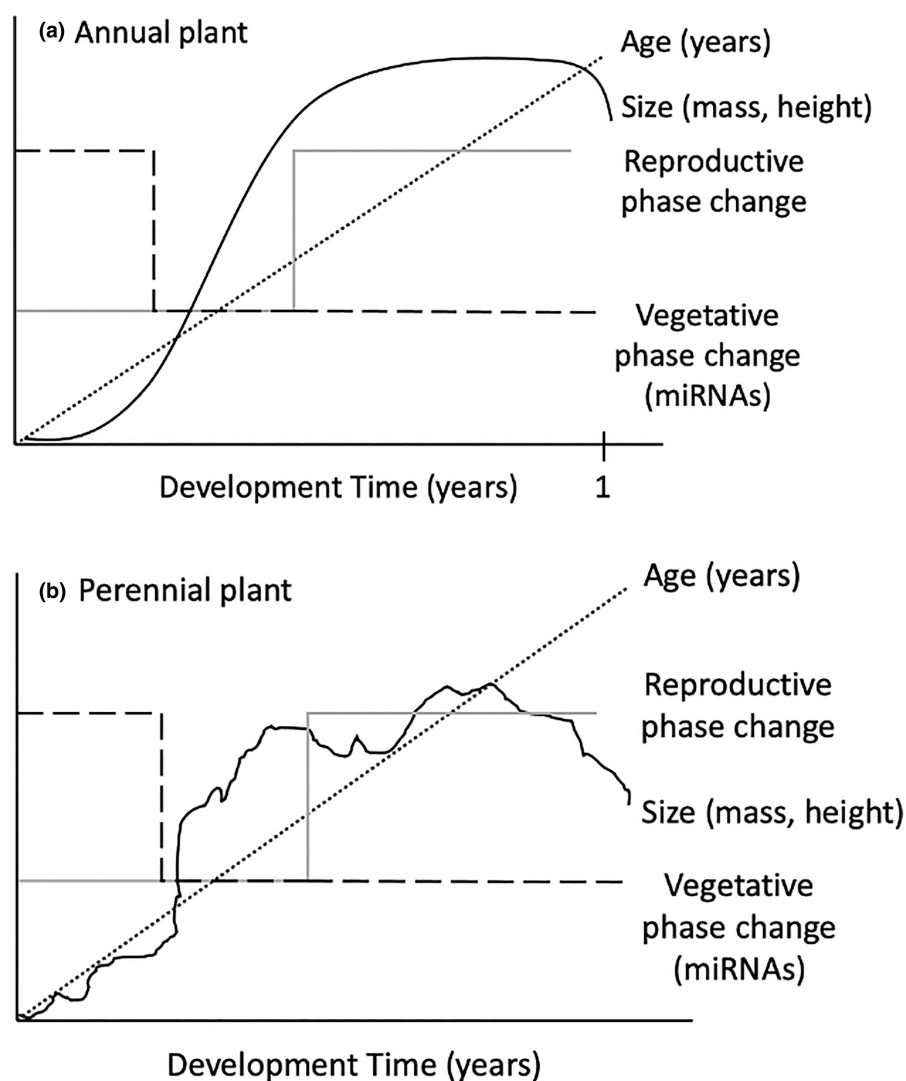


FIGURE 1 Example developmental trajectories for simultaneous changes in plant age, size and ontogeny (vegetative and reproductive phase change), conceptualized separately for short-lived annual species (a) and long-lived perennial species (b). As plants develop and grow, they increase in age and size while passing through ontogeny, resulting in multiple axes of developmental trait variation. Ontogeny is the passage through genetically regulated phase changes (Jones, 1999; Poethig, 2013) and is thus a categorical axis of development. In contrast to ontogeny, age and size are continuous axes of development. Size often increases nonlinearly or exponentially (Tessmer et al., 2013) under favourable conditions in short-lived annual plants (a), while trajectories are more complex and variable in long-lived plants (b), reflecting more dynamic extrinsic and intrinsic conditions over longer time periods (Bowman et al., 2013).

ontogenetic stages, particularly for long-lasting stages such as the juvenile stage of forest trees that spend decades in the understory (Lusk, 2004).

3 | CAUSES OF ONTOGENETIC TRAIT VARIATION

3.1 | Proximate causes of ontogenetic trait variation

As plants pass through ontogeny, changes in trait expression are caused by intrinsic and extrinsic drivers, as well as their interplay. Intrinsic factors include genetically regulated shifts in trait expression, while extrinsic factors drive ontogenetic trait variation via phenotypic plasticity. Because phenotypic plasticity of morphological and anatomical traits is largely expressed through the development of new tissues, phenotypic plasticity contributes to ontogenetic trait variation. Moreover, developmental trait shifts occur along a trajectory, and plasticity to current environmental conditions depends on prior trait expression and environments, leading to a dynamic interplay, or 'ontogenetic contingency', between intrinsic and extrinsic factors over a plant's lifetime (Diggle, 2002; Pigliucci, 1998; Watson et al., 1995).

Transitions from the juvenile to vegetative adult phase and from the vegetative to reproductive adult phase are regulated by microRNAs, including the master age regulators miR156 and miR172, as well as miR159, miR166 and miR396 (Ma et al., 2020; Teotia & Tang, 2015), which promote adult vegetative trait expression (He et al., 2018; Xu et al., 2016). The networks of genes regulated by these microRNAs, including the Squamosa Promoter Binding Protein-Like transcription factors, are well characterized in *Arabidopsis* and some annual crops such as maize and include genes responsible for observable trait shifts across ontogeny, including leaf morphology and trichome density (He et al., 2018; Huijser & Schmid, 2011; Lawrence et al., 2021; Poethig, 2013; Xu et al., 2016). Documentation of similar patterns of expression (e.g. declines in miR156 and increases in miR172 with plant age) in diverse woody species suggests their function may be widely conserved within plants (Ahsan et al., 2019; Leichty & Poethig, 2019; Wang et al., 2011), although clear links to ontogenetic variation in functional traits are not yet broadly established.

