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Review: Intraspecific trait variation in plants: a renewed focus on its role in ecological processes

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- **Background** Investigating the causes and consequences of intraspecific trait variation (ITV) in plants is not novel, as it has long been recognized that such variation shapes biotic and abiotic interactions. While evolutionary and population biology have extensively investigated ITV, only in the last 10 years has interest in ITV surged within community and comparative ecology.
- **Scope** Despite this recent interest, still lacking are thorough descriptions of ITV's extent, the spatial and temporal structure of ITV, and stronger connections between ITV and community and ecosystem properties. Our primary aim in this review is to synthesize the recent literature and ask: (1) How extensive is intraspecific variation in traits across scales, and what underlying mechanisms drive this variation? (2) How does this variation impact higher-order ecological processes (e.g. population dynamics, community assembly, invasion, ecosystem productivity)? (3) What are the consequences of ignoring ITV and how can these be mitigated? and (4) What are the most pressing research questions, and how can current practices be modified to suit our research needs? Our secondary aim is to target diverse and underrepresented traits and plant organs, including anatomy, wood, roots, hydraulics, reproduction and secondary chemistry. In addressing these aims, we showcase papers from the Special Issue.
- **Conclusions** Plant ITV plays a key role in determining individual and population performance, species interactions, community structure and assembly, and ecosystem properties. Its extent varies widely across species, traits and environments, and it remains difficult to develop a predictive model for ITV that is broadly applicable. Systematically characterizing the sources (e.g. ontogeny, population differences) of ITV will be a vital step forward towards identifying generalities and the underlying mechanisms that shape ITV. While the use of species means to link traits to higher-order processes may be appropriate in many cases, such approaches can obscure potentially meaningful variation. We urge the reporting of individual replicates and population means in online data repositories, a greater consideration of the mechanisms that enhance and constrain ITV's extent, and studies that span sub-disciplines.

Key words: Community ecology, comparative ecology, effect traits, functional traits, functional ecology, intraspecific trait variation, ITV, levels of organization, response traits, trait-based ecology.

INTRODUCTION: A HISTORICAL PERSPECTIVE

For centuries, humans have described phenotypic variation across and within plant species. Domestication of crops by indigenous peoples was only possible through careful observation of intraspecific variation in traits such as grain size, and targeted breeding (Zizumbo-Villarreal and Colunga-GarcíaMarín, 2010; Abbo *et al.*, 2012). Historical records reveal the first mention of environmentally driven intraspecific variation in the fourth century BCE (Stegmann, 2020). In 1786, the German novelist Johann Wolfgang von Goethe noted shifts in willow leaf morphology across an elevation gradient (Stegmann, 2020). During the 19th century, Charles Darwin and Alfred Russel Wallace sought to explain the underlying mechanisms that drove variation in form and function, and posited that variation within species was an essential building block necessary for

natural selection (Darwin, 1859). Later studies described how variation within species determines niche width/breadth (Van Valen, 1965) and how niche overlap determines community assembly and structure (Gleason, 1926; Clements, 1936). In the mid- to late 20th century, (John) Philip Grime (1965) reared plants from different habitats under controlled conditions to understand how ‘susceptibilities’, or traits, drove sub-optimal performance in particular environments. Such studies were insightful, as they could be used to investigate the mechanisms controlling a species’ distribution and predict its occurrence within a community. This sub-discipline has since been referred to as comparative, functional or trait-based ecology [see Shipley *et al.* (2016) for a more comprehensive history], which recognizes the utility of plant traits rather than taxonomy for characterizing community and ecosystem processes.

Relative to evolutionary and population ecology, which have a long and rich history of investigating variation within species, community and trait-based ecological studies have predominantly explored variation across species. In particular, trait-based or comparative approaches often seek to examine patterns of variation in easily measurable plant traits across a large number of species spanning wide ecological gradients. This focus on variation across species arose naturally from the search for general ecological principles and rules that could be applied to all species. One popular approach is to position species along axes based on morphological and physiological traits to understand their life-history strategy. For example, the highly cited leaf economics spectrum (Wright *et al.*, 2004) describes trade-offs among plant traits influencing resource acquisition and leaf carbon economy. Species on the ‘slow’ end of the spectrum have thick, long-lived, nutrient-poor leaves, while ‘fast’ species exhibit the opposite pattern. While the utility of these large-scale and species-wide approaches at local scales has been called into question (Anderegg *et al.*, 2018), a study in this Special Issue (Gorné *et al.*, 2020) detected evidence of the leaf economics spectrum within a single species under homogeneous environmental conditions. This is a significant finding, as previous studies have concluded that selective pressures imposed by environmental conditions rather than genetic constraints (e.g. pleiotropic effects) control the evolution of the leaf economics spectrum (Donovan *et al.*, 2011). Studying patterns of trait covariation *within* species thus provides novel opportunities to consider the forces driving trait covariation *across* species, as we will highlight below.

The increasing popularity of trait-based studies, coupled with the advent of online data repositories, has resulted in a large number of published datasets that report species means (e.g. TRY; Kattge *et al.*, 2011). Many ecological studies have drawn their conclusions on the basis of these species-level datasets, explicitly or implicitly assuming that variation within species is smaller than variation across species (McGill *et al.*, 2006). It is also generally assumed that even when ITV is considerable, it should not obscure trends across species or alter a species’ trait-based rank within a community (Grime and Hunt, 1975; Grime, 1979). While there is some empirical support for this claim (Albert *et al.*, 2010; Hulshof and Swenson, 2010; Siefert *et al.*, 2015), in other instances a species’ rank has been shown to depend on the extent of ITV (Fajardo and Siefert, 2016). Several key empirical studies published in rapid succession challenged the use of species means and put forth a call to action for more studies of its extent (Albert *et al.*, 2010; Hulshof and Swenson, 2010; Jung *et al.*, 2010; Messier *et al.*, 2010). Since that time, the ecological significance of ITV has been reviewed numerous times (Albert *et al.*, 2011, 2012; Bolnick *et al.*, 2011; de Bello *et al.*, 2011; Lepš *et al.*, 2011; Violle *et al.*, 2012; Siefert *et al.*, 2015; Shipley *et al.*, 2016), yet there remain critical gaps in our understanding of how ITV influences higher-order ecological processes, including species interactions and ecosystem resilience.

In the last decade there has been a notable rise of interest in ITV among trait-based and community ecologists, which has motivated the publication of this Special Issue. The studies that form part of this Special Issue have been chosen for their novel focus on downstream effects of ITV on population-

community- and ecosystem-scale processes. To provide context for how ITV influences ecological processes, we briefly review the mechanisms underlying ITV, drivers and sources of ITV, and the extent of ITV across underrepresented plant functional traits (e.g. anatomy, chemical defence) and organs (e.g. woody stems rather than leaves), focusing on terrestrial plants. Here, plant functional traits are defined as morphological or physiological traits that indirectly influence fitness via effects on growth, survival and reproduction (Violle *et al.*, 2007), but in some cases we describe trait variation in the context of whole-plant metrics. Our goals are to incentivize ecologists to quantify intraspecific trait variation (ITV) and make these data available, similar to what has occurred with species means, and to establish research questions that will more effectively address existing knowledge gaps.

