

# Variability in Plant–Herbivore Interactions

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## Keywords

herbivory, plant, herbivore, defense, species interactions, ecological variability

## Abstract

Plants and herbivores are remarkably variable in space and time, and variability has been considered a defining feature of their interactions. Empirical research, however, has traditionally focused on understanding differences in means and overlooked the theoretically significant ecological and evolutionary roles of variability itself. We review the literature with the goal of showing how variability-explicit research expands our perspective on plant–herbivore ecology and evolution. We first clarify terminology for describing variation and then review patterns, causes, and consequences of variation in herbivory across scales of space, time, and biological organization. We consider how incorporating variability improves existing hypotheses and leads to new ones. We conclude by suggesting future work that reports full distributions, integrates effects of variation across scales, describes nonlinearities, and considers how stochastic and deterministic variation combine to determine herbivory distributions.

**Diversity:** the number of discrete types (e.g., species, genotypes) present, their relative abundances, and their multivariate variation in space and time

**Variation:** the measured differences in a system; can be summarized with dispersion metrics (e.g., variance); also used to mean change in a factor across a gradient (e.g., elevational variation)

**Variability:** the propensity of a process to yield differences or variation in outcomes

**Variability-explicit research:** research that examines the causes and/or consequences of differences in variability by including metrics of variation as a response, predictor, or experimental treatment

## 1. INTRODUCTION

Herbivory—the interaction between plants and their consumers—occurs in nearly every ecosystem on Earth and is one of life’s dominant interactions (Strong et al. 1984). Over a century of research has uncovered the many ways herbivory has shaped the ecology and evolution of plants and herbivores (Crawley 1983, Endara et al. 2023). Plant distribution, density, and quality influence herbivore performance, abundance, and population dynamics (Beatley 1969, Larsson et al. 2000, Mattson 1980). Likewise, herbivore attack can greatly reduce plant fitness and population abundances (Maron & Crone 2006). In response to herbivory, plants have evolved an astounding diversity of defensive plant traits, from spines to toxic chemicals to tolerance of tissue removal (Strauss & Zangerl 2002). In return, herbivores have evolved countless specialized adaptations—from behaviors to morphological traits—for locating and consuming their host plants (Karban & Agrawal 2002). The reciprocal effects of this interaction are indisputably central to plant and herbivore biology.

Although herbivory is ubiquitous, it is also highly variable through space and time (**Figure 1**). For example, the larch budmoth (*Zeiraphera griseana*) in the Alps and the spruce budworm (*Choristoneura fumiferana*) in New Brunswick vary 100,000-fold in density across years, and their damage varies from nearly unobservable to complete defoliation (Turchin 2003). Attacks by sawflies on willows, gall flies on sagebrush, and gall wasps on oaks consistently vary by an order of magnitude among neighboring plants of the same species (Fritz et al. 1987, Wetzel & Strong 2015). In many tropical tree species, damage can be highly variable even within individuals, with chewing damage often an order of magnitude higher for young leaves than for mature leaves (Coley 1980). This remarkable variation has inspired decades of research on its causes and consequences. Variability has even been called “a key to understanding plant–herbivore interactions” (Denno & McClure 1983, p. 1).

Despite our fascination with variation, the majority of herbivory research, as in most fields of ecology, is focused on means. For example, biogeographic and macroevolutionary studies have shown that the mean level of herbivory across species tends to decline with latitude and differ among plant clades (Turcotte et al. 2014). However, these studies have largely overlooked latitudinal or phylogenetic differences in the amount of variation itself. A growing chorus has pointed out the potential importance of variability and advocated for an increased focus on the role of variability in ecological and evolutionary processes (Benedetti-Cecchi 2003, Bolnick et al. 2011, Holyoak & Wetzel 2020, Ruel & Ayres 1999, Shaw & Shaw 2014, Shoemaker et al. 2020, Violle et al. 2012). Herbivory researchers have begun to respond to this call, with work examining multiple types of variation, including genetic (Crutsinger et al. 2006), phytochemical (Wetzel & Whitehead 2020), physiological (Pearse et al. 2018), population (Underwood 2007), and community (Salazar et al. 2016). A general understanding of variability, however, has yet to emerge, in part because variability-explicit research is spread across disparate literatures, siloed by scales of biological organization, and complicated by differences in terminology.

With this review, we aim to advance our understanding of the role of variability in plant–herbivore interactions by reaching across scales and subfields. We start by clarifying variability and related terms because they are often used inconsistently by biologists. Next we highlight the importance of variability in ecology and evolution by summarizing theoretical work. Finally, we review what is known about variability in herbivory at three scales: within plant individuals, among plant individuals within populations, and among populations and communities. Within each scale, we revisit foundational hypotheses and show how considering variability improves their ability to explain observed patterns or leads to novel hypotheses. Our goals are to provide an entry point for researchers interested in variability, spur growth in variability-explicit research, and help grow our perspective on plant–herbivore ecology and evolution.



**Figure 1**

Plant–herbivore interactions often exhibit high variation. For example, neighboring individuals of the same species often have large differences in levels of herbivore feeding damage, as in these photos of (a) water oak (*Quercus nigra*) and (b) sagebrush (*Artemisia tridentata*). The water oak on the left has many cut-out areas on its leaves that have been consumed by chewing herbivores, while the one on the right has relatively low herbivore damage. Similarly, the sagebrush on the left is highly infested by flies feeding internally via the galls they induce (*brown swellings*), while the individual on the right is gall free. Variation is also common within plant individuals. For example, damage often varies many-fold across leaves within individuals, as in these photos of (c) common milkweed (*Asclepias syriaca*) with an aggregation of the milkweed tussock moth (*Euchaetes egle*) feeding on a single leaf and (d) okra (*Abelmoschus esculentus*) with high Japanese beetle (*Popillia japonica*) damage (cut-out areas) on some leaves (left) but not others (right). Photos provided by (a) Phil G. Hahn, (b) Brian D. Inouye, (c) William C. Wetzzel, and (d) Ikponmwo N. Egbon.

## 2. A THEORETICAL PRIMER ON VARIABILITY

### 2.1. What Is Variability?

We use variability to mean the propensity for a process to produce different outcomes (Wagner & Altenberg 1996). Variation, in contrast, is the magnitude of differences among units in a system. In other words, variability is a feature of underlying processes, whereas variation is a feature of an observed pattern (i.e., data). Well-known drivers of interaction variability in ecology include organismal plasticity, demographic stochasticity, and population dynamics; these factors and more combine to create an underlying probability distribution for a given interaction. For example, the expected probability distribution for damage from a particular herbivore among plants in a population may be jointly driven by factors such as nutrient heterogeneity, plant induced defenses, and herbivore mobility. The amount of herbivore damage an individual receives and the distribution among a specific group of plants at a specific time and place are based on this true underlying

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#### Interaction variability:

the propensity of the strength of a species interaction to vary through space and time

#### Probability distribution:

a function that describes the probabilities of possible outcomes

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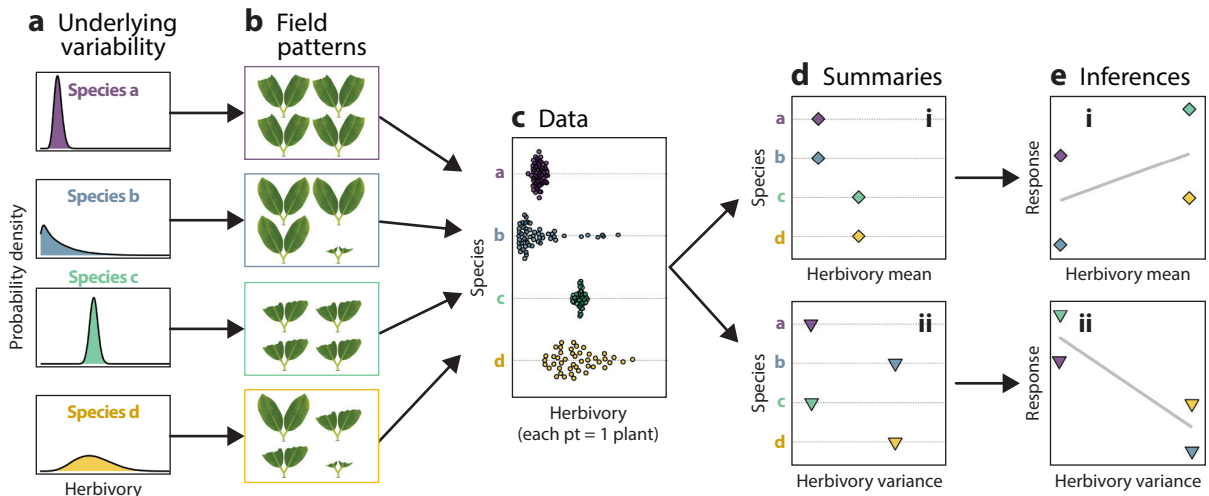
**Heterogeneity:** the variability of a pattern; spatial heterogeneity, for example, has been described as composed of spatial variance and spatial pattern

**Variance:** measure of dispersion calculated by averaging the squared deviations of each observation from the mean; often used to mean the spread of a distribution in general

distribution. Thus, any particular data set on the distribution of herbivory is a sample from one realization of an underlying distribution, and the observed variation is unlikely to reflect the full underlying variability of the system.

Recognizing the distinction between the underlying distribution and the data we take from it has two implications for how we gather data. First, the estimate of a mean has less uncertainty than estimates of higher moments, so if we want to know about variance and skew we need larger sample sizes. Second, if we want to ask about the causes or consequences of variability, we need multiple samples of distributions in situations with higher and lower levels of observed variation—it is not enough to measure a distribution once. For example, understanding drivers of variability among plants in a population requires measuring the distribution of damage in many different populations (and/or the same population many times) and analyses that explicitly consider metrics of population-level variation as response variables.

In addition to variation, other features of frequency distributions likely matter for plant–herbivore interactions, including skew and kurtosis, which describe the symmetry and tails of a distribution. As such, we advocate for the field to embrace distributional thinking, a term we use as shorthand for studying the full probability distributions of variables. Distributional thinking emphasizes examining the causes and consequences of differences in probability distributions across systems or gradients, explicitly using multiple aspects of distributions beyond just means as inputs or outputs of interest (**Figure 2**). Distributional thinking is also valuable because it encourages an explicit consideration of hierarchical scales of biology; one cannot calculate a variance without multiple measurements taken at a nested smaller scale. For example, comparing herbivory



**Figure 2**

Using distributional thinking to understand herbivory. (a) Variability in herbivory is the propensity for a system (in this case, a plant population) to produce levels of herbivory that differ among units (e.g., plant individuals). It could be a function of abiotic and biotic variation, plasticity in interacting species, stochasticity, and other processes. This variability can be visualized as the density function describing the probability of each amount of herbivore damage (herbivory) a plant individual could receive. (b) These underlying distributions shape patterns of damage observed in the field. (c) A researcher would record data, for example, the percent herbivore damage (herbivory) on 50 individuals of each of four study species. (d, i) Distributions of data have traditionally been summarized with a focus on their means, (d, ii) but studies could also examine variances, coefficients of variance, Gini coefficients, or other distributional features. (e, i) Researchers have traditionally focused on how differences in means relate to response variables (e.g., plant fitness) or predictor variables of interest (e.g., plant defense traits, herbivore community characteristics). (e, ii) We advocate for expanding beyond means to consider how variation, quantified with the variance or other metrics, relates to response or predictor variables.

distributions across populations will require sampling multiple individuals within each population, to calculate population means, variances, and skews. Similarly, comparisons of within-individual distribution will require data from multiple leaves, leaflets, or other plant modules per individual.

## 2.2. Why Study Variability?

We see two equally valid reasons for studying variability explicitly. The first is that variability pervades natural systems and cries out for explanation. Natural historians and biologists have spent centuries documenting patterns in the natural world, and this knowledge is foundational for ecology and evolution. Charting patterns in the amount of variation itself should be central to that effort. A second reason to study variability is that theory tells us that it has crucial ecological and evolutionary consequences. We see three major theoretical foundations for the study of variability.

First, variability is what generates variation, which itself is a prerequisite for natural selection and evolution. Less obviously, theory indicates that selection and rates of evolution depend not just on mean effects but also on the variability, skew, and other features of distributions of fitness (Wilson & Levin 1986). In particular, variability is central to the evolution of phenotypic plasticity (Ghalambor et al. 2007). Thus, knowledge of which systems have more or less variability or different distributional shapes is important for our understanding of the evolution of plant–herbivore interactions.

Second, a theme that pervades theoretical ecology is that variability acts through ecological nonlinearities to make the outcome of ecological processes substantially different from what would occur in the absence of variability. Nonlinear functions, ubiquitous in biology, include fitness functions, density dependence in population growth, and physiological processes. Studies have shown significant consequences of variability in all of these contexts. For example, because plant nutrient concentration influences herbivore performance typically through concave-down performance curves, herbivore populations will have lower mean performance in plant populations with variable nutrient concentrations, all else equal (Wetzel et al. 2016). Essentially, the steep parts of these curves, where small differences in nutrients lead to big differences in performance, pull down mean herbivore performance. This phenomenon is known as Jensen’s inequality, but there are also other important nonlinear mechanisms (see the sidebar titled *Theoretical Mechanisms by Which Variability Can Influence Response Variables*). These mechanisms are inevitable mathematical rules that give variability the power to shape ecological and evolutionary processes (Bolnick et al. 2011, Denny & Benedetti-Cecchi 2012, Holyoak & Wetzel 2020, Inouye 2005a, Shoemaker et al. 2020), and their effects have been confirmed empirically in a small number of systems (Stockhoff 1993). However, how these mathematical rules interact with the complexity of biological systems is still poorly understood and an open area of research (Pearse et al. 2018).

Finally, variability can matter because of biological responses to variation itself, such as behavioral or physiological responses to variation in the environment. For example, variable plant environments challenge the behavioral and information-processing abilities of whiteflies and other herbivores in ways that lead to reduced herbivore performance and increased vulnerability to predators (Bernays 1999, 2001; Schultz 1983). Crucially, direct biological responses to variation can be studied only by examining the effects of different levels of variation, unlike the effects of variation via nonlinear functions, discussed above, which can be inferred indirectly from the shape of the nonlinear response function. Direct biological responses are likely to be more idiosyncratic and less predictable than nonlinearity effects because they will depend on the biology of the study system (Pearse et al. 2018, Underwood et al. 2005). We expand upon these effects in each section below as we review empirical patterns of variability in plant–herbivore interactions and herbivory at within-individual, among-individual, and among-population scales.

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**Distributional thinking:** moving beyond a focus on centrality (means, medians) to using full probability distributions or facets other than centrality (e.g., spread, skew) for theory or practice

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## THEORETICAL MECHANISMS BY WHICH VARIABILITY CAN INFLUENCE RESPONSE VARIABLES

### Jensen's Inequality

When  $Y = f(X)$  is nonlinear and strictly concave or convex, Jensen's inequality states that  $f(\bar{X}) \neq \overline{f(X)}$ , where the bar indicates a mean. For example, for the common saturating (concave) function  $Y = \frac{X}{\beta + X}$ , variance in  $X$  will always cause a lower value of  $Y$  than when  $X$  is not variable. Ecological examples of Jensen's inequality are abundant, as so many relationships between predictors and responses in ecological systems are nonlinear (e.g., Inouye 2005b, Ruel & Ayres 1999, Violle et al. 2012). The strength of the effect of variability will depend on both the amount of variation in the predictor and the degree of nonlinearity.

### Critical Thresholds

A second context in which variability affects the mean response is when a relationship has a critical threshold or step function. If values above a threshold lead to a new response, then variability of a predictor can have an effect independent of the mean. This mechanism is related to Jensen's inequality, in that the relationship between a predictor and the response must be nonlinear but need not be strictly concave or convex. For example, suppose that a plant dies if it suffers greater than 50% leaf damage in a season but otherwise survives. In a population in which plants receive a mean of 40% plant damage, the proportion of a population that survives depends on the distribution of the plant damage among individuals, including the variance, skew, and kurtosis of the distribution of leaf damage. In populations with identical means, the population with greater variability in damage will have a great proportion of individuals above the critical threshold. In agricultural contexts, it is common for there to be a fixed threshold of acceptable damage for marketability or economically based damage thresholds for decisions to spray pesticides (Paredes et al. 2022).

### Extremes

A third way variability can influence ecological responses is if the most extreme values in a predictor have a disproportionate effect on a response,  $Y = f(\text{maximum}(X))$ , such that the response depends on the maximum observed values of  $X$  (or alternatively, its minimum). The most extreme values that are observed for  $X$  of course depend on the full distribution of the variable, including variances and particularly the weight of distribution tails, which depend on skew and kurtosis. Interest in climate extremes has surged in recent years, but the extremes of biological distributions are also important, such as the individual in a population with the highest load of disease propagules (affecting disease dynamics) or tallest individual in a patch (affecting patch finding by herbivores).

### Variation per se

In some systems, species may respond directly to variation itself, such that  $Y = f(\text{var}(X))$ , through behavioral or physiological mechanisms. This could arise if, for example, plant nutrient or defense variation was costly to herbivores by forcing them to repeatedly reacclimate their digestive physiology to spatiotemporally changing conditions (Wetzel & Thaler 2016). Often the direct effects of variation depend not just on the amount of variation but also on the spatiotemporal pattern with which organisms encounter it, leading Pearse et al. (2018) to refer to these effects as time-sensitive or time-dependent processes. Unlike the mechanisms described above, they are not simply a product of static statistical averaging and may be one of the most generalizable consequences of variation for herbivores. Similarly, plants can respond directly to variation in herbivore damage, with fitness outcomes dependent not just on the amount of damage but also on its distribution in time and space (see Section 2).

## 3. VARIABILITY WITHIN PLANT INDIVIDUALS

Historically, most studies of herbivory have considered plant individuals as their primary unit of replication and focused analyses on the total amount of damage per plant. The same total amount

of damage, however, could be distributed across a single plant in many ways. From the perspective of an herbivore, a single plant can represent a complex habitat with multiple food sources that vary in nutrients, defenses, and seasonal availability (Orians & Jones 2001). Consequently, damage may vary among different organs (e.g., leaves versus roots), among organs of the same type (e.g., flower to flower), or even within a single organ (e.g., fruit exocarp versus mesocarp). Temporally, damage may vary across years, seasonally, or even diurnally (Hay et al. 1983). Our understanding of the causes and consequences of this variability, however, is limited by a dearth of studies that explicitly quantify or manipulate levels of within-plant variation in herbivory across multiple plants and then use that variation as a predictor or response variable. In this section, we aim to encourage more such studies by reviewing patterns and causes of within-plant variation in damage and then discussing the consequences of this variation for plant and herbivore ecology and evolution.

### 3.1. Patterns and Causes of Within-Plant Variation

One of the most apparent axes of within-plant variation in damage is variation across different organs, including roots, stems, flowers, and fruits. Differences in damage across organs can often be driven by different herbivore communities and feeding guilds, but many herbivores also move between plant parts (Novotny et al. 2010). For example, the turnip sawfly (*Athalia rosae*), a specialist on Brassicaceae, feeds on leaves during early instars but later moves to flowers (Bandeili & Müller 2010). In addition to differences driven by herbivore biology, variation in damage across organs may be driven by plant traits, including physical structure, nutrients, and defenses. Optimal defense theory, one of the most cited ideas in plant–herbivore biology, proposes that plants should allocate defenses across different tissues based on the fitness value of each tissue, their probabilities of attack, and the costs of defense (McKey 1974, Rhoades 1979). This often leads to the prediction that reproductive tissues should be more defended than leaves (McCall & Fordyce 2010), but comparative studies have shown inconsistent defense allocation patterns (McCall & Fordyce 2010, Schneider et al. 2021). Few studies, however, have attempted to link variation in defenses across organs directly to variation in herbivore interactions across organs (i.e., in the identity of the herbivore or in the intensity of attack). Consequently, we know little of what leads some plant species to have more or less variability in traits or damage across organ types. Variability-explicit studies will be essential to understanding how defenses (or other traits) drive variability in herbivore attack and vice versa.

In addition to variation across organs, plants often experience high variation in damage among organs of the same type. For example, 73.5% of the total variance in leaf herbivory in the tropical plant *Piper polytrichum* occurred among leaves on the same plant, compared to 26.5% occurring among plant individuals (Wetzel & Meek 2019). Although much of the variation in damage across repeating organs may be driven by stochastic processes, plant traits, including nutrients and defenses, can also vary enormously from leaf to leaf (Møller et al. 2023), flower to flower (Pozo et al. 2014), fruit to fruit (Blanchard & Bowers 2020, Sobral et al. 2019), and even spatially within single leaves (Shelton 2005). This variation can be shaped by a variety of genetic and environmental factors (reviewed in Herrera 2009, 2017). Importantly, evidence has shown that subindividual trait variability—plasticity but also canalized spatial variation among units—can itself be a heritable trait under genetic or epigenetic control (Eisenring et al. 2021; Herrera et al. 2019, 2021). Thus, subindividual trait variability can shape variability in herbivory, but variability in herbivory can also be a selective force that shapes trait variability (Sobral et al. 2019). Indeed, how herbivores select for chemical variability and diversity within plants is a major recent focus within chemical ecology (e.g., Kessler & Kalske 2018, Richards et al. 2015, Wetzel & Whitehead 2020, Whitehead et al. 2021). By explicitly considering the role of variability, this work is expanding our perspective

on Ehrlich & Raven's (1964) notion of a chemically mediated coevolutionary arms race between herbivores and their host plants, moving from a focus on evolution of individual compounds to the evolution of variability itself.

Most studies of subindividual variation in herbivory have focused on plant traits that vary across repeating organs as an explanatory mechanism, but this variation is not just a bottom-up process. Herbivores from different feeding guilds and with different feeding behavior cause characteristically different spatial damage patterns. Herbivore behavior affects not only the amount of leaf-to-leaf variation per plant but also the spatial patterns of damage within individual leaves. For example, flea beetles (Chrysomelidae: Alticini) typically spread their damage relatively evenly within leaves via many small feeding holes, whereas many lepidopteran species cluster their damage more unevenly within leaves, starting feeding at one site and feeding contiguously outward. These patterns may be driven by a variety of factors beyond plant traits, such as predation avoidance (Ren et al. 2018) or larval aggregation behaviors (Inouye & Johnson 2005), but few studies have linked quantitative metrics of within-plant variation to hypothesized drivers.

Along with spatial variation, plants also experience temporal variation in herbivory at scales from hours to years. At both interannual and seasonal scales, a single individual plant can experience extreme shifts in the identities and densities of herbivores (Klapwijk et al. 2013, Mazía et al. 2012, Owen-Smith 2014). Temporal variation within plant individuals is further shaped by ontogenetic life stages (Barton & Koricheva 2010, Boege & Marquis 2005) and individual leaf ontogeny (Barton et al. 2019, Coley & Barone 1996, Kursar & Coley 1991). In general, damage tends to be concentrated on younger plants and younger leaves, though this pattern depends on growth form and other factors (Barton & Koricheva 2010, Barton et al. 2019). Within-individual temporal variation is a function of seasonal shifts in herbivore abundance and ontogenetic shifts in plant nutrients, chemical defenses, physical properties, and indirect defenses, among other factors (Barton & Koricheva 2010, Quintero et al. 2013). Indeed, within-plant temporal variation in defense can rival the variation found across genotypes and species (Holeski et al. 2012). One astounding example is horoeka (*Pseudopanax crassifolius*), which changes from having camouflaged leaves as a seedling to having linear, downward-pointing leaves with conspicuously colored spines as a sapling to having no spines and typical leaf coloration as an adult. Evidence suggests that, historically, these changes reduced ontogenetic variation in herbivory, largely by reducing sapling-stage herbivory from the giant moa (*Dinornis robustus*), an extinct herbivorous flightless bird that could reach foliage on saplings but not mature trees (Fadzly et al. 2009). Still, despite strong interest and numerous documented examples of temporal variation in herbivory, we found no studies that sought to explain why some plants would experience more or less temporal variation by specifically calculating metrics of within-plant temporal variation in herbivory and relating those metrics to hypothesized drivers.

At smaller timescales (hours to days), there have been more explicit efforts to quantify the extent of within-plant temporal variation in damage, as well as its underlying drivers. In particular, there has been extensive empirical and theoretical interest in the inducibility of plant resistance traits as a key mechanism that can shape temporal dynamics in herbivore preference, performance, and damage rates (e.g., Kessler & Baldwin 2002, Poelman et al. 2010, Underwood et al. 2005). Induced resistance or defense is a form of plasticity in which plants increase defenses in response to herbivory or cues about the presence of herbivores (Karban & Baldwin 1997). The extent of within-plant inducibility of defense traits is known to vary quantitatively across plant genotypes and depending on the type and extent of damage (Agrawal et al. 2002, Underwood 2000). However, variation in inducibility of defense is not often explicitly linked to variation in observed damage in the field (but see Underwood et al. 2005), and many other factors may also contribute to fine-scale variation in herbivore damage. For example, both herbivore activity and diverse aspects of



plant metabolism vary across the diel cycle (Davis et al. 2022, Zhang et al. 2021), leading to strong fine-scale variation in damage patterns that may interact with inducibility to shape overall levels and patterns of temporal variability.

### 3.2. Consequences of Within-Plant Variability

Clearly, different plants experience strikingly different levels of within-plant spatial and temporal variability, but the fitness, ecological, and evolutionary consequences of this variability for plants and herbivores are poorly understood. In addition to improving our understanding of the causes of variability, explicitly quantifying or manipulating within-plant variation in damage will allow researchers to understand the broad ecological and evolutionary consequences of that variation.

Multiple studies have shown that the spatial and temporal distribution of herbivore damage has large consequences for plant growth or fitness (Marquis 1996, Mauricio et al. 1993, Zangerl et al. 2002). Studies of damage patterns across leaves or branches within individuals have often shown that plants have a higher tolerance for dispersed damage than for concentrated damage (e.g., Avila-Sakar et al. 2003, Marquis 1992). For example, Mauricio et al. (1993) found that spatially concentrated damage patterns among leaves within *Raphanus sativus* reduce plant fitness more than dispersed damage patterns. Temporally, early-season damage from monarchs on milkweeds has strong effects on plant growth, whereas late-season damage has stronger effects on reproduction (Rasmussen & Yang 2023). At an even finer temporal scale, McMunn (2017) found that damage in the afternoon but not other times of the diel cycle induced resistance to later herbivory in sagebrush (*Artemisia tridentata*).

Considering the complex consequences for fitness, the amount and pattern of within-plant variation in damage could have broad consequences for the evolution of plant traits related to defense. A key example is the evolution of induced defenses. Induced defenses are hypothesized to benefit plants experiencing variable herbivory by saving resources in the absence of herbivore attack, by matching plant defense phenotypes to detected attackers, or by countering herbivore variability with within-plant defense variability that serves as a moving target (Adler & Karban 1994, Agrawal 1999, Karban 2011, Karban & Baldwin 1997, Karban & Myers 1989). There is strong theoretical support for the idea that high temporal variation in herbivory should select for high inducibility (Adler & Karban 1994, Ito & Sakai 2009, Karban et al. 1997), as well as some support from observational data, although this idea has not been tested experimentally. For example, wild radish populations with high interannual variation in herbivore pressure tend to have strong induction (Karban & Nagasaka 2004) and tropical understory trees that experience constantly high herbivory can have low defense plasticity (Bixenmann et al. 2016). Similarly, high spatial variation in damage across different organs or among organs of the same type should lead to tissue-specific defenses (e.g., Köllner et al. 2004, Whitehead et al. 2013) that can be induced or expressed constitutively only in the most susceptible plant parts.

A better understanding of the consequences of within-plant variation in damage requires more studies that explicitly quantify and/or manipulate the distribution of within-plant damage, as well as the application of distributional thinking to further refine hypotheses central to plant defense and plant–herbivore interactions. For example, applying distributional thinking to optimal defense theory reveals that its central tenet—that tissues should be defended in proportion to their fitness value—is an oversimplification. Defense allocation should depend not just on static metrics of fitness value but rather on the entire (likely nonlinear) functions relating fitness to the amount of herbivore damage on each tissue type. In leaves, fitness is likely an accelerating negative function of damage (concave down), where plants can often tolerate low levels of damage to leaves with no apparent loss to fitness (Marquis 1984), while high levels of defoliation can lead to steep declines in fitness, even in trees (Hernández-Barríos et al. 2012). On the other hand, a small

amount of damage to flowers might greatly reduce fitness by preventing reproduction or reducing attractiveness to pollinators, resulting in a decelerating negative damage–fitness function (concave up). This idea, as far as we know, has not been tested broadly, but evidence from wild parsnip indicates that reproductive parts are far more likely to receive extensive damage than leaves even though their overall probability of receiving any damage is similar (Zangerl & Rutledge 1996). Applying Jensen’s inequality (see the sidebar titled Theoretical Mechanisms by Which Variability Can Influence Response Variables), variable damage to reproductive tissue will make realized population mean fitness higher than expected, while variable damage to leaves will make population mean fitness lower than expected. We should thus expect less differentiation in defense allocation between leaves and reproductive tissues in environments with variable herbivore attack rates, a novel hypothesis that arises from distributional thinking.

## 4. VARIABILITY AMONG PLANT INDIVIDUALS WITHIN POPULATIONS

Biologists have long been fascinated by the fact that one plant can receive extensive damage, while another nearby plant receives very little. Most studies on herbivory in natural populations have focused on this scale, quantifying damage to multiple plants and asking how differences in damage among plants relate to diverse factors such as plant defense traits, resource availability, and herbivore behavior. However, surprisingly few studies have investigated drivers or consequences of among-plant variation by quantifying variation (or other features of distributions) across multiple populations and relating those metrics to other variables. These studies could be conducted across multiple populations of the same species, or across populations of different species in a community, either of which could shed new light on many of our foundational hypotheses in plant–herbivore biology. Here, we provide a starting point for studies of this nature by reviewing what is known about patterns, drivers, and consequences of population-level variation.

### 4.1. Patterns and Causes of Variation in Damage Among Plants

Decades of plant–herbivore research have documented biotic and abiotic factors resulting in differences in herbivory among plants within a population and thus potentially influencing the distribution of herbivory within populations. For example, plant chemical composition, nutrients, and phenology all influence herbivore attack and performance (Boecklen et al. 1990, Fritz & Simms 1992, Mopper & Simberloff 1995). Herbivory can also be influenced by the local environment created by neighboring plants, such as shading (Louda et al. 1987). The local density of conspecific plants can increase [resource concentration hypothesis (Root 1973)] or decrease [resource dilution (Otway et al. 2005)] herbivory on a focal plant; the relative frequency of a second plant species can also increase (associational susceptibility) or decrease (associational resistance) herbivory (Underwood et al. 2014). Plant diversity can influence herbivore behavior (Bernays 1999), and it has been suggested that local plant diversity should generally decrease herbivory (Root 1973). However, tests of this idea have found mixed results (Andow 1991, Jactel et al. 2021), perhaps in part because taxonomic or genotypic diversity (richness or evenness) is often a poor measure of variation in the plant phenotypes that ultimately influence herbivory. More recent studies focused on traits find that diversity in chemistry in a local neighborhood can influence herbivory (e.g., Bustos-Segura et al. 2017; Glassmire et al. 2016, 2020; Schuman et al. 2015).

Far less is known about what drives spatial distributions of herbivory among plants, relative to our understanding of what drives the amount of herbivory on a single plant or mean herbivory for a population. Theory and some data suggest that inducible resistance in plants can increase aggregation of insects and their damage in the short term and, in the long term, create even

distributions of damage by influencing herbivore movement (Roslin et al. 2008, Underwood et al. 2005). Interplant communication is similarly hypothesized to modify herbivore movement, making distributions of damage more even (Rubin et al. 2015). Little is known about whether this happens in practice, though one study suggests that it can (Karban & Yang 2020).

It has also been suggested that characteristics associated with plant apparency might influence the distribution of herbivory among plant individuals (Coley 1983), although this idea is largely untested. Feeny (1976) coined the term *apparent* to describe plant species that are bound to be found by herbivores, with traits hypothesized to increase apparency including plant size, life span, and abundance. Coley (1983) hypothesized the long-lived, shade-tolerant tropical tree *Trichilia cipo* should receive more even damage than the patchily distributed, fast-growing gap specialist *Cecropia insignis* because *T. cipo*'s slow growth and wider distribution would lead it to be found by herbivores more consistently. Although that study did not find a difference in the distribution of damage among individuals, this could be because it controlled for another aspect of apparency (plant size) that likely influences the distribution of damage. If large plants are easier for herbivores to find, among-plant variation in damage should be low due to the law of large numbers. That is, large plants should receive more herbivore feeding bouts than small plants; because the average of a number of events converges on the expected value as the number of events increases, larger plants should have per-individual damage levels closer to the mean and thus a more even distribution of herbivory among plants. Further, large plants also tend to retain their green tissues longer, which would lead large plants to average over temporal variation in herbivore pressure as well.

Herbivore traits can also influence the distribution of herbivory. For example, the metabolic rate and body size of grassland herbivores, from insect herbivores to large mammals, can affect herbivore activity budgets and feeding behavior, thus influencing the distributions of damage each species leaves (Belovsky & Slade 1986). Herbivorous insects often aggregate (e.g., Bergelson et al. 1986, Faeth 1990, Morris et al. 1992, Root & Cappuccino 1992, Turchin 1989), although the degree of aggregation can vary among herbivore species even on a single host plant species (Root & Cappuccino 1992). Herbivore aggregation should increase variance in damage among plants and cause skewed distributions, aggregating most damage on a few plants. Conversely, herbivore traits that deter individuals from laying additional eggs in the same location, such as pheromones used by herbivorous flies (Roitberg & Prokopy 1987) or visual responses used by *Heliconius* butterflies (Williams & Gilbert 1981), should lead to more even distributions of feeding damage, reducing variation among individuals.

Decades of work in population ecology have sought predictors of temporal variability, examining what makes some systems exhibit stable population dynamics with low temporal variation whereas others exhibit dynamics that are highly variable and skewed across years (Myers & Cory 2013, Wallner 1987). For example, work has shown that endophagous herbivores, such as gall-forming insects, tend to have relatively low variability in population size through time, even as they often have very high variability in numbers among plant individuals (Price 2003). This stability has been hypothesized to be a result of contest competition among endophagous herbivores for a limited number of high-quality oviposition sites (Price 1994). In contrast, many Lepidoptera species exhibit outbreaking or cyclical dynamics, in which they fluctuate between low densities and densities high enough to defoliate their hosts (Myers & Cory 2013). From the plant perspective, delayed inducible responses to herbivory have been hypothesized to be a key plant trait that contributes to such fluctuations in density and damage (e.g., Haukioja 1980). This is supported by a theory showing that lagged density dependence leads to variance in population size over time, but the role of delayed inducible plant resistance in herbivore population cycles has been empirically difficult to pin down. Elder et al. (2013) nicely demonstrate how experimental characterization of

induction can be combined with models to infer effects of induction on insect herbivore outbreaks. More work that combines data on variation with mechanistic models would be useful.

It would be natural to assume that distributions of herbivory among plants should reflect underlying plant trait distributions or the aggregative tendency of herbivores. For example, there is substantial variance in plant traits within populations (Siefert et al. 2015), and the shapes of trait distributions can vary across abiotic gradients (Asner et al. 2017). Although the correlation between herbivory and traits is thought to be important, it is often surprisingly weak (Carmona et al. 2010), as is the correlation between insect preference and offspring performance (Gripengberg et al. 2010). These discrepancies could be due to the dynamic nature of plant–herbivore interactions, including inducible resistance and plant–plant communication, which can create feedback between plant traits and herbivory, making the distribution of plant traits changeable over time. The distribution of herbivory should also be influenced by herbivore movement, and when herbivores are mobile, the distribution of herbivores at a particular time may not correspond with the pattern of herbivory that accumulates over time. Aggregations of newly hatched insects may cause less herbivory than a few large individuals, and insects that move to track particular plant traits or ontogenetic stages may be aggregated at any one point in time and yet distribute damage evenly among plants over time (e.g., Underwood et al. 2005). Importantly, the distribution of herbivory among plants should also be influenced by stochasticity. Even if all plants in a population had the same traits and same microenvironments, chance would likely lead to differences in damage among plants, and the distribution of that damage would likely not be even.

Although herbivores themselves are typically aggregated—on particular host plants or in herds—we know surprisingly little about the distribution of their damage. Very few studies report the shapes of the distributions of traits or damage per plant on a random sample of plants. One of the very few such studies reports distributions of herbivore damage across kelp at several spatial scales, finding that damage by isopods is highly aggregated at all scales (Poore et al. 2014). Most studies of differences in means, especially more recent ones, report uncertainty around those means (e.g., Bach 1981), and in some cases one could use the uncertainty to infer information about the damage distributions. For example, Moyes et al. (2000) report *Brassica* damage means and standard errors for multiple populations; because the standard errors are larger than the means and damage must be non-negative, we can infer that the distribution of damage must be aggregated. Some studies report measures of spatial distribution of damage among plants such as Moran's *I* (Hagen & Suchant 2020, Hakes & Cronin 2011). Spatial autocorrelation cannot be used to infer the full distribution of damage among plants, but it does show variation at the scale of patches within a population. Several studies report mean, variance, and skew for immobile herbivores, such as gall makers (Egan & Ott 2007, Wetzel 2014) and leaf miners (Faeth 1990), with herbivores highly aggregated on some plants relative to others. For these sessile herbivores the distribution of herbivory should largely mirror the distribution of the herbivores.

## 4.2. Consequences of the Distribution of Herbivory Among Plants Within a Population

Variance and skew in the distribution of herbivores are thought to have a major influence on ecology. Herbivore aggregation can stabilize population dynamics by providing plants with refuges from overexploitation (Hassell & May 1974), reducing the probability of large cycles or extinction (Crawley 1983). Variance and skew in the vital rates and density dependence herbivores experience among plants can also influence herbivore population dynamics (Agrawal et al. 2004, Helms & Hunter 2005, Underwood 2007, Wetzel 2014) in ways that likely feed back to influence plant population dynamics and evolution. When herbivores are distributed unevenly across plