New Phytologist

Review

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Looking to the past to understand the future: linking evolutionary modes of response with functional and life history traits in variable environments

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Received: *17 June 2022*
Accepted: *22 September 2022*

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Contents

New Phytologist (2023) 237: 751–757
doi: 10.1111/nph.18605

Key words: bet hedging, coordinated strategies, fast–slow continuum, functional traits, phenology, phenotypic plasticity.

Summary

In a variable world, plants must have strategies to deal with environmental conditions as they change. Understanding these strategies is critical since climate change not only affects mean conditions but also affects variability and predictability of those conditions. Doing so requires identifying how functional and life history traits interact throughout the life cycle to drive responses, as well as exploring how past variability will shape future responses. Here, I highlight relevant life history theory for predicting strategies in relation to the nature of environmental variability, relate theory to empirical studies integrating functional and life history traits to understand responses, and identify key areas for future research that will facilitate the application of this understanding toward predicting responses to climate change.

I. Introduction

Our world is inherently variable, and this variability is increasing. Climate change is not only shifting mean conditions, but also altering patterns of variation and shifting seasonal timing and conditions (IPCC, 2021). To persist in variable and changing environments, plants must have strategies to address these challenges, includingphysiological, morphological, and life history traits that mediate responses to variability. Understanding these strategies, and their ability to address current and future variability, requires exploration of patterns of environmental variability, the traits that mediate responses throughout the life cycle, and the consequences of those responses for fitness and population dynamics.

Evolutionary modes of response to environmental variability generally fall into two categories. First, individuals may get better at matching traits to the environment as it changes, through the rapid evolution of traits via natural selection or the evolution of phenotypic plasticity (Simons, 2011; Botero *et al.*, 2015). Second, traits that buffer individuals or lineages from the risk of having the wrong phenotype as the environment changes may evolve, including bet-hedging or other buffering strategies (Cohen, 1966; Simons, 2011; Botero *et al.*, 2015). Theory suggests that the adaptive nature of these responses depends on the timescale of variation, how predictable that variation is, and its effect on the mean and variance of fitness (Cohen, 1967; Seger & Brockmann, 1987; Botero *et al.*, 2015).

New Phytologist

In addition to identifying modes of response, predicting responses to variation requires identifying traits that lead to tracking vs buffering the effects of environmental variability and how these traits interact throughout the life cycle. These traits fall into two main categories: life history traits and functional traits (Box 1). While the field of life history evolution has long focused on the evolution of traits in response to environmental variation, the study of functional traits has focused more on responses to mean conditions or across environmental gradients (McGill *et al*., 2006; Kühn *et al*., 2021; but see Angert *et al*., 2007). Integrating these perspectives provides an insight into mechanisms driving responses to variability. Of course, the entire phenotype, including traits expressed throughout the life cycle, drives responses and ultimately determines fitness and population dynamics.

Box 1 Definitions and descriptions.

Timescale of variation: frequency or cycling of environmental variability, which can be evaluated on absolute scales (hours, days, years, and decades) or relative to lifespan or generation time.
Predictability of variation: temporal pattern of variability indicating correlations among conditions, such as autocorrelations in conditions or cross-correlations from one condition (e.g. day length) with another (e.g. temperature).

Modes of response

Adaptive tracking: evolution by natural selection in response to environmental conditions as they change.
Bet hedging: evolutionary mode of response in which variance in fitness is reduced, but that reduction entails some cost to (arithmetic) mean fitness, often categorized as conservative bet hedging or diversified bet hedging.
Conservative bet hedging: bet hedging in which variance in *individual* fitness is reduced at a cost to mean fitness. Typically, this type of bet hedging corresponds with generalist or 'safe' strategies that perform reasonably well across a range of conditions. For example, reproducing at a smaller size or younger age to reduce variance in fitness driven by stochastic risk of mortality (Rees *et al*., 2004, 2006).
Diversified bet hedging: bet hedging in which variance in the fitness of a *lineage* is reduced at a cost to mean fitness. Here, individuals of the same lineage display a diversity of phenotypes. Example: Delayed germination in desert annual plants, in which some seeds in a maternal lineage will germinate readily, and other seeds will instead remain dormant and germinate later (Gremer & Venable, 2014).
Phenotypic plasticity: changes in phenotype expressed by the same genotype in response to environmental conditions.
Irreversible phenotypic plasticity: phenotypic plasticity that is permanent such as germination or the transition to reproduction (bolting) for monocarpic species.
Reversible phenotypic plasticity: phenotypic plasticity that is not a permanent change, such as upregulation of physiological processes or behavioral changes.