MECHANISMS UNDERLYING PLANT ITV

Intraspecific trait variation results from genotypic variation and variation in trait expression within genotypes (i.e. phenotypic plasticity) (Schlichting, 1986; Sultan, 1987; Pigliucci, 2001). Whereas genotypic variation encompasses genetic differences among individuals or populations, phenotypic variation involves non-genetic changes in traits (Abrams, 1994). Genetic variation can result from local adaptation to particular habitats (i.e. ecotypic variation) and from genetic differentiation among populations due to drift, developmental noise or random mutations (Scheiner, 1993). The latter can result in variation among individuals reared in identical environments. Whether ITV is driven by phenotypic plasticity, local genetic adaptation, or both, is influenced by the extent of gene flow (Via and Lande, 1985; Van Tienderen, 1991; Baythavong, 2011) and the degree of environmental heterogeneity.

Phenotypic plasticity has a heritable genetic basis (Scheiner, 1993), and populations and species vary in their plasticity (Bradshaw, 1965; Schlichting and Smith, 2002). Whether plasticity or fixed trait expression is more likely to evolve in response to changing environmental pressures is unclear but relevant for predicting plant responses to climate change and other global threats (Christmas *et al.*, 2016). Studies of plasticity are more common for plants than are studies of local adaptation, most likely due to the ease with which plasticity is quantified, and evidence suggests that plasticity plays an important role for plant populations experiencing rapid environmental change (Nicotra *et al.*, 2010). Although phenotypic plasticity is often assumed to be adaptive, it may also be neutral, non-adaptive or maladaptive (Ghalambor *et al.*, 2007). In this Special Issue, March-Salas *et al.* (2020) report that although phenotypic plasticity in flowering time due to shifting precipitation patterns had a heritable basis, there was no evidence for rapid evolutionary change across three generations. These results contrast with earlier reports of rapid evolution of fixed traits (March-Salas *et al.*, 2019) and suggest that rapid adaptation to changing climate may be slower for phenotypically plastic traits than fixed traits.

A growing body of work has revealed that extensive ITV occurs across generations. Such transgenerational effects have now been described for many plant functional traits (Bossdorf *et al.*, 2008; Sultan *et al.*, 2009; Herman and Sultan, 2011;

Holeski *et al.*, 2012) and are typically referred to as epigenetic variation, defined as interactions among molecular processes that alter gene expression and function without changing the underlying DNA sequence (Richards, 2006; Holeski *et al.*, 2012). DNA methylation has been identified as an important mechanism underlying transgenerational effects (Jablonka and Raz, 2009; Richards *et al.*, 2010, 2017). In this Special Issue, Puy *et al.* (2020) used experimental demethylation in *Arabidopsis thaliana* populations and determined that epigenetic forces were responsible for driving variation in specific leaf area (SLA), but also plant growth (and therefore productivity) in response to waterlogging and fertilization. The authors also found that demethylation influenced competitive interactions within monocultures and mixed stands. Determining the role of transgenerational plasticity for species interactions and community processes is an exciting and promising area of research, as it has the potential to unite evolutionary biologists and community ecologists towards a common goal.

The key mechanisms underlying ITV at different levels of organization are summarized in a conceptual diagram (Fig. 1). Intraspecific trait variation within and across individuals is driven by abiotic and biotic cues that induce phenotypic plasticity. Traits can also vary across plant developmental stages, i.e. ontogeny, and in some cases the extent of ITV is constrained by biomechanical or biophysical properties (see section Extent

of plant intraspecific trait variation). At the population and community level, ITV can drive variation in whole-plant performance, altering population dynamics but also species interactions. Over time, local genetic adaptation and epigenetic forces further enhance ITV, shifting community dynamics in conjunction with abiotic and biotic filters. Changes in the extent of ITV, coupled with shifts in trait means, can produce downstream effects on ecosystem fluxes and vegetation dynamics, driving shifts in species distributions and global fluxes.

The role of abiotic and biotic factors in driving ITV

While trait variation between species (BTV) is often evaluated over large abiotic gradients, ITV is strongly driven by microenvironmental heterogeneity in abiotic and biotic factors, including irradiance, air temperature and aridity, as well as competition and herbivory. The extent of ITV and the directionality of its response have been shown to vary across gradients of light availability (Carlucci *et al.*, 2015; Burton *et al.*, 2017), climate (Bloomfield *et al.*, 2018; Kühn *et al.*, 2020; Westerband *et al.*, 2020), soil pH (Dong *et al.*, 2020) and soil nutrient availability (Siefert and Ritchie, 2016; Niu *et al.*, 2020). In this Special Issue, Westerband *et al.* (2020) report greater ITV in leaf chlorophyll content and leaf area as environments became