Current research on the regulation of plant ontogenetic phase change has focussed primarily on two transitions between three phases: vegetative juvenile to adult and adult vegetative to reproductive. Although phases are categorical, shifts in trait expression across phase transitions are necessarily gradual, requiring the development of new tissues. In many plant species, there are more than three phases, with additional phases early in ontogeny as seeds germinate, and as seedlings become autotrophic and initiate developmental trajectories (Jones, 2001; Poethig, 2003). Although gene expression patterns associated with the germinant–seedling autotrophic transition have been described and they suggest a role for microRNAs (Ha et al., 2017; Vidal et al., 2014), genetic regulation of

other early ontogenetic shifts remains unclear. Identification of regulatory mechanisms underlying these early and complex trait trajectories would confirm whether additional phases occur during early ontogeny and reveal whether plants share a universal progression of developmental phases.

Developmental trait variation occurs not only due to genetically regulated phase change (i.e. ontogeny) but also as a consequence of phenotypic plasticity as plants acclimate to changing environmental conditions (Figure 2). Phenotypic plasticity is common and widespread, driving variation in diverse plant traits in response to many environmental factors, although the directionality and magnitude of these changes are highly variable (Fritz et al., 2018; Matesanz & Ramirez-Valiente, 2019; Poorter et al., 2012; Sultan, 2000). Because environmental conditions often change considerably as plants grow and develop, particularly for long-lived species, phenotypic plasticity to these changing conditions can lead to developmental trait variation. For example, many forest trees grow from low-light conditions as juveniles in the understory to high-light conditions as they reach the canopy, and it is therefore difficult to determine whether ontogenetic trait differences, such as smaller leaf area, less palisade tissue and lower leaf mass per area (LMA) in seedlings than mature trees (Fortunel et al., 2020; Ishida et al., 2005), reflect genetically programmed shifts associated with phase change, or plasticity to low- versus high-light conditions.

It is likely that for many species, developmental trait variation reflects simultaneous effects of ontogeny and phenotypic plasticity, as well as interactions between them (Callahan et al., 1997; Pigliucci, 1998; Winn, 1996b; Wright & McConnaughay, 2002). Interactions between ontogeny and plasticity may occur for multiple reasons. First, ontogeny is itself plastic. For example, the timing of the juvenile–vegetative adult phase change varies in response to light availability in *Acacia koa* (Rose et al., 2019). Second, plasticity within ontogenetic stages may alter the magnitude of ontogenetic trait variation (Figure 2), highlighting how genetically regulated shifts in trait expression across ontogeny do not necessarily lead to fixed trait trajectories (de Soyza et al., 1996; Moriuchi & Winn, 2005). Third, a plant's phenotype reflects plasticity in previous stages as in 'ontogenetic contingency' (Diggle, 2002; Pigliucci, 1998; Watson et al., 1995). For example, carotenoid production varies considerably throughout ontogeny in response to changing light conditions, and recent research has revealed that epigenetic mechanisms underlie this variation, effectively linking plasticity at earlier stages to phenotypes at later stages (Anwar et al., 2021). As a consequence of such 'ontogenetic contingency', ontogenetic trajectories are unique to individuals and their specific sequence of environment–phenotype variation.

In order to estimate the role of phenotypic plasticity in ontogenetic trait variation, experiments are needed to characterize trait expression across ontogenetic stages under manipulated environmental heterogeneity. To maintain consistency in treatments across ontogenetic stages that also differ in size, it is important that conditions of resource availability and not simply resource levels be manipulated. For example, to characterize plasticity in net photosynthesis