Types of traits

Functional traits: morphological, physiological, or phenological attributesofspeciesthatinfluencesurvival, growth, andreproduction.
Life history traits: traits describing the timing of life cycle events, such as the timing and extent of growth, development, reproduction, and life span, and also phenology.
Phenology: timing of life history events, such as germination, emergence, growth, or reproduction, typically considered within a growing season or calendar year.

II. Responses to environmental variation depend on scale and predictability of variation

Evolutionary modes of response to variability critically depend on the pattern of variation, including timescale and predictability (Cohen, 1967; Botero *et al*., 2015; Fig. 1; Box 1). Adaptive tracking via evolution or phenotypic plasticity is a favored mode when there is some level of predictability, which allows for matching phenotypes to the environment as it changes. When the pattern of variation is long relative to the generation time of the organism, adaptive tracking is favored, while plasticity is favored with variation at shorter time frames (Simons, 2011; Botero *et al*., 2015; Fig. 1; Box 1). In environments with little-to-no predictability, strategies to buffer from risk are needed. This can be achieved through bet hedging, either at the individual level (conservative bet hedging, CBH), which is favored at short timescales, or across individuals within a lineage when variability is at longer time scales (diversified bet hedging, DBH; Fig. 1; Box 1; Slatkin, 1974; Seger & Brockmann, 1987; Starrfelt & Kokko, 2012).

Applying this framework to plants requires consideration of their unique characteristics. First, plants have a remarkable range of lifespans, including very long lifetimes. Long-lived species may have fewer generations per cycle of environmental variability and thus rely more on conservative bet hedging in unpredictable environments. For example, trees may allocate carbon to storage at the cost of growth to hedge against the risk of drought or predation (Chapin *et al*., 1990; Childs *et al*., 2010; Richardson *et al*., 2013; Blumstein *et al*., 2022), though evidence for this is mixed and needs additional study (Wiley & Helliker, 2012; Bachofen *et al*., 2018; Blumstein *et al*., 2022). Reproducing at a smaller size or younger age can also hedge against stochasticity in mortality risk (Rees *et al*., 2006). Conversely, annual and short-lived plants may rely more on diversified bet hedging. The classic example is annual plants that spread the risk of germinating at unfavorable times by having some seeds germinate readily, while others remain dormant and germinate later (Cohen, 1966; Gremer & Venable, 2014). Second, dormancy and developmental delay are quite common in plants and can blur lines between timescales, and life stages may experience variability differently. For example, annuals emerge for one growing season, but their seeds may survive in seed banks for years to decades (Baskin & Baskin, 2014). Third, modularity and indeterminate growth in plants facilitate plastic responses within an individual's lifetime, which may create even more possibilities for reversible plasticity (Bradshaw, 1965; Chapin *et al*., 1993). Furthermore, modularity can enable plants to shrink or return to previous stages (regression), which can provide a demographic buffer against variability (Salguero-Gómez & Casper, 2010).

While these modes are often treated as separate, they are not mutually exclusive. Phenotypic plasticity may help populations track-shifting optima and provide time for adaptive tracking (Chevin & Hoffmann, 2017). Similarly, plasticity and bet hedging may coevolve in variable environments with partially reliable

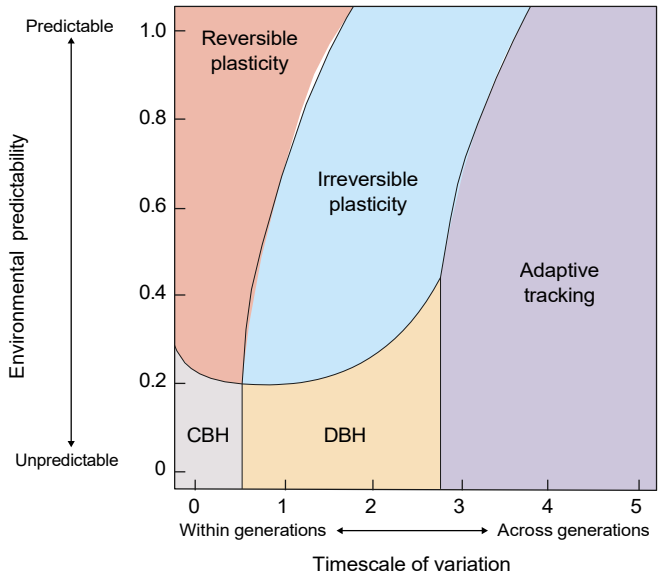


Fig. 1 Evolutionary modes of response to environmental variation under different levels of environmental predictability (level of correlation between an environmental cue and future conditions) and relative timescale of environmental variation (number of generations per cycle of environmental variability; redrawn from Botero *et al*., 2015). Illustrated are regions of parameter space that favor each mode of response. CBH, conservative bet hedging; DBH, diversified bet hedging. See Box 1 for definitions of modes of response.