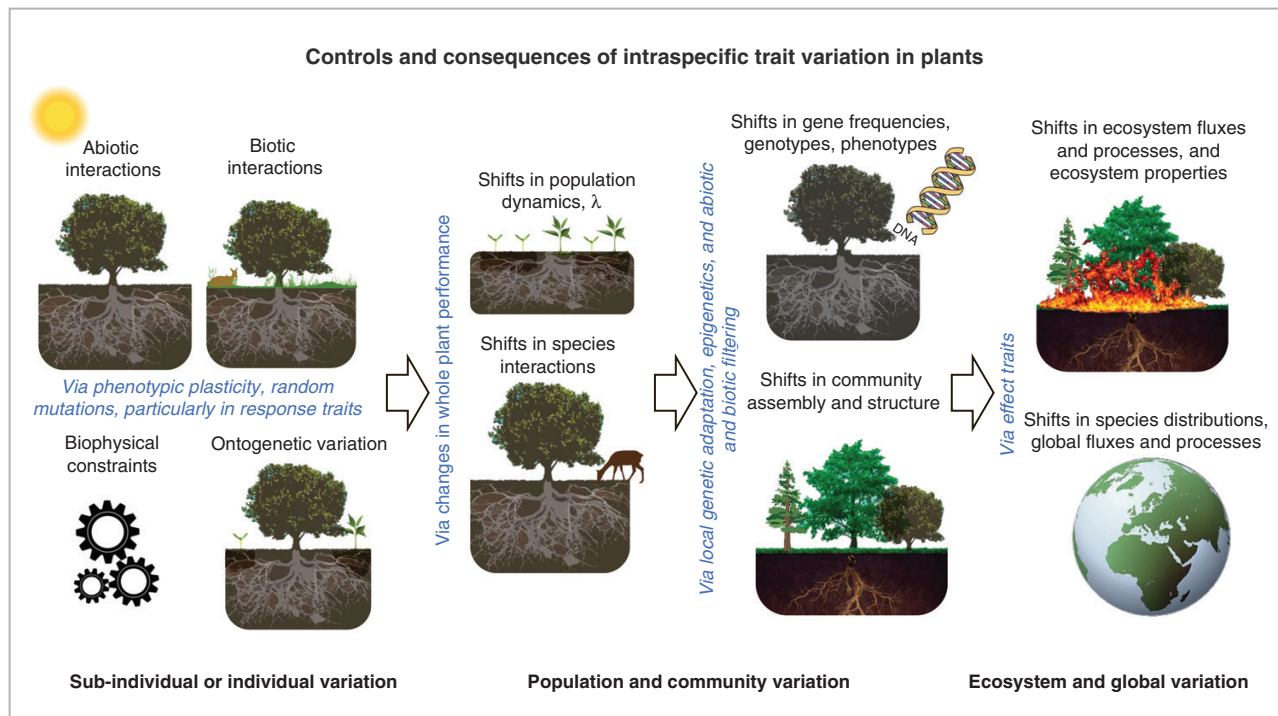


FIG. 1. Controls and consequences of ITV in plants across levels of organization. The mechanisms that influence ITV are shown in blue. Trait variation within (sub-individual) across individuals can be induced by abiotic and biotic forces that trigger plastic responses but can also result from ontogenetic variation. This is particularly relevant for response traits, i.e. those that respond to abiotic and biotic factors. Biophysical properties constrain the extent of variation within individuals. At larger scales, high ITV can influence individual plant performance and, consequently, population dynamics. Shifts in performance also mediate species interactions. Over time, population-level variation results from local genetic adaptation and/or epigenetic forces, which bring about changes in gene frequencies over time. Shifts in species interactions will ultimately drive changes in community assembly and structure, via biotic filtering, while abiotic filtering continues to operate. Finally, variation in community properties triggers shifts in ecosystem properties (e.g. fire regimes), and will be evident at the largest scales, as species distributions change. While not shown, shifts in species distributions and ecosystem and global properties will induce shifts in response traits, beginning the cycle again.

more humid in Hawaiian forests, and Kühn *et al.* (2020) report that the extent of within-population variability in leaf traits associated with carbon economy, e.g. SLA, leaf dry matter content (LDMC) and carbon:nitrogen ratios, increased with elevation in species native to Tenerife (Canary Islands, Spain). Studies such as these are useful for identifying sources driving within-ITV.

Intra-annual variation in abiotic properties, e.g. seasonality in climate, drives a significant portion of ITV, but its importance varies across traits. For example, growing season explained only a small portion of the total variation in leaf mass per area (LMA; 0 and 20% from two studies), and a much larger portion of the variation in leaf nutrient concentrations (9–40 %) (Fajardo and Siefert, 2016; Bloomfield *et al.*, 2018). A recent study found that LMA of a South African shrub declined with increasing precipitation when a high proportion of annual rainfall occurred in the winter months, but exhibited the reverse trend when rainfall occurred in summer or throughout the year (Moore *et al.*, 2020). These findings suggest that by describing seasonally driven ITV we may better understand why trait–climate relationships in particular species deviate from the species-wide trends. Quantifying the extent of temporal variation in traits can improve the accuracy and precision of models estimating ecosystem function.

Interactions between abiotic and biotic factors are less frequently reported with regard to their effects on ITV, despite the important role of species interactions in shaping plant trait strategies (Agrawal, 2020). Using a field experiment, Jessen *et al.* (2020) found that grazing by mammalian herbivores on tundra plants influenced their plasticity in height, SLA and leaf carbon:nitrogen ratios in response to fertilization, but the direction of the response varied across species. Competitive interactions can also exert a significant effect on ITV. The ‘niche packing’ hypothesis posits that highly diverse plant communities should be characterized by low ITV, due to increased interspecific competition and strong selection for reduced niche overlap (Violle *et al.*, 2012). Conversely, the ‘individual variation’ hypothesis posits that when species diversity is high, ITV is enhanced rather than constrained (Clark, 2010) (see section Effects on higher-order processes). There is empirical evidence to support both hypotheses (Helsen *et al.*, 2017).

When examined within species, several studies found that patterns of trait variation across environmental gradients differ from those observed at the species level (Siefert *et al.*, 2014; Dong *et al.*, 2020), which may result from high ITV. While a meta-analysis on a global dataset reported consistent species-wide patterns for LMA, leaf nitrogen concentrations and stable carbon isotope values ($\delta^{13}\text{C}$) across an elevation gradient (Midolo *et al.*, 2019), these patterns do not always hold when evaluated for below-ground traits. In this Special Issue, Taseski *et al.* (2020) examined patterns of root trait variation across a hydrological gradient in Australian species, and found that root tissue density (RTD), the ratio of root dry mass to root volume, decreased with soil organic matter (SOM) across and within species, while specific root length (SRL), which is often considered the below-ground equivalent of SLA, decreased with increasing SOM in some species but not others. This finding is surprising given that RTD and SRL may be expected to covary, as RTD reflects tissue construction costs while SRL reflects root

absorptive capacity. However, the best model for SRL included within-ITV while the best model for RTD did not. Studies such as these are useful, as they clarify the extent to which ITV influences species-wide patterns of trait variation.

Role of ontogeny

Ontogenetic trait variation results from developmentally regulated shifts in trait expression that may be coordinated with environmental cues or occur independently of the environment (Mason *et al.*, 2013). Heteroblasty is a classic example of ontogenetically derived ITV, referring to abrupt and extreme changes in phenotype within individuals throughout development (Zotz *et al.*, 2011). For example, in *Acacia koa*, juvenile leaves have higher rates of mass-based photosynthesis while the mature phyllode, a flattened petiole and rachis that mimics a leaf, have higher photosynthetic water use efficiency (the ratio of photosynthetic capacity to water loss) and tolerance to high irradiance (Pasquet-Kok *et al.*, 2010).

Ontogenetic trait variation can be an equally, if not more important, driver of trait variation than environmental cues, although in many instances the two cannot be disentangled. In this Special Issue, Funk *et al.* (2020) determined that a facultatively drought-deciduous shrub, *Artemisia californica*, expressed significant variation in LMA, leaf nitrogen concentration and leaf photosynthetic traits with age but not watering treatment, while only leaf water potential varied (becoming more negative) under drought conditions. Also in this Special Issue, Martin and Isaac (2020) found that larger coffee plants displayed leaf traits associated with conservative resource use compared with smaller plants, and that the effect of plant size on several leaf traits was largely robust to variation in light and soil nutrient availability. Variation in soil nutrient availability affected the strength of trait–trait relationships (e.g. LMA–leaf nitrogen), but the overall patterns were similar across fertilization treatments.

Ontogenetic variation in plant functional traits can mediate higher-order processes, such as species interactions. For example, Bond *et al.* (2004) determined that heteroblasty in two woody species was associated with defence from herbivory by large birds, such that juvenile morphology resulted in lower susceptibility to damage. Indeed, ontogenetic trajectories have been described for both plant defence traits and levels of herbivory across numerous plant species (Barton and Koricheva, 2010), and these ontogenetic shifts can also involve tri-trophic interactions with natural enemies (Quintero *et al.*, 2013). Ontogenetic variation is also likely to be ecologically important under fluctuating environmental conditions. If environments are fluctuating at a rate that exceeds that of phenotypic plasticity, or if environments are highly unpredictable, mismatches between traits and environmental conditions across ontogeny are more likely to occur.