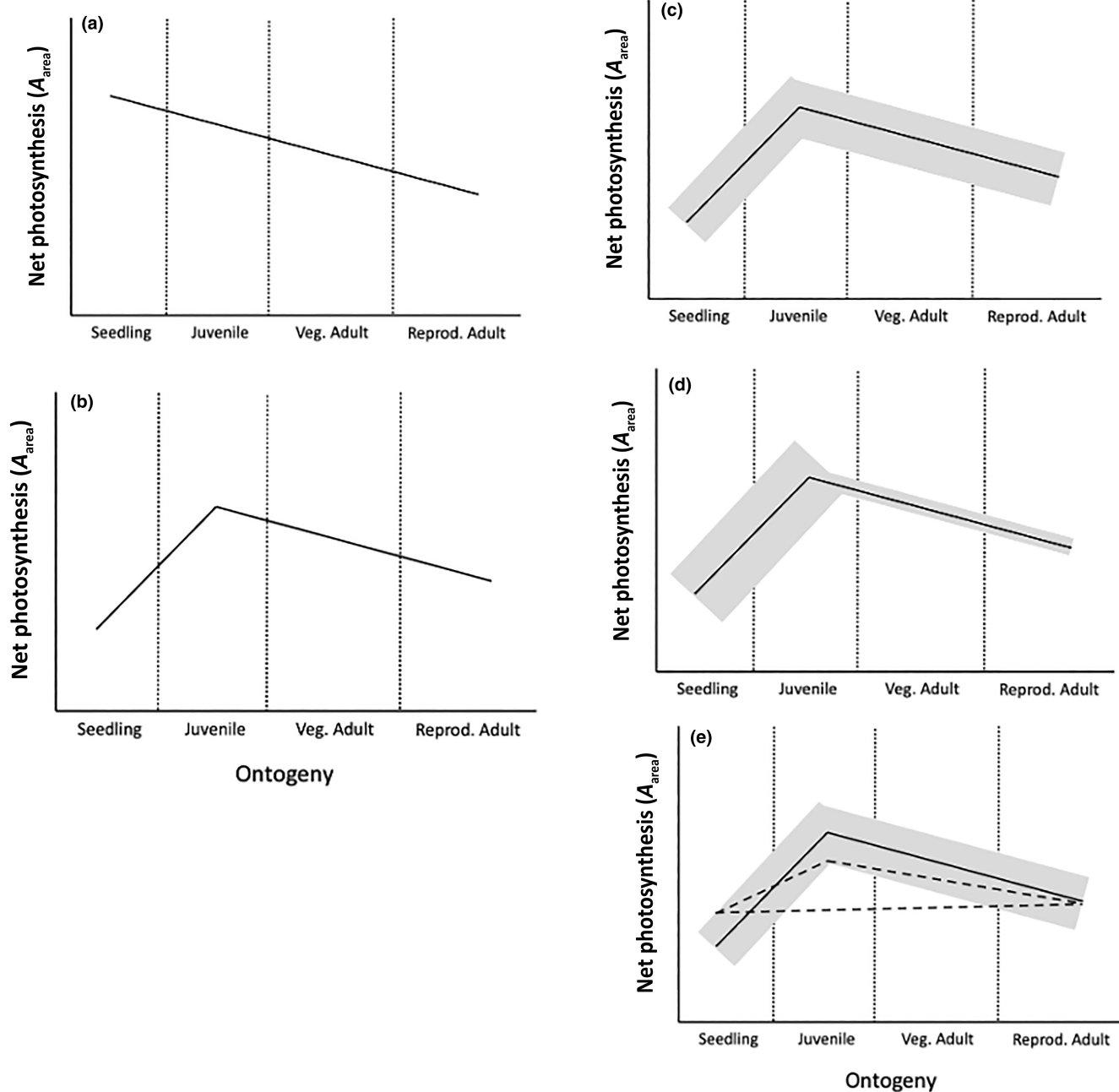


FIGURE 2 Possible ontogenetic trajectories in photosynthetic rates through ontogeny in which a single trajectory is depicted in each panel. In the narrow sense, each line represents the trajectory of a single individual plant (genotype) or that of a sibship. In the absence of phenotypic plasticity, the trait may vary linearly (a) or nonlinearly (b) through ontogeny. Phenotypic plasticity results in more complex and unpredictable ontogenetic trajectories (line) in (c–e). The drivers, biotic and abiotic cues, of trait plasticity are highly variable among environments and species and so are not depicted in this general model.

(A_{area} $\mu\text{mol}/\text{m}^2/\text{s}$) to water limitation will require changing watering treatments across ontogeny to account for simultaneous effects of increasing size on water use. Such experiments will benefit from a norm of reaction approach with sibships to more precisely characterize trait variation throughout ontogeny and with respect to environmental heterogeneity (Simms, 2000). Genotypic replication via cloning is discouraged because cloned material maintains the age and ontogenetic stage of the source plant (Mencuccini et al., 2007) and so cannot be used to characterize whole-plant ontogeny.

Using this experimental approach, we can identify cases in which net photosynthesis is not plastic, for example declining across ontogeny in a fixed trajectory (Figure 2a). For species germinating under light-limited conditions, as is typical for many plants, a fixed ontogenetic trajectory would be predicted to be nonlinear, reflecting anatomical and physiological constraints in the seedling stage (Figure 2b). On the contrary, phenotypic plasticity in net photosynthesis may be detected, leading to a range in trait expression throughout ontogeny, depicted as the grey area surrounding the

mean trajectory (Figure 2c). The magnitude of trait plasticity may be consistent throughout ontogeny (Figure 2c), or may be greater early in ontogeny (Figure 2d), as is commonly reported (Avramov et al., 2017; Niinemets, 2004; Winn, 1996b). Considering the potential range of trait expression via plasticity, there is a large number of possible ontogenetic trajectories, depicted with dashed lines in Figure 2e. It is even feasible that no ontogenetic shifts are observed if only subsets of ontogenetic stages are sampled, and plasticity happens to lead to similar trait expression in the observed stages (Figure 2e, flat dashed line). This scenario illustrates how plasticity can result in the apparent lack of ontogenetic trait variation.

3.2 | Ultimate causes of ontogenetic trait variation

Master regulator genes provide a mechanism by which plants may evolve distinct phenotypes in response to variable selection pressure across ontogenetic stages. When environmental change is predictable across plant ontogeny, genetically fixed ontogenetic trait variation is expected to enhance fitness by minimizing the costs of phenotypic plasticity (DeWitt et al., 1998). While environmental shifts through ontogeny are likely to be highly variable among biomes and so difficult to characterize with general models, research to date has largely focussed on a few common scenarios, which form the basis for two mechanistic hypotheses for the evolution of ontogenetic trait variation (Figure 3). The first hypothesis considers how light quality and quantity typically change from shady conditions during germination and early ontogeny to more open and sunny conditions in later ontogeny (Thomas & Winner, 2002), hereafter referred to as the '*Light Hypothesis*'. Selection pressure from these distinct light environments may drive the evolution of predictable shifts from 'shade leaves' early in ontogeny to 'sun leaves' late in ontogeny, leading to ontogenetic increases in photosynthetic rates and LMA and decreases in stomatal pore density, leaf nitrogen concentration and leaf area (Coste et al., 2005; Delagrange et al., 2004; Givnish, 1988; Houter & Pons, 2012; Pasquet-Kok et al., 2010). While shady to sunny ontogenetic transitions are most common for forest trees, it is also likely that grassland species germinate into shady conditions and even that some desert and alpine species that recruit under the canopy of nurse plants will experience predictable shifts from shady to sunny conditions as they develop, thus identifying this as a widespread and common prediction for the evolution of ontogenetic trait trajectories.