information (Cohen, 1967; Wong & Ackerly, 2005). For example, a fraction of seeds may germinate in response to good germination rains, but the remaining seeds stay dormant as a hedge against the risk that good germination rains may be followed by unfavorable conditions (Cohen, 1967; Gremer *et al*., 2016). On the contrary, plasticity may itself be a bet-hedging strategy if a genotype produces offspring with different levels of plasticity (Haaland *et al*., 2021). Thus, we may see a combination of modes evolve and plants may be particularly effective at combining strategies.

III. Functional and life history traits mediate responses to variability

Understanding and predicting responses to variability, and how they will mediate responses to future change, requires identifying traits mediating those responses. Ultimately, fitness depends on performance throughout an entire lifespan, which requires integrating the consequences of functional and life history traits expressed across stages. Thus, identifying the linkages between traits throughout the life cycle is an important challenge in predicting responses to variability. Indeed, traits do not evolve in isolation, but instead reflect coordinated strategies that respond to, and are shaped by, the environment.

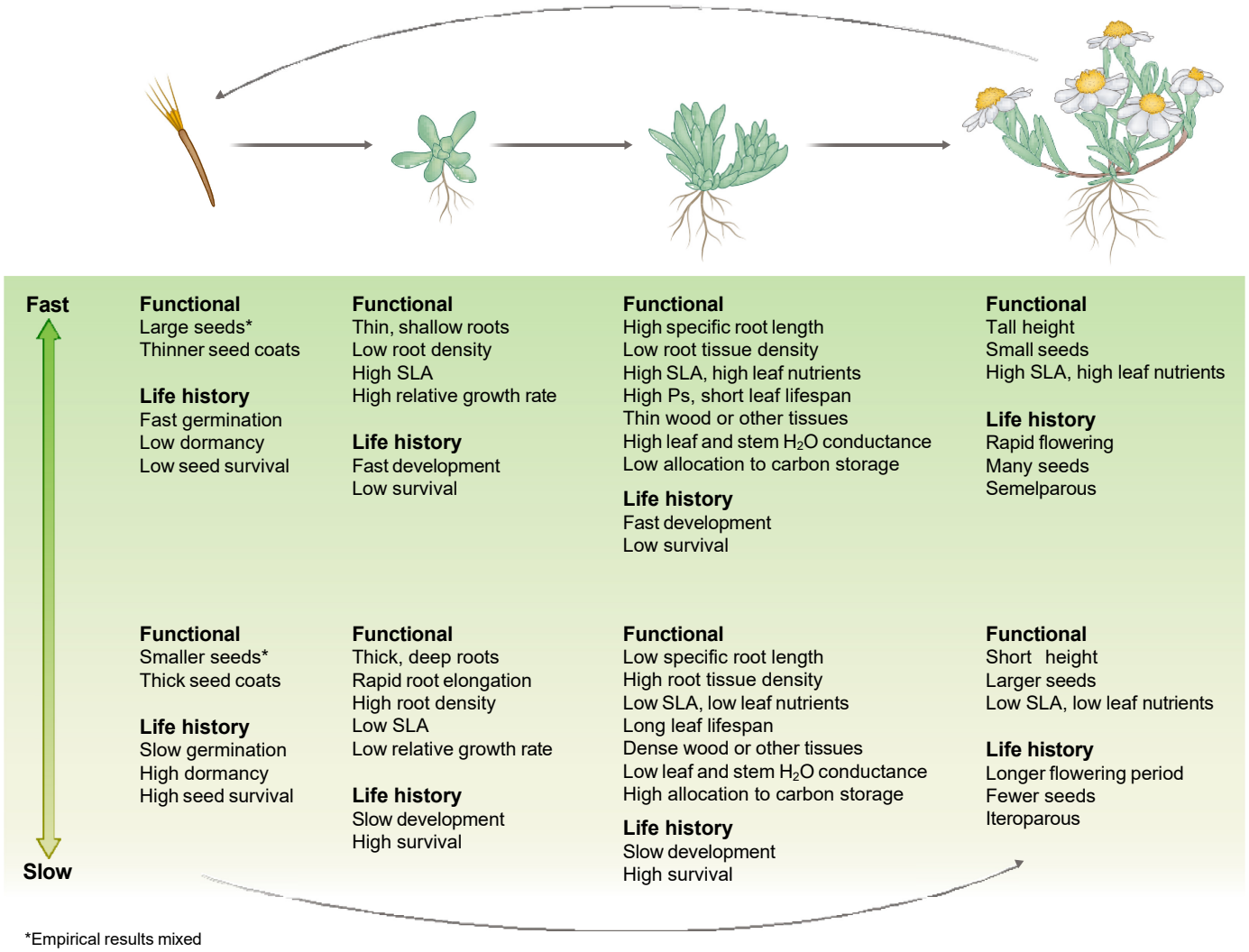
Numerous frameworks describing coordinated strategies have been developed, each highlighting different aspects of traits, demography, and environmental response (Raunkiaer, 1934; MacArthur & Wilson, 1967; Grime, 1977). The fast–slow continuum highlights trade-offs between survival and reproduction (Harvey & Zammuto, 1985; Franco & Silvertown, 1996). 'Fast' life histories include rapid growth, high reproductive rates, and short life spans, while 'slow' life histories have slower growth, lower reproductive rates, and long-life spans. Parallel frameworks exist in the plant functional trait literature, with several spectra constructed using trait data from global datasets. Most prominent is the 'world-wide leaf economic spectrum' (LES), which describes coordinated leaf traits that reflect 'fast' vs 'slow' responses to resource availability and allocation (Wright *et al*., 2004). According to the LES, fast-growing species have traits associated with a rapid return on investment, including high leaf nutrient concentrations, high rates of photosynthesis, and short leaf life spans, while slow-growing species display the opposite traits. Similarly, 'fast' hydraulic traits, which enable a rapid supply of water, support 'fast' LES traits, while 'slow' hydraulic traits that withstand low water availability are linked with 'slow' LES traits (Reich, 2014). Recently, other trait spectra have been proposed, including for roots (Carmona *et al*., 2021) and wood (Chave *et al*., 2009), with calls for generating additional spectra for seeds and seedlings (Larson & Funk, 2016; Saatkamp *et al*., 2019). These frameworks highlight the coordination of traits across tissues and life stages and reveal clear parallels with the fast–slow continuum (Fig. 2).