EXTENT OF PLANT ITV

Evidence is growing that the extent of ITV is non-negligible, although clear patterns have yet to emerge. In a global analysis, Siefert and colleagues (2015) reported that, on average, ITV

TABLE 1. Recommendations for quantifying ITV, which will facilitate a deeper understanding of its causes and its ecological significance across levels of organization. We focus on experimental design and analysis and data collection techniques; detailed research questions are outlined in the main text

Question	Solutions
What are the mechanisms, drivers, and sources of ITV?	<p><i>Design and analysis</i></p> <ul style="list-style-type: none"> • Use mixed linear models to account for hierarchical relationships (e.g. species/individual/branch) • Apply variance partitioning analysis to determine sources of trait variation, e.g. site, across species, within species, climate, soil. Report total variation alongside these analyses • Use common garden experiments to separate plasticity from genetic differentiation, and incorporate with field studies whenever possible • Quantify spatiotemporal patterns in ITV alongside BTV. Search for parallels or discrepancies • Use multivariate environmental variables, e.g. integrate aridity and soil texture, in regressions • Use phylogenetic analyses if traits are suspected to be highly conserved among closely related species • Test for patterns of covariance and for underlying biophysical or developmental constraints on ITV, e.g. hydraulic constraints on tree height <p><i>Data collection</i></p> <ul style="list-style-type: none"> • Apply nested sampling designs, e.g. region/site/plot • When collecting trait data, track the identity of the individual plant but also the individual branch or stem • Measure biotic forces, e.g. competition and herbivory, but also interactions between abiotic and biotic variables, e.g. herbivore intensity over soil gradients
How does ITV influence individual higher-order processes?	<p><i>Design and analysis</i></p> <ul style="list-style-type: none"> • Measure traits that are likely to be under selection, rather than always using commonly measured traits such as SLA, and use integrative traits that capture multiple functions. Consider using ‘effect’ traits, i.e. traits that directly influence ecosystem processes • Analyse trait–performance relationships across a range of ages/sizes, genotypes, environmental conditions and levels of organization and test for interactions, e.g. genotype × environment to understand phenotypic variation but also trait × environment × size, to understand consequences for performance • Incorporate ITV within demographic models, and calculate demographic rates for co-occurring species • Simulate ITV when data are lacking, using published datasets to explore sensitivities of population growth or community dynamics to ITV <p><i>Data collection</i></p> <ul style="list-style-type: none"> • Measure traits across a range of plant ages or sizes, and environments • Measure at least one metric of plant performance, i.e. growth, survival, reproduction, but ideally more than one as there may be trade-offs among them • Measure ITV in traits of interacting species, e.g. plant and its pollinator
What is the extent of ITV and are there key generalities?	<p><i>Design and analysis</i></p> <ul style="list-style-type: none"> • Quantify extent of intraspecific trait variation (e.g. CV, SD) and distributions of data • Investigate changes in CV across environmental gradients • Report population means or individual level (replicate) data rather than species means in published trait databases • Report underlying genetic structure/variation • Investigate ITV in underrepresented traits or functions: biomass allocation, anatomy, defence, chemistry, hydraulics, architecture • Investigate ITV in underrepresented plant functional groups, biomes, across latitudinal gradients, and at global scale <p><i>Data collection</i></p> <ul style="list-style-type: none"> • Randomly sample individuals or organs • Repeatedly sample over time to assess temporal variation • Sample more extensively within species (ideally 20 if reporting CV but at least 5). Measure more extensively if environmental conditions are particularly heterogeneous (e.g. sites spanning topographic gradients) • Expand the breadth of traits measured to include roots, stems and reproductive organs • Use a combination of individual traits and multifunctional (integrative traits) and consider whether focal traits are likely to be under strong selection, e.g. wood density may be more meaningful along aridity gradients than chlorophyll content

accounts for 25 % of total trait variation within communities. Nonetheless, the extent of ITV varies dramatically among traits and species; ITV can be equivalent to or surpass BTV for LMA (Fajardo and Siefert, 2018; Tautenhahn *et al.*, 2019), LDMC (Kang *et al.*, 2014; Read *et al.*, 2017; Benavides *et al.*, 2019), leaf nutrient concentration (Fajardo and Siefert, 2016; Burton *et al.*, 2017; Umaña and Swenson, 2019a), dark respiration rate (Bloomfield *et al.*, 2018), height (Luo *et al.*, 2016; Tautenhahn *et al.*, 2019), biomass allocation (Umaña *et al.*, 2018) and stem wood density (Kang *et al.*, 2014). Indeed, a recent study of five grassland species determined that 9 of 14 focal traits had higher ITV than BTV, which was thought to be driven by the exceptionally wide geographical ranges of the focal species (Tautenhahn *et al.*, 2019).

While meta-analyses are appropriate for determining the global mean and sources of ITV across species, biomes and

environmental gradients, estimates of ITV vary in quality as a consequence of variation in sampling methods. Many studies estimate ITV from very few individuals, even for widespread species, and there is no consensus regarding the scale at which within- versus across-population ITV is separated. There have also been calls to forego traditional sampling protocols when investigating community properties (Violle *et al.*, 2012), as the most frequently used metric [94.4 % of papers versus 1.9–7.4 % (Yang *et al.*, 2020a)] of ITV, the coefficient of variation (CV), has been found to underestimate ITV in nearly 50 % of examined cases, and is particularly prone to underestimating ITV when the data suffer from kurtosis, small sample sizes or skewness (Yang *et al.*, 2020a). We emphasize that our understanding of ITV’s extent would be improved by more consistent and comprehensive sampling methods across studies (Table 1) and may clarify many of the idiosyncratic patterns that are

commonly observed in the ITV literature. Given that low ITV is a key assumption for using species means in ecological studies (Garnier *et al.*, 2001; Lecerf and Chauvet, 2008; Messier *et al.*, 2010), accurately determining its extent is paramount for understanding its drivers and ecological consequences. Below we summarize the extent of ITV reported across traits, biomes and levels of organization, from studies published since Siefert *et al.* (2015). The values reported were primarily generated from variance partitioning or variance decomposition analysis (Supplementary Data Table S1).

Variation across types of traits

Our understanding of ITV is limited by research biases as most studies quantifying the extent of ITV have focused on leaf nutrient concentration, height and leaf morphology. Of the leaf morphological traits, SLA, or its reciprocal, LMA, is the most well-studied and expresses considerable within-species variation (Supplementary Data Table S1). The ITV in leaf nitrogen and phosphorus concentrations and plant height follow SLA in order of the frequency with which they are reported (Supplementary Data Table S1).

Overall, ITV tends to be greater for leaf nutrient concentrations than for leaf morphological traits (Siefert *et al.*, 2015; Supplementary Data Table S1), greater in photosynthetic traits relative to anatomical traits, and greater for whole-plant metrics, such as height, relative to leaf traits (Siefert *et al.*, 2015; Supplementary Data Table S1). These differences likely reflect varying degrees of phenotypic plasticity and genetic regulation. For example, a large-scale study of widespread European herbs sampled across extensive temperature and precipitation gradients reported a mean ITV of only 18 % for two leaf anatomical properties, stomatal density and guard cell length (Tautenhahn *et al.*, 2019), suggesting low phenotypic plasticity and limited local adaptation. Stem anatomical traits, including wood density and specific stem density, have been shown to exhibit the same pattern of relatively low ITV (Burton *et al.*, 2017), although this is not always the case (Umaña and Swenson, 2019b).