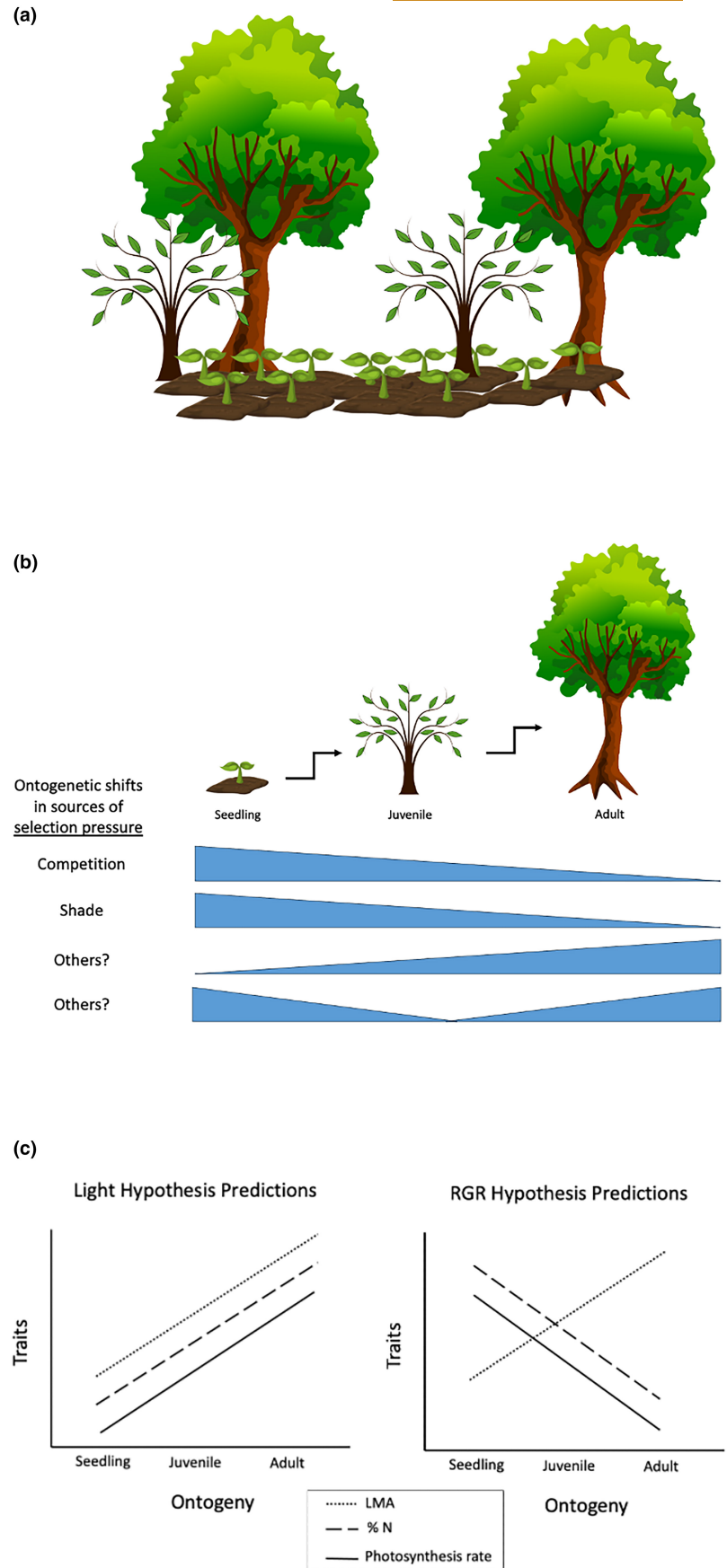
The second evolution of ontogeny hypothesis considers the benefit of maximizing growth during early ontogeny, followed by predictable declines in relative growth rate in later ontogenetic stages (Dayrell et al., 2018; Mason et al., 2013), hereafter referred to as the '*RGR Hypothesis*'. In many communities, seedlings germinate in high densities under conditions characterized by water, nutrient and space limitation. Escape from these stressful conditions through vigorous growth may be the most successful seedling and juvenile strategy because as plants grow larger, they have greater access to resources (both below- and above-ground) and are also

able to tolerate biotic threats more easily (Barton & Hanley, 2013). Thus, seedlings and juveniles are predicted to benefit from fast relative growth rates characterized by higher photosynthetic rates and leaves with lower LMA and higher stomatal pore area, nitrogen and phosphorus concentrations than adult plants (Evans, 1998; Pasquet-Kok et al., 2010; Smith et al., 1997; Wright et al., 2004). It follows, then, that later ontogenetic stages are expected to have been selected not only for vigour alone, but also for stress tolerance, leading to resource allocation to more diverse functions, and thereby leading to lower relative growth rates. In addition to the *Light* and *RGR Hypotheses*, additional species-specific predictions have been made for the evolution of ontogenetic trait variation in response to predictable shifts in temperature (Darrow et al., 2001), water availability (Brodribb & Hill, 1993; Lucani et al., 2019; Pasquet-Kok et al., 2010) and wind (Burns, 2005). Consideration of additional species and biomes is needed to determine the generality of ontogenetic trait patterns with respect to the diverse environmental factors that vary as plants pass through ontogeny.

Despite the expectation that ontogenetic trait variation occurs, at least in part, due to evolutionary responses to predictable environmental change during a plant's lifetime, relatively little research has examined the potential for ontogenetic trajectories to evolve by natural selection (Barton & Boege, 2017; Poorter, 2007; Winn, 1999). Because plant function depends on coordinated expression of interdependent traits (Agrawal, 2020; Damián et al., 2020; Reich, 2014), multivariate analyses that consider the evolution of trait syndromes are likely to be the most informative. One important question is whether trait covariance that is well documented among species also occurs within individuals throughout ontogeny. For example, leaf traits associated with leaf economics (e.g. carbon and nitrogen content, LMA and chlorophyll content) are more integrated at the adult than at the juvenile stage, leading to an ontogenetic shift in leaf modularity (Damián et al., 2018). High modularity in the adult stage indicates strong selection for the conservative leaf economic strategy, while weaker modularity in the juvenile stage suggests a relaxation of trait covariance, potentially allowing for increased capacity of plastic adjustment and/or a greater diversity of leaf functional solutions early in ontogeny. However, trait covariance quantified under controlled conditions (e.g. greenhouse or garden) may not correspond to trait covariance under field conditions, further complicating our understanding of multivariate trait evolution throughout ontogeny (Laughlin et al., 2017).

In order for ontogenetic trait trajectories to evolve via natural selection, they must present heritable genetic variation associated with differential fitness. While extensive research has documented heritable genetic variation in functional traits and characterized links between traits and fitness under diverse environmental contexts, these studies are typically constrained to a single ontogenetic stage (e.g. seedlings or adults), leading to largely separate understandings of the traits under selection in seedlings versus adults (e.g. regeneration and adult niches; Poorter, 2007), or ignoring stage altogether. But of course, the regeneration and adult niches are not independent and are linked within plants via ontogeny. Although relatively

FIGURE 3 Conceptual model linking shifting sources of selection pressure as plants pass through ontogeny to predicted changes in functional traits across stages. In many communities, especially forests but also grasslands, plants experience predictable decreases in competition intensity and shade as they develop from the seedling to juvenile to adult stage (a). These result in changing selection pressure for traits that maximize fitness to different environmental conditions across ontogeny (b). It is likely that many other section factors can also change across ontogeny in variable ways, including nonlinear patterns (b). Ontogenetic variation in functional traits is predicted to have evolved in response to these changing selection pressure regimes (c).



few studies have begun to investigate the evolvability of ontogenetic trait trajectories, these studies provide compelling evidence that evolution by natural selection is likely. For example, relatively high broad-sense heritabilities have been detected for an ontogenetic increase in leaf nitrogen concentration ($H^2=0.24$) and ontogenetic decrease in LMA ($H^2=0.15$) in a long-lived tree, *Populus tremuloides* (Cole et al., 2020). Broad-sense heritabilities for ontogenetic decreases in area-based assimilation and stomatal conductance rates are greater under dry than wet conditions in a Mediterranean annual grass (Maherali et al., 2009). Other examples of genetic variation in ontogenetic trait trajectories (Barton, 2007; Winn, 1996a) support the prediction that they could evolve via natural selection.

Ontogenetic trajectories may also evolve via shifting selection pressure on different traits at different stages (Figure 3). For example, in *Turnera velutina*, fitness is linked to secondary chemistry in the seedling stage and trichome density in the adult stage, leading to ontogenetic patterns in both traits (Ochoa-López et al., 2020). In coastal dune plants, growth and reproduction were not only linked to high chlorophyll content throughout ontogeny but were also associated with stomatal regulation in seedlings and high water-use efficiency in juveniles, revealing how stress may select for different traits across ontogeny (Lum & Barton, 2020). Such complex links between traits and fitness across ontogeny could explain the numerous examples of weak relationships between functional traits and performance that confound scientists (Paine et al., 2015; Yang et al., 2018) if trait–fitness relationships are being examined at stages in which traits are not under selection. Characterization of trait–fitness links throughout ontogeny and with respect to meaningful shifts in environmental conditions will provide new insights into the evolvability of ontogenetic trait trajectories.

4 | GENERAL PATTERNS IN PLANT ONTOGENETIC TRAIT VARIATION

4.1 | Compiling the evidence

Studies reporting ontogenetic trait variation were identified through literature searches using systematic review methods (Gusenbauer & Haddaway, 2020). Additional search details and a summary of trait variation patterns are reported in the Supplementary Materials (Supplementary Methods, Supplementary Tables S1–S4). Synthesis across studies is challenging due to the inconsistent use of terminology (see Section 2); many publications report ontogeny for the characterization of trait variation across plant size or age. Nonetheless, if the plants sampled seemed to also span ontogenetic stages, they were included as examples of ontogeny. Studies documenting trait variation between the juvenile and adult stages are far more common than those characterizing trait variation between seedling and juvenile plants. Evidence for ontogenetic trait variation comes from both tropical and temperate biomes, but is biased with respect to plant growth form, with the majority of studies focussing on woody plants (Tables S1–S4).

4.2 | Evidence for the light and RGR hypotheses

Because most studies address predictions about light and growth rate variability across ontogeny, these hypotheses are assessed here. Undoubtedly, plants have evolved ontogenetic trait variation in response to other environmental factors (Figure 3), and identifying these should be a future research priority. The most commonly sampled trait, LMA, demonstrates remarkably consistent increases from the seedling to juvenile (Table S1), and juvenile to adult stages (Table S2), although there are a few exceptions, notably in crops (Table S2). An increase in LMA through ontogeny is predicted by both the *Light* and *RGR Hypotheses* to maximize light use and relative growth rate through ontogeny, illustrating the multifunctionality of plant traits and how these hypotheses are not mutually exclusive. Leaf area, thickness and stomatal conductance (g_s) are also commonly measured, but these show variable ontogenetic patterns among species (Tables S1 and S2), potentially reflecting relatively weak trait coordination with LMA within individuals, high plasticity in these traits due to microscale heterogeneity, or more complex ontogenetic patterns selected for by factors other than those associated with the *Light* and *RGR Hypotheses*.