Critical connections between these typically disparate life history and functional spectra have been made. Life history traits require time-intensive monitoring to quantify, but global demographic databases have lowered this barrier, facilitating global analyses of life histories, as have global functional trait databases (Adler *et al*., 2014; Salguero-Gómez, 2017; Kattge *et al*., 2020). Functional traits associated with slow growth, longer lived tissues, and stress tolerance correspond with 'slow' life histories, while traits associated with rapid responses align with 'fast' life history traits (Fig. 2). A key strength of these studies is the incorporation of multiple traits, which improves upon weak relationships using single traits (Swenson *et al*., 2020; Fig. 2).

While these global analyses are powerful, they have focused on mean traits and conditions. However, coordination among traits may vary across local-scale environmental gradients (Diaz *et al*., 2016; Flores-Moreno *et al*., 2019) and throughout ontogeny (Falster *et al*., 2018; Emery & La Rosa, 2019), limiting generalization of global-scale findings to local- and regional-scale findings. Flores-Moreno *et al*. (2019) demonstrated stronger interdependence of functional traits in wetter environments, with traits varying more independently in arid environments. Kelly *et al*. (2021) demonstrated that relationships between life history and functional traits were stronger in more arid environments. Less well studied is trait variation through ontogeny and in relation to variability. An experimental study of three *Lasthenia* species showed significant differences in functional traits across development and in response to mean and variance in water levels (Emery & La Rosa, 2019). Furthermore, *Lasthenia* responses aligned with patterns of variability, since fitness for the species that experiences higher variation in the field was less sensitive.