Compared with leaf traits, fewer studies report the CV for hydraulic, root or reproductive traits (e.g. floral characters). The paucity of data for stems and roots makes it difficult to draw broad conclusions regarding the extent and sources of ITV across plant organs, which is necessary for understanding trait covariance patterns at the species level. The quartile coefficient of dispersion (a metric similar to but more robust than the CV) values range from 6 to 42 % for hydraulic properties depending on the trait (Rosas *et al.*, 2019) whereas branch-level properties, such as wood radial growth, have CV values up to 56 % in Scots pine spanning large latitudinal and environmental gradients (Martínez-Vilalta *et al.*, 2009). From the few studies that have examined root traits, relatively high ITV has been detected for root chemical content and specific root length, although this can vary dramatically among species, with ITV ranging from 15 to 95 % (Supplementary Data Table S1). Relatively few studies have reported the CV for floral traits, with the exception of floral morphology (variation in the size, shape and colour), which can determine the extent of reproductive isolation and therefore speciation (Dormont *et al.*, 2019). From a global

study, the CV for reproductive architecture and morphology is estimated to be 20 % (Kuppler *et al.*, 2020).

Previous studies have suggested that plant traits should be coordinated with one another in similar ways across organs, leading to whole-plant functional strategies (Reich, 2014). For example, leaves and stems are inextricably linked and their traits should covary with one another in similar ways whether evaluated across or within plant species. Despite this assertion, trait covariance patterns observed across species can be weaker when evaluated within species due to high ITV (Laughlin *et al.*, 2017; Read *et al.*, 2017; Kumordzi *et al.*, 2019; Nolting *et al.*, 2020). For example, if a trait varies strongly across an environmental gradient within a single species due to plasticity, it can weaken the trait covariance patterns observed across species, which reflects evolutionary adaptations. In a study of six widespread species in Puerto Rico, species-level trait covariance patterns (e.g. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, leaf carbon concentration, leaf nitrogen concentration, leaf area, SLA, thickness) were inconsistent when evaluated within species (Umaña and Swenson, 2019b). In this Special Issue, Heyduk *et al.* (2020) report extensive genotypic variation in the upregulation of crassulacean acid metabolism (CAM) photosynthesis, and weak covariance between leaf anatomical and photosynthetic traits for $\text{C}_3 + \text{CAM}$ hybrid *Yucca* species spanning a large latitudinal gradient. The authors determined that cell size and intercellular air space, which are integral components associated with CAM photosynthesis, were not associated with CO_2 assimilation in the hybrid despite their known functional associations. Also in this issue, Bachle and Nippert (2020) detected weak covariance between leaf microanatomical properties (e.g. mesophyll area) and SLA, a whole-leaf property, in a C_4 grass sampled across climate gradients. This is surprising given that mesophyll area is a lower-level component of SLA, and the two should thus be coordinated. However, the authors demonstrate that SLA had much higher ITV (reported as the CV) than the anatomical traits and did not vary significantly across the study sites while the anatomical properties exhibited the reverse trend (low CV but significant trait–environment relationships). These findings suggest that we should consider the role of ITV when evaluating species-level trait covariance patterns. Weak covariance may also reflect poor selection of focal traits, which can be ameliorated by reporting multiple traits at once or using multivariate traits (Table 1).

Extent of ITV across levels of organization

The ‘spatial variance partitioning assumption’ offers a spatially explicit framework depicting the relationship between intraspecific (ITV) and interspecific (BTV) trait variation across levels of biological organization (within-individual to within-, then among-population) (Albert *et al.*, 2011). According to this model, at small scales the amounts of ITV and BTV are low and increase with spatial scale, saturating at different points along the continuum. Intraspecific trait variation plateaus when the scale encompasses the entire species’ distribution. These patterns lead to general predictions, such as reductions in the extent of ITV at larger scales, and higher BTV than ITV at larger scales. However, at the local or community scale, the model

lacks precision for whether ITV will exceed BTV because this depends on species distributions, gene flow, environmental heterogeneity and the traits of interest. In some cases, predictions do not hold (see section Extent of Plant ITV).

Although the extent of ITV within individual plants (10–18 % of total variation; [Supplementary Data Table S1](#)) is typically less than that observed within or among populations (within, 5–75 %; among, 22–38 %), it may still be biologically meaningful. For example, in this Special Issue [March-Salas et al. \(2020\)](#) reared common sainfoin, *Onobrychis viciifolia*, in a multigeneration experiment and reported that within-individual and within-population variability in flowering phenology and seed number per inflorescence increased when precipitation was less predictable. The authors also determined that intra-individual variability is plastic and under stabilizing selection, suggesting clear links between ITV and fitness under variable environments. In some cases, variation within individuals, or ‘sub-individual variation’ ([Herrera, 2017](#)), can exceed variation among individuals in a population. Such variation may be biologically meaningful for plants, given that their modular nature permits greater sub-individual variation than would be expected in most animals ([Herrera, 2017](#)). There is also evidence that within-individual variation is partly constrained by biophysics ([Fig. 1](#)), which considers how physical laws and properties operate on organisms. For example, maximum tree height appears to be constrained by gravity and friction, which create high hydraulic resistance within the xylem vessels, tissues that serve as conduits for water between the roots and canopy. Even when soil moisture is not limiting to plant growth, trees are constrained to 120 m or less (although historically as tall as 130 m has been reported), because above this height water stress becomes too great, limiting leaf expansion and photosynthesis ([Koch et al., 2004](#)).

Considering the prescribed methods of sampling plant functional traits ([Perez-Harguindeguy et al., 2013](#)), which constrain variation by avoiding shaded, older or blemished leaves, it is probable that ITV is greater than has been appreciated and would be better incorporated via random sampling of individuals and tissues within individuals ([Table 1](#)).

Extent of ITV across biomes and habitat types

While an increasing number of studies report the extent of ITV, variable patterns across species, biomes and traits make a general model elusive. For example, LMA and leaf area in woody species have been shown to exhibit ITV (reported as the CV) as low as <5 % or as high as 90 %, depending on whether they were sampled in boreal or tropical forest ([Bastias et al., 2017](#)). Similarly, ITV in height varies considerably across species and biomes ([Supplementary Data Table S1](#)), from as low as 5 % (from variance decomposition analysis) in understory plants of Oregon ([Burton et al., 2017](#)) to as high as 90 % (reported as the CV) in the pocosin-to-savannah ecotone of North Carolina ([Mitchell et al., 2017](#)). Habitats characterized by high microenvironmental heterogeneity over small spatial scales, such as forest understories and alpine meadows, typically exhibit higher ITV at local scales relative to homogeneous environments ([Burton et al., 2017](#); [Chalmandrier et al., 2017](#); [Read et al., 2017](#); [Kumordzi et al., 2019](#)), and in these cases ITV may

surpass BTV. Additional research may help clarify the role of climate, resource availability and plant growth forms in driving ITV’s extent.

EFFECTS ON HIGHER-ORDER PROCESSES

Various studies have clarified the role of ITV in the context of eco-evolutionary dynamics, species’ niche breadths and community assembly and structure ([Jung et al., 2010](#); [Violle et al., 2012](#); [Shipley et al., 2016](#); [Fajardo and Siefert, 2019](#)). However, more work is needed to clarify how ITV influences higher-order processes, including population growth and persistence, invasion success, species distributions, ecosystem function (e.g. productivity), and resilience and resistance to disturbance. Intraspecific trait variation can have demonstrable effects on whole-plant performance and population performance ([Fig. 1](#)), and can induce changes in species interactions, which determine community assembly and structure. Over time, ecosystem-level processes will also change alongside community shifts, and large-scale shifts in vegetation will follow. We emphasize that there are feedbacks between these processes, as changes in vegetation type and ecosystem function influence the extent of ITV.