Patterns in photosynthesis are particularly informative because these are predicted to undergo distinct ontogenetic shifts (Tables S1 and S2), increases associated with greater light availability (*Light Hypothesis*) and decreases due to a shift from high to low relative growth rate (*RGR Hypothesis*). Evidence was detected in support of the *Light Hypothesis* in trees as increases in light-saturated assimilation rate measured on a per-area basis (A_{area}), as well as the *RGR Hypothesis* as juvenile–adult ontogenetic decreases in A_{area} in two crop, one grass and three tree species (Tables S1 and S2). Thus, based on photosynthetic data, ontogenetic trait variation in trees seems largely driven by adaptation to predictable increases in light availability, while selection for RGR may occur in various growth forms. However, this conclusion may oversimplify the multiple challenges woody plants face during ontogeny which can span decades, and it is limited by a relatively small species pool. Few studies to date have included more than 2 stages, or incorporated traits beyond LMA, A_{area} , A_{mass} , leaf area and g_s (Tables S1 and S2), which precludes robust general patterns.

4.3 | Ontogenetic patterns in hydraulic traits

A consequence of ontogenetic shifts from shade to sun tolerance (*Light Hypothesis*) or from fast to slow RGR strategy (*RGR Hypothesis*) would be more sclerophyllous leaves in the adult stage, which could contribute to an ontogenetic increase in drought resistance. Indeed, seedlings are often reported to be particularly vulnerable to drought (Comita & Engelbrecht, 2014), and although this is generally attributed to developmental constraints associated with their small size leading to shallow roots, minimal stored nonstructural carbohydrates and underdeveloped woody tissue (Comita & Engelbrecht, 2014; Marod et al., 2002;

O'Brien et al., 2020), low drought tolerance in seedlings may also be directly selected for to enhance fast RGR and shade-tolerant strategies during establishment (Brodribb & Hill, 1993; Lucani et al., 2019; Mediavilla & Escudero, 2004; Mediavilla et al., 2021; Pasquet-Kok et al., 2010).

Beyond leaf morphology, few studies have characterized ontogenetic trends in traits regulating water balance and hydraulic function (Tables S3 and S4). The limited evidence available indicates an ontogenetic increase in water-use efficiency (Tables S3 and S4). In contrast, ontogenetic patterns in stomatal density, stem/wood density and mid-day or predawn leaf water potential are variable among species (Tables S3 and S4). Clearly, additional research is needed that expands beyond leaf morphology to determine whether general patterns in ontogenetic trajectories of water-use traits occur across species and biomes, and this research is increasingly urgent considering the increase in consecutive days without rainfall and annual declines in rainfall in many parts of the world (Masson-Delmotte et al., 2021).

Aside from ontogenetic drivers of hydraulic function as plants develop, there is ample evidence that plant size contributes to water balance, although these patterns are beyond the scope of this review (Lachenbruch et al., 2011).

4.4 | Ontogenetic patterns in other traits

There are many promising avenues for future research characterizing ontogenetic trajectories in functional traits. For example, very few studies have incorporated below-ground traits, obscuring the degree to which shoot and root traits are coordinated throughout ontogeny (Havrilla et al., 2021). Ontogeny can also influence phenology, although this is not well described. For example, spring leaf flushing occurs earlier in seedlings than in adult trees (Vitasse, 2013), a presumably adaptive ontogenetic pattern enabling seedlings to maximize photosynthesis and growth before the canopy closes. Consistent with the prediction that juvenile stages have faster RGR, leaf longevity has been reported to be shorter early in ontogeny (Mediavilla et al., 2013; Seiwa, 1999). How climate change will affect ontogenetic variation in phenology is unknown, but is likely to be important considering the widespread evidence for phenological changes due to global warming (Parmesan, 2007; Parmesan & Hanley, 2015).

5 | HOW DOES THE ONTOGENETIC DIMENSION OF INTRASPECIFIC TRAIT VARIATION INFLUENCE TRAIT-BASED ECOLOGY?

5.1 | Population dynamics

Population dynamics depend on demography and life history, processes that explicitly incorporate ontogeny. For example, demographic models project population growth by integrating vital rates (survival

and growth) throughout the life cycle of plants, and while demographic data are often based on size rather than ontogeny per se, they nonetheless capture phase changes (Merow et al., 2014; Rüger et al., 2018). However, despite growing efforts to integrate functional traits into demographic studies for mechanistic insights (Adler et al., 2014; Hérault et al., 2011; Lasky et al., 2015; Salguero-Gómez et al., 2018; Visser et al., 2016; Westerland & Horvitz, 2017), ontogeny is often neglected from the trait analyses so that species means of adult plant traits rather than individual trait data associated with ontogenetic trait variation are incorporated into the models. This leads to a scale mismatch between the vital rates quantified at the individual scale and functional traits quantified at the population (or species) scale (Iida & Swenson, 2020; Yang et al., 2018). This mismatch could account for the reported weak links between vital rates and traits, which have stymied the integration of functional traits into population dynamics (Laughlin et al., 2020; Liu et al., 2016; Paine et al., 2015).