The next critical link is between coordinated strategies and modes of response to variability, which is even more challenging to make. Doing so requires substantial data, including trait variation in response to conditions and subsequent effects on fitness. One way forward is to test relationships between the fast–slow

New Phytologist



*Empirical results mixed

Fig. 2 Coordinated functional and life history traits throughout the plant life cycle. Life stages include seeds, seedlings, growth phase for established plants, and reproductive plants. A selection of functional and life history traits that correspond to the fast–slow continuum (top two rows, fast traits; bottom two rows, slow traits) are listed for each life stage. Ps, photosynthetic rate (μmol of carbon m^{-2} s^{-1}); SLA, specific leaf area (leaf area per unit mass).

continuum with patterns of local climatic variability using global databases. Species with 'slow' strategies are expected in environments with short-to-intermediate timescales of variability, while 'fast' strategies may be more responsive to variability and would be associated with environments exhibiting higher predictability (Fig. 3).

Such links have been made for Sonoran Desert winter annual plants after decades of study. This iconic system experiences strong variability in temperature and precipitation, within and among growing seasons (Huxman *et al.*, 2013). In response, species have evolved germination strategies that integrate both bet hedging and plasticity to cues (Gremer & Venable, 2014; Gremer *et al.*, 2016). Species vary in degree of bet hedging, which aligns with differences in later functional traits (Huang *et al.*, 2016; Cuello *et al.*, 2019). Large-seeded species experience lower seed survival, which lowers the value of delayed germination, and thus have higher germination fractions. These species tend to have stress-tolerant functional traits during their growth phase, including high water-use efficiency and low specific leaf area. Thus, they have 'fast' traits for germination, but 'slow' functional growth traits (Fig. 2). Other species have smaller seeds, high seed survival, and low germination fractions, rely more on bet hedging at the seed stage ('slow' germination traits), and have 'fast' functional traits such as high relative growth rates. If these patterns generalize across systems, then we may see traits associated with slow strategies for life stages that are most affected by variability and fast strategies for those that are not.

Generalizing across systems will require viewing variability in relation to coordinated strategies. For example, the Sonoran Desert supports species with a range of lifespans, from annuals to long-lived shrubs and cacti (Robichaux, 1999). These species experience variability differently such that annuals and long-lived species experience it at longer and shorter time scales, respectively. While annuals rely on diversified bet hedging through delayed germination, longer lived species utilize strategies consistent with conservative bet hedging, such as storage of carbon or water, or adult plant dormancy (Childs *et al.*, 2010; Gremer *et al.*, 2012; Fig. 3). Thus,

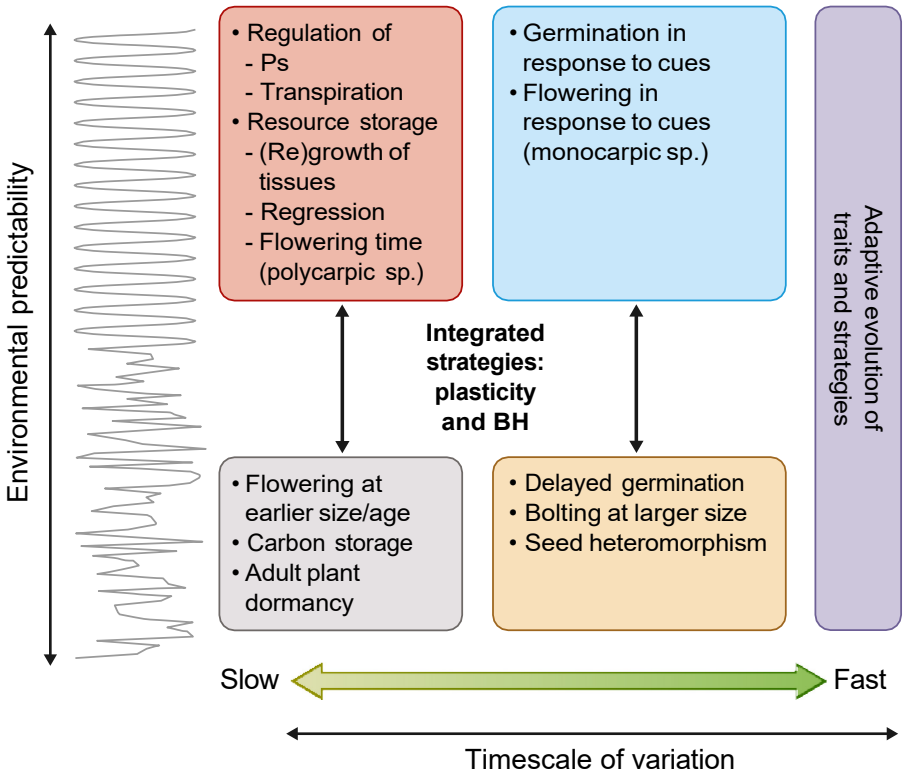


Fig. 3 Coordinated strategies in relation to evolutionary modes of response to variability, with examples. Colors correspond to regions favoring different modes of evolutionary response in Fig. 1 (red, reversible plasticity; blue, irreversible plasticity; light gray, conservative BH; yellow, diversified BH; purple, adaptive tracking). See Box 1 and text for definitions. BH, bet hedging; monocarpic, plants that reproduce once in their lifespan (semelparous); polycarpic, plants that reproduce multiple times (iteroparous); Ps, photosynthetic rate; sp., species.