Individual performance

Linking ITV to higher-order ecological processes, such as population and community dynamics, requires strong associations between traits and performance (growth, survival and reproduction), yet these connections are often weak ([Paine et al., 2015](#); [Funk et al., 2020](#); [Swenson et al., 2020](#)) or context-dependent ([Heschel et al., 2004](#); [Angert et al., 2014](#)). Trait–performance relationships have also been shown to vary substantially when evaluated across species and spatial scales. For example, wood density is a strong predictor of growth for species across biomes ([Kunstler et al., 2016](#)) but appears to be a weak predictor of growth and competitive ability within two widespread *Nothofagus* species ([Fajardo, 2016](#)). One possible explanation for this weak link is high ITV, as traits may have positive effects on performance at one developmental stage or size but have weak or opposite effects at another ([Falster et al., 2018](#)). Clarifying how ITV influences plant performance will require sampling across environment gradients and plant developmental stages or sizes ([Table 1](#)).

Because plant function is largely driven by suites of traits working synergistically and traits can vary substantially within individual plants, it is reasonable to assume that not all trait–performance relationships will be biologically meaningful. An increasing number of studies are calling for trait–performance relationships to be evaluated using suites or networks of traits ([Table 1](#)) rather than individual traits ([Laughlin and Messier, 2015](#)). In this Special Issue, [Nolting et al. \(2020\)](#) determined that the power to predict plant size for five *Protea* species from the Western Cape Region of South Africa was vastly improved with a multivariate regression (including physiological and structural traits) versus univariate regressions, and physiological traits had clear links to plant size and reproductive effort despite higher ITV than BTV in physiological traits. It is

also evident that individual performance metrics are not always effective predictors of population-level performance, as there may be trade-offs between growth, survival and reproduction across a plant's lifetime (Laughlin *et al.*, 2020).

Demand is increasing for the use of more functionally integrative (reflecting various functional roles) and phenotypically integrative (combining individual-level biomass allocation data with organ-level data) traits to examine trait–performance relationships (Yang *et al.*, 2020b). Specific leaf area, one of the most widely measured traits, expresses some of the highest levels of ITV among plant functional traits (Supplementary Data Table S1) and has multiple functional roles (e.g. regulating light capture, nutrient retention, resistance to structural damage). Yet in some habitats SLA may be under weaker selection than other traits. For plants inhabiting sandy plains in Brazil, midday water potential was much more strongly associated with dominance rankings than SLA (Rosado and de Mattos, 2017), and water potential has been described as an integrative trait (Ackerly, 2004; Dias *et al.*, 2020). Because researchers may be biased or incorrect in their selection of the most ecologically relevant traits, additional steps must be taken towards identifying integrative and biologically relevant traits and quantifying their ITV (Table 1).

When using species means over individual replicates, the ability to detect meaningful trait–performance relationships may be stymied when ITV is high. In this Special Issue, Yang *et al.* (2020b) found that to generate more accurate predictions of tree growth on the basis of traits required data at the level of individuals rather than species means. The authors argue that individuals within and across species express significant variation in how they allocate carbon, resulting from underlying ontogenetic variation or microenvironmental heterogeneity. Thus, a consequence of high ITV may be a weak ability to predict plant performance, particularly when traits are averaged across populations or species. It is also important to consider the role of ITV in obscuring higher-order interactions between traits, plant performance and environmental conditions. For example, rooting depth should increase plant performance under conditions of drought, but high seasonally driven ITV could weaken the relationship between rooting depth and soil moisture when averaged across the entire year. Similarly, ontogenetically driven ITV can also obscure expected relationships. In this Special Issue, Funk *et al.* (2020) determined that younger individuals of a drought-deciduous shrub had higher ITV across a moisture gradient relative to older individuals, and there was only weak evidence to support the prediction that trait–performance relationships were stronger for younger individuals, as they may be more vulnerable to drought. Thus, to generate more accurate and meaningful predictions of trait–environment and trait–performance relationships, future studies should consider random or systematic sampling of individuals across a range of sizes or developmental stages (Table 1). Alternatively, mixed effects models can be used to account for random effects of plant size, age or developmental stage, and can be used to separate ITV from BTV even when ITV is not the focal response variable.

Population-scale processes

The extent of variation in plant phenotypes is at the very core of evolutionary biology and population biology. Among

evolutionary biologists, a population's mean absolute fitness is often considered in terms of an individual's lifetime contribution of offspring to a population. Among demographers, the average lifetime fitness is considered equivalent to the population growth rate for overlapping generations. In both disciplines, a key aim is to capture variation across individuals in terms of their growth, survival and reproduction, i.e. vital rates. Variation in vital rates, but also traits that influence vital rates, can contribute substantially to population persistence, and to vegetation dynamics (see section Ecosystem-scale processes) and are described below.

Coupled with individual-level variation in vital rates (demographic stochasticity), the extent to which functional traits vary among individuals can play a key role in determining whether that population will persist over time. Across populations, phenotypic variation in traits relevant to abiotic stress tolerance, such as drought, can reveal a population's capacity to adapt to changing environmental conditions (Nicotra *et al.*, 2010; Valladares *et al.*, 2014). In this Special Issue, Welles and Funk (2020) used a common garden experiment to compare drought acclimation responses across wild radish populations spanning an aridity gradient in California (USA), and found that populations from arid regions expressed higher leaf nitrogen concentration, low LMA and earlier flowering than those from mesic regions. While this phenotype is consistent with a drought escape strategy, the authors also reported greater investment in below-ground biomass among arid populations, which is more consistent with a drought tolerance strategy. These findings suggest that intermediate strategies are likely to confer an advantage over strictly drought-escapist or drought-tolerant strategies, and reveal the importance of population-level ITV for the evolution of plant ecological strategies.

Evolutionary studies often regress traits onto mean fitness to study traits under selection, while demographic models can evaluate the sensitivity of population growth rates to lower-level parameters that influence vital rates, i.e. examine the effects of plant functional traits on population dynamics. In the last several years, interest has surged in demographic models that more explicitly integrate functional traits (Adler *et al.*, 2014; Westerband and Horvitz, 2017; Jenouvrier *et al.*, 2018; Salguero-Gómez *et al.*, 2018; Smallegange and Ens, 2018), leading to 'trait-based population models'. For example, Westerband and Horvitz (2017) used integral projection models to measure the sensitivity of population growth rates to light-saturated leaf photosynthesis across a range of plant sizes and a range of light environments. Snell *et al.* (2019) highlight how ITV in seed dispersal influences population dynamics, persistence and spatial spread, but also community processes including assembly, composition and coexistence. For example, infrequent long-distance dispersal events by robins was a stronger determinant of the spatial spread of an invasive shrub than more common, short-distance dispersal events (Horvitz *et al.*, 2015). Integral to the more widespread use of such models are trait databases such as the StrateGo Network (Salguero-Gómez, 2018) and the COMPADRE Plant Matrix Database (Salguero-Gómez *et al.*, 2015), which have increased the availability of demographic and functional trait data measured on the same individuals. Carrying out functional and demographic fieldwork on the same individuals in the field is highly labour-intensive but should be prioritized (Blonder *et al.*, 2018).

The capacity to integrate ITV within species distribution models (SDMs) is on the horizon. When resource availability is temporally variable, populations that contain extensive variation in traits regulating resource uptake and use are more likely to include genotypes or individuals that can withstand potentially unfavourable conditions (Hooper *et al.*, 2005; Bolnick *et al.*, 2011). Species distribution models and individual-based models have the capacity to include ITV to generate more accurate predictions of population and community dynamics (Moran *et al.*, 2016), although computational limitations make this a significant challenge (Zhang and DeAngelis, 2020). Chardon *et al.* (2020) compared a traditional SDM with models that assumed variation across genetic groups or habitat types, reporting how the latter strongly outperformed the former. As technology advances, limitations of these approaches will be reduced.

Community-scale processes

Because abiotic and biotic filters act on individuals rather than species, phenotypic variation within and among individuals can influence community composition and community dynamics (Violle *et al.*, 2012). Within-plant variation can broaden a species' ecological breadth and thus alter the number and strength of inter- and intraspecific interactions (Bolnick *et al.*, 2011; Herrera *et al.*, 2015). It has been argued that high within-individual phenotypic variation resulting from divergent responses to environmental cues can promote species richness by reducing interspecific competition relative to intraspecific competition (Clark, 2010). High phenotypic variation may also constrain species richness (Hart *et al.*, 2016), and it is likely that both dynamics occur (Helsen *et al.*, 2017).

A number of reviews have suggested that community-scale studies should incorporate ontogenetically derived or temporal patterns of ITV, multivariate and covarying traits, and information regarding the underlying genetic basis and heritability of trait variation and the abiotic drivers of ITV (Albert *et al.*, 2011; Bolnick *et al.*, 2011, Violle *et al.*, 2012). Although relatively uncommon, in cases where ITV contributes more strongly to community-level trait variation than BTV, community assembly models that do not incorporate ITV may produce misleading or erroneous conclusions, as has been described previously (Violle *et al.*, 2012). We note that recently developed community assembly models are now capable of incorporating ITV to predict species abundances, maximize functional diversity and achieve particular functions in restored communities, such as drought tolerance (Laughlin *et al.*, 2012, 2018); however, these models may require high replication within species for effective parameterization (Laughlin *et al.*, 2012).

Although it has received less attention, another goal of community-based research is to understand the consequences of ITV for plant–herbivore interactions, plant–microbial interactions and invasion. For example, chemical resistance and extrafloral nectaries, small glands that occur at the base of the leaf, declined across ontogeny in a multi-year study of clonally replicated aspen trees, and this ontogenetic component of ITV was itself heritable, as demonstrated in this Special Issue by Cole *et al.* (2020). This ontogenetically driven variation in

defence and resistance to herbivores suggests a shift towards herbivory tolerance with plant age, consistent with previous studies revealing ontogenetic shifts from a dependence on resistance to tolerance across ontogeny (Boege *et al.*, 2007; Massad, 2013). With regard to invasion, a number of studies have reported greater phenotypic plasticity of functional traits in non-native invasive species relative to natives (Funk, 2008; Hiatt and Flory, 2020) and non-invasive species (Davidson *et al.*, 2011), which may result in more extensive ITV among invasives. However, studies that quantify the extent of ITV in natives and invasives are relatively rare, and the relative contributions of genotypic variation and phenotypic plasticity are usually not determined. Rarer still are studies that quantify the extent of ITV in natives and invasives across relevant environmental gradients. In this Special Issue, Westerband *et al.* (2020) determined that the extent of ITV in leaf phosphorus concentration, leaf chlorophyll content and leaf area was positively correlated with available soil moisture and mean annual rainfall in natives, whereas soil moisture and rainfall were positively correlated with ITV in leaf thickness and photosynthetic water use efficiency in invasives. These findings suggest differential plasticity and local adaptation in response to climate among native plants and non-native invaders in Hawaii. Similarly, Kühn *et al.* (2020) determined that while the phenotypic trait spaces of native and non-native species within Tenerife (Canary Islands, Spain) overlapped, the extent of ITV in LDMC and SLA decreased with elevation in invasives but increased with elevation in natives. These studies reveal distinct patterns of within-species variation that will likely mediate species interactions, and are further evidence that evaluating ITV, as opposed to BTV alone, can yield novel insights regarding species interactions and community processes. Whether or not high ITV across populations is driven by plasticity, local adaptation, or both, is integral to understanding resistance to invasion (Richards *et al.*, 2006; Hulme, 2008; Davidson *et al.*, 2011), as high ITV has been shown to produce significant overlap in traits between native plants and their non-native invaders, which can increase resistance to invasion (Funk *et al.*, 2008).

Ecosystem-scale processes

The extent of ITV can influence ecosystem properties via 'effect' traits, i.e. traits that influence ecosystem processes such as nutrient and water cycling (Lavorel and Garnier, 2002; Suding *et al.*, 2008). These traits include leaf nitrogen concentration, leaf lifespan, respiration and leaf area index (LAI; the amount of leaf area per unit ground surface area), and previous studies have determined that effect traits can strongly influence ecosystem properties, including net primary production (Reich, 2012). Shifts in ecosystem properties will subsequently trigger changes in 'response' traits (Lavorel and Garnier, 2002; Suding *et al.*, 2008), traits that respond strongly to environmental gradients. Thus, there are feedbacks between ITV's extent and ecosystem properties such as productivity, nutrient cycling and resistance to disturbance that warrant further study.

Although the extent of ITV appears to vary widely across traits, species and habitats, even simple efforts to incorporate ITV in ecosystem models appear to improve their predictive

power. [Lecerf and Chauvet \(2008\)](#) found that intraspecific variation in litter quality across distinct geographical origins largely explained variation in decomposition rates. [Reich et al. \(2014\)](#) determined that including intraspecific variation in gymnosperm needle longevity, biomass allocation and nitrogen content across biogeographical gradients improved the ability to predict primary production and LAI. [Lu et al. \(2017\)](#) modelled land area fractions and found that the model's predictive power increased when both ITV and BTV were integrated into models. Similarly, [Sakschewski et al. \(2015\)](#) modelled trait variation (ITV and BTV) using a distribution of values rather than a constant value per plant functional type and were able to represent plant functional diversity more realistically at the local and regional scales. [Reich et al. \(2014\)](#) acknowledge that, in some cases, including more realistic variation within species reduces model performance, but such steps are vital as they lay the groundwork for future advances in ecosystem modelling approaches.

Clarifying the extent and drivers of ITV can also refine our understanding of how community-level properties shift in response to ecosystem properties ([Fig. 1](#)). For example, [Mitchell et al. \(2020\)](#) experimentally manipulated fire return intervals in a long-leaf pine ecosystem in southeastern USA and reported lower community-weighted mean values of SLA in plots that had experienced more burns, and higher SLA values in less frequently burned plots, indicating a community-level shift towards more resource-conservative strategies (associated with lower SLA) with increasing fire frequency. This study captures links between ecosystem properties and ITV, and similar studies could be used to predict shifts in community-weighted trait means under changing environmental conditions ([McGill et al., 2006](#)).