Refining our approach to incorporate ontogenetic trait variation in population dynamic studies will provide a more nuanced mechanistic understanding of plant performance throughout ontogeny and may also shed light on population stability under global threats such as climate change (Moran et al., 2016). That climate influences plant population dynamics is well documented (Dahlgren et al., 2016; Doak & Morris, 2010; Sletvold et al., 2013; Ticktin et al., 2016), and it has been shown that climatic variables can affect vital rates in different ways across ontogeny (Doak & Morris, 2010; Hart-Fredeluces et al., 2020). Furthermore, climate change could alter the predictability of environmental conditions across ontogeny, leading to trait–environment mismatches. This may be particularly relevant for species with fixed ontogenetic trajectories and limited phenotypic plasticity, characteristic of heteroblasty, and could increase the vulnerability of these species to climate change.

5.2 | Community structure and dynamics

Scaling from populations to communities can benefit from the incorporation of functional traits for mechanistic insights (Laughlin et al., 2020). Although there is growing appreciation for the role of intraspecific trait variation in community structure and dynamics (Albert et al., 2011; Bolnick et al., 2011; Violle et al., 2012; Westerland, Funk, et al., 2021), intraindividual variation such as that due to ontogeny is rarely represented. Indeed, for the most part, ontogeny has been intentionally excluded from trait-based community ecology as a consequence of prescribed methods to collect data on 'reproductively mature' individuals (Pérez-Harguindeguy et al., 2013). As a consequence, the vast repositories of functional trait data, such as the TRY database (Kattge et al., 2020), are poor resources for investigating the role of ontogenetic trait variation in ecology. This is unfortunate because ontogenetic trait variation is likely to influence many components of community structure and dynamics, including species fundamental niches, temporal niche partitioning, functional diversity, and community responses to climate change and biological invasions.

The fundamental niche represents the full set of abiotic and biotic conditions that support a species via positive population growth (Carscadden et al., 2020). Depending on niche breadth and overlap among species, we can gain insights into the species interactions and resource-use strategies that structure communities, and functional trait variability can in some cases be a good proxy for niche breadth (Cadotte et al., 2013). Niche breadth is predicted to be narrow during early ontogeny, associated with specific recruitment conditions and referred to as the 'regeneration niche' (Grubb, 1977; Larson & Funk, 2016). As plants mature, abiotic tolerance is predicted to increase, leading to ontogenetic niche expansion (Donohue et al., 2010). Ontogenetic trait variation offers some support for these predictions, with the tendency for plants to shift from fast to slow RGR strategies and to increase in drought resistance across ontogeny (Section 3). However, an increase in abiotic stress tolerance is not necessarily associated with an increase in niche breadth as quantified using functional trait variation. For example, tolerance of high light and drought during adult stages may arise through a shared trait syndrome (e.g. high LMA, leaf thickness, WUE and small leaf area), emerging as a shift in niche position away from that of the juvenile stage, rather than niche expansion. With ontogenetic niche shifts, the fundamental niche is broader at the species scale than at any single ontogenetic stage (Carscadden et al., 2020). Without comprehensive trait data for all stages, it is difficult to determine whether species fundamental niches generally include niche shifts, representing a change in functional strategy, or expansion, representing an increase in the range of potential functional strategies, across ontogeny.

Associated with ontogenetic niche shifts, the abiotic and biotic filters that determine community composition can change as plants develop (Lasky et al., 2015; Piao et al., 2013). As a consequence, community assembly will differ at the regeneration, juvenile/sapling, and adult plant stages. For example, in a temperate forest in the Ozark Mountains, functional diversity of leaf morphology (area and LMA) differed between sapling and adult stages, with stronger trait–environment relationships detected for adults than saplings, suggesting abiotic filters are particularly important for community assembly at the adult stage (Spasojevic et al., 2014). Ontogenetic niche shifts may also reveal when biotic filters influence community assembly. For example, the intensity of competition can change across ontogeny due to ontogenetic niche shifts in co-occurring species and because of shifting species pools (Lasky et al., 2015; Piao et al., 2013). A major challenge of trait-based community assembly research, particularly with consideration of whole-plant ontogeny, is to characterize how different traits relate to fitness across ontogeny in order to provide meaningful indicators of filters operating at various stages (Craine et al., 2012). This same complexity underlies the challenge in identifying sources of selection pressure across ontogeny (Section 3.2).

5.3 | Ecosystem dynamics

The degree to which intraindividual ontogenetic trait variation scales up to influence ecosystem dynamics has rarely been examined. Most

ecosystem models implicitly focus on the contributions of adult plants, which are assumed to dominate global carbon, nutrient, and hydrological dynamics (Pan et al., 2013; Schimel et al., 2019). Yet, the integration of functional traits to ecosystem models often includes experimental data from seedlings (Hartmann & Trumbore, 2016), and the extrapolation of these results to understanding dynamics of adult plants has been questioned (Hartmann et al., 2018). Depending on the age structure and size stratification of the community, ontogenetic shifts in plant functional traits could drive ecosystem dynamics. For example, even-aged forest stands such as plantations have been observed to decline in productivity with age (Hinckley et al., 2011), a pattern consistent with the predicted shift from fast to slow relative growth rates across ontogeny. The role of ontogenetic trait variation in ecosystem dynamics for communities with greater diversity and demographic complexity deserves attention.