multiple strategies can address the same variability, mediated by coordination of traits expressed throughout a lifespan.

IV. Using the past to understand the future

Understanding modes of response and links to coordinated strategies can provide insights into the effects of climate change and whether alternative strategies can evolve. Primarily, work in this area has been theoretical and needs empirical testing. Nonetheless, the theory provides expectations for outcomes of change. Shifts in timescale or predictability that stay within parameter space favoring each mode of response may be generally well tolerated. However, evolutionary tipping points can occur at transitions between modes (Fig. 1; Botero *et al*., 2015). For example, in models, extinction was likely between conditions favoring plasticity vs bet hedging, which could be due to the difficulty of addressing particular combinations of predictability and timescale, or the challenges for trait evolution across modes (Botero *et al*., 2015; Haaland & Botero, 2019). Thus, theory explains why some changes may not have strong effects, while others can be catastrophic. Furthermore, it highlights the need to understand patterns of variability under which responses have evolved to predict consequences of future change.

Climate change has and will continue to influence patterns of variability, including increasing extreme events (Swain *et al*., 2018; Papalexiou & Montanari, 2019), increasing amplitude of variation, and changes in patterns of climate cycling (Dillon *et al*., 2016; Rodgers *et al*., 2021). How these shifts relate to timescale and predictability is less clear. Patterns of increasing temporal autocorrelation would increase predictability (Di Cecco & Gouhier, 2018; Bernhardt *et al*., 2020). Conversely, changes in extreme events and cycling would reduce predictability and could either increase or reduce timescale. Correlations among cues, such as temperature, precipitation, and photoperiod, are also changing, influencing cue perception and their reliability (Bonamour *et al*., 2019; Bernhardt *et al*., 2020). These shifts will interact with evolutionary modes and coordinated strategies to determine fitness and persistence. Since 'slow' strategies incorporate conservative bet hedging and buffering, they may be less responsive and more resistant to change but recover more slowly once perturbed (Salguero-Gómez, 2017; Fig. 3). Conversely, 'fast' strategies may have stronger and more rapid responses, with the potential for faster evolution due to shorter generation times (Chapin *et al*., 1993; Fig. 3). Indeed, studies have shown species with 'fast' traits to be more responsive to changing precipitation (Zhang *et al*., 2020; Compagnoni *et al*., 2021). The success of these rapid responders depends on the longer term pattern of variation and whether the benefits of extremely good conditions outweigh risks of extremely bad ones (Lawson *et al*., 2015; Liu *et al*., 2019). Integrated strategies that employ plasticity to respond to new changes while hedging against risks of catastrophe may be particularly successful in confronting change. However, these hypotheses need further testing, at global and local scales.

V. Conclusions

How do shifts in mean and variance in environmental conditions interact with functional and life history strategies to drive performance in changing environments? The answers to this question require understanding (1) the nature of environmental

New Phytologist

variation past, present, and future, (2) where in the life cycle variation is most influential, and (3) how coordinated strategies relate to the timescale and predictability of local climatic variation. Recent research has provided ways forward, through a renewed focus on coordinated strategies and multivariate phenotypes. Key challenges remain in linking these phenotypes to evolutionary modes of response, how they mediate fitness in the face of changing variability, and whether the evolution of alternative traits and strategies is possible.

Acknowledgements

I am grateful to Drs J. Schmitt, S.Y. Strauss, M. LaForgia, S. Worthy, and members of my research group for valuable discussion about modes of response, coordinated strategies, and responses to variability and how to link these typically disparate fields of study. Dr D. Ackerly provided insightful guidance on the manuscript. I would also like to thank Dr H. Slater for her guidance and patience through the process, as well as the reviewers for their excellent suggestions for improving the manuscript. Figs 2 and 3 were initially developed using Biorender. Funding was provided by NSF DEB (1831913).

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