Dynamic vegetation models (DVMs) simulate changes in vegetation cover with climate at regional and global scales. Similar to SDMs, DVMs typically assume a single mean trait value per plant functional type ([Van Bodegom et al., 2012](#); [Fisher et al., 2018](#)); however, recent reviews have identified ITV as a key research priority for the next generation of DVMs ([Hartig et al., 2012](#); [Scheiter et al., 2013](#); [Moran et al., 2016](#)). [Berzaghi et al. \(2020\)](#) summarize state-of-the-art DVMs that can incorporate ITV, describing limitations of each type. One type of model, 'plastic models of intraspecific variability', requires users to describe the relationships between traits and their environment; however, these lack heritable variability as they assume that adaptations to changes in environmental drivers are instantaneous. These models are also difficult to generalize across a wide range of species and environmental conditions. Another class, 'eco-evolutionary' models, draws on quantitative genetics to simulate adaptive evolution but requires information regarding underlying genetic architecture of focal traits (e.g. numbers of alleles and loci determining a trait). Thus, parameterizing these models requires more extensive data than are currently available. Another key limitation of this type of model, and of models in general, is the problem of complexity. While including ITV would *likely* produce more realistic estimates of long-term vegetation dynamics, such models are often computationally intensive, difficult to parameterize and prone to high uncertainty ([Berzaghi et al., 2020](#)). An alternative to explicit integration of ITV is to simulate ITV based on a

combination of empirical observations and theory ('prescribed trait distribution' models) ([Berzaghi et al., 2020](#)). However, this technique would require a deeper and more synthetic understanding of the underlying mechanisms that constrain or enhance ITV, which is still lacking. By investigating the extent of ITV for underrepresented traits, species and biomes, and by exploring controls of ITV across spatial scales, we will be able to generate a much-needed, deeper and more synthetic view of ITV's role at the ecosystem level.

FUTURE DIRECTIONS

The recent surge of interest in understanding the extent of ITV has culminated in a number of ecological studies that are descriptive in nature. Relatively fewer ITV studies examine the underlying mechanisms controlling or enhancing ITV. Significant progress has been made towards understanding how population and community dynamics are influenced by ITV, and how ITV is maintained over time, but we can do more to draw connections across disciplines and sub-disciplines.

Here, we summarize a few key areas of future research and outline strategies for quantifying ITV ([Table 1](#)) in ways that will elucidate its ecological significance. First, simultaneously analysing shifts within and across species will help identify the potentially different mechanisms that underlie ITV and BTV. For example, does the extent of variation within species versus across species respond in similar ways to an abiotic gradient? Is this driven by species turnover, local adaptation or phenotypic plasticity? The first question can be addressed using nested sampling designs accompanied by linear mixed models and variance partitioning analysis, while the second can be addressed via common garden experiments. It is laborious to determine the underlying mechanisms producing ITV, be it phenotypic plasticity, genetic adaptation or epigenetic forces. But combinations of field studies and common garden experiments will be a powerful tool for understanding the role and importance of ITV.

Second, to clarify the consequences of ITV across levels of organization, we should first focus on traits likely to be under selection in a given context, which may include traits underrepresented in the current literature or traits that integrate across multiple functions. We should aim to quantify relationships between traits of interest and whole-plant performance metrics over a range of plant ages, sizes and environments, as well as population growth rates of co-occurring or interacting species. There are already approaches for including ITV within demographic models, and these should be more fully utilized. Given that population growth rates can be estimated in a variety of ways, including ratios of population sizes, such approaches are useful for understanding whether a particular trait value is adaptive. For example, by measuring the amount of trait variation at the population level, coupled with estimates of population growth for multiple species spanning environmental gradients, one can test for correlations between trait values and population growth rates across species. This simple approach can reveal the sensitivity of population growth rates (equivalent to fitness) to ITV. When ITV data are lacking, they can be simulated based on published datasets, although caution is

needed when employing such approaches given the research biases outlined above.

Third, an extensive body of research has clarified the extent of ITV in a few but well-represented plant functional traits, including SLA and height, and largely ignored roots, anatomical properties, hydraulic traits, seed traits and traits associated with herbivore defence, among others. Efforts to scale ITV across levels of organization will be facilitated by making ITV data for these underrepresented traits more widely available, and will enhance our ability to detect patterns of ITV at regional and global scales (Kuppler *et al.*, 2020). This paucity of ITV data could be addressed by incorporating ITV within larger studies, particularly through undergraduate and graduate student projects, or via citizen science projects. The National Phenology Network within the USA (<https://www.usanpn.org/>) provides a platform for the general public to record phenological data, and can be used to track shifts in phenological responses over time. Similar platforms can be generated for other easily measurable plant traits, such as leaf width or plant height. We emphasize that while many studies of ITV report the CV, this metric can be biased for low sample sizes, as explained above, and more extensive sampling is needed, particularly for heterogeneous habitats. Yang *et al.* (2020a) determined that the least amount of bias in the CV occurred with sample sizes greater than 20 for almost all traits and species. This means that when reporting ITV in plant functional traits, the number of individual replicates within a species should be greater than 20, whenever possible. Variance partitioning analysis is an alternative and complementary approach that describes the total amount of variation explained within versus across species.

Lastly, greater efforts should also be made to capture temporal variation in traits, due to environmental variation or ontogeny. When coupled with nested experimental designs, mixed effects models can be used to partition variation among these sources (e.g. species, individual, branch, climate, soil). We also agree with previous calls to dispense with traditional sampling protocols whenever possible, and to use random sampling instead. This will reveal ITV's true extent.

CONCLUDING REMARKS

Our review has largely focused on identifying how ITV can inform ecological processes from the individual to ecosystem scale. From previous studies (Siefert *et al.*, 2015), it is recommended that ITV be studied when (1) it explains a large proportion of total variation in traits across and within communities, (2) the study is conducted on a local scale, and (3) the study is conducted in a species-poor community (because large ITV broadens niche width). In these cases, the use of species means may lead to spurious conclusions. Here, our synthesis of recently published studies found that ITV's extent across spatial scales does not match predictions, as ITV is sometimes larger than BTV (Supplementary Data Table S1). For example, Tautenhahn *et al.* (2019) measured functional trait variation in 56 grassland sites across Europe, and found that ITV exceeded BTV for 9 of 14 traits. Thus, we suggest a modification of the recommendations of Siefert *et al.*, as it is perhaps an oversimplification to conclude that regional or global studies can omit ITV, and that ITV will not be important in habitats with high environmental heterogeneity.

The advent of online data repositories has resulted in a greater availability of functional trait data, and these publicly available datasets are increasingly being used to study ITV, despite their limitations. Incremental steps can and should be taken towards increasing the availability and type of ITV data within these data repositories, as this information can be used to clarify the mechanisms underlying ITV patterns. Little effort is required to report population means, rather than species means, and to report estimates of variation around means as well as data distributions. As highlighted by this Special Issue, we have much to gain from investigating not only the extent of within-species variation but also its controls and ecological consequences.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Table S1: summary of ITV extent for plant functional traits from studies published since the Siefert *et al.* (2015) meta-analysis.

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