6 | KNOWLEDGE GAPS AND RESEARCH PRIORITIES

In summary, ontogeny is a widespread and common source of intraspecific trait variability that can evolve by natural selection and which may drive higher order processes at the scale of populations and communities. In contrast to early predictions, ontogenetic trait variation is not simply developmental noise (Evans, 1972), but is regulated by a shared suite of micro RNAs and displays consistent structure and directionality among species and biomes. Common ontogenetic trajectories are consistent with predictions that plants undergo shifts in trait expression to maximize relative growth rate and shade tolerance early in ontogeny followed by a shift to a conservative strategy to tolerate high light and drought at the expense of relative growth rate later in ontogeny (Figure 3). Nonetheless, there are exceptions to these general patterns, and some biomes and plant growth forms remain poorly sampled. In particular, more research is needed to: (i) characterize ontogenetic trajectories within individuals using a norm of reaction approach; (ii) determine the extent of genetic variation and heritability of ontogenetic trajectories to assess their evolvability; (iii) identify the role of master regulatory genes in driving ontogenetic trait changes in wild species under natural conditions in order to understand its generalizability; (iv) extend trait analyses throughout plant life stages in order to assess the number of ontogenetic phases and potential nonlinearities in ontogenetic trajectories; (v) synthesize abiotic with biotic drivers of the evolution of ontogenetic trajectories; and (vi) incorporate ontogenetic intraspecific trait variation in population, community and ecosystem-scale studies. These recommended future directions will require new approaches and tools in conjunction with clear definitions and a greater diversity of plants and biomes, as further described below.

Mixed approaches are needed to characterize ontogenetic trajectories in plant functional traits. For insights into their evolvability, a combination of longitudinal and snapshot surveys would shed light on the genetic variation and heritability of trajectories. Snapshot

surveys entail sampling plants of varying ontogenetic stages within a single time and place, and they benefit from consistent conditions at sampling time across stages and feasibility. However, different individuals are sampled among ontogenetic stages, and because ontogeny is a feature of genotypes, snapshot surveys do not actually characterize ontogenetic trajectories in the narrow sense. Instead, longitudinal studies that can be depicted as ontogenetic norms of reaction are needed to more precisely characterize ontogenetic trajectories in functional traits. Longitudinal studies are logistically challenging, particularly for long-lived plants and so are not common. Furthermore, longitudinal studies cannot easily distinguish changes in plant traits due to genetic regulation (i.e. ontogeny in the strict sense) and plasticity to shifting environmental conditions. Thus, the ideal approach characterizes trait expression within individuals through ontogeny while also maintaining homogeneous environmental conditions. Such conditions are unlikely in natural populations, and so these studies might best be conducted in glasshouses or gardens, or potentially as part of long-term ecological networks and experiments.

Leveraging recent advances in molecular tools, additional research is needed to examine ontogenetic trait variation in nonmodel systems. For example, we lack evidence for the role of master regulator microRNA genes in trait expression across ontogeny under field conditions in wild species. These studies will help clarify the number of ontogenetic stages within species, the timing at which regulated phase changes occur, and how environmental conditions may alter the timing of those transitions. To date, few studies have characterized trajectories across more than two stages (Fortunel et al., 2020; Iida & Swenson, 2020; Lum & Barton, 2020), and early stages are rarely sampled (e.g. embryonic, postgermination and seedling stages) and integrated with later ontogenetic stages (Larson et al., 2020).

A greater diversity of plant species, growth forms and biomes is needed to determine whether the common trajectories described for forest trees occur in other ecosystems. Other sources of selection pressure may be more important than competition or shade tolerance in different ecosystems and for different plant growth forms. While ontogenetic increases in plant defence traits such as secondary compounds and physical deterrents (Barton & Koricheva, 2010; Boege & Marquis, 2005) align with the observed shift from fast to slow RGR strategies, the role of microbial interactions remains poorly integrated. For example, the timing of microbiome interactions could contribute to early ontogenetic trait variation (Metcalfe et al., 2019), although this is not well documented within the context of the whole-plant ontogeny. A holistic approach that synthesizes biotic and abiotic factors throughout ontogeny is needed to provide a more complete characterization of the evolution of ontogenetic trajectories.

Filling these knowledge gaps will enhance our understanding of the evolution and mechanisms of ontogenetic trait variation, which can then improve applications to higher order processes. For example, incorporation of ontogenetic variation functional traits to demographic models may improve our understanding of population dynamics. Ontogenetic trait variation may elucidate filters operating

at different stages during community assembly. And ontogenetic trait variation may enhance the integration of experimental data to forecast ecosystem dynamics of carbon, water and nutrients. Broadscale efforts to explicitly sample functional traits across all ontogenetic stages are needed to provide these insights and should be a research priority, particularly as global change continues to threaten biodiversity in complex ways across plant ontogeny.

AUTHOR CONTRIBUTIONS

Kasey E. Barton conceived the ideas, gathered the evidence, and wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

Kasey Barton is an associate editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

No data were used in this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary Methods

Table S1. Ontogenetic patterns of functional traits underlying predicted shifts in shade tolerance (*Light Hypothesis*) and relative growth rate (*RGR Hypothesis*) strategies from the seedling to juvenile phases. For each record, the plant growth form (T = tree, S = shrub, H = herb, G = grass) and number of species examined (#Spp) is reported. Ontogeny was usually defined categorically as stages, and the number of stages at which traits were examined is reported (Ontogeny # Stages), but in some cases, Age or Size were used as proxies for ontogeny and were sometimes sampled at multiple size or age classes; when trait variation was examined as a linear response to quantitative variation in size or age.

Table S2. Ontogenetic patterns of functional traits underlying predicted shifts in shade tolerance (*Light Hypothesis*) and relative growth rate (*RGR Hypothesis*) strategies from the juvenile to adult phases. Column details, trait abbreviation, and units as in Table 1.

Table S3. Ontogenetic patterns of functional traits associated with hydraulic function and drought resistance, from the seedling to juvenile phase. Column details are as in Table 1.

Table S4. Ontogenetic patterns of functional traits associated with hydraulic function and drought resistance, from the juvenile to adult phases. Column details, trait abbreviations, and units as in Table 3.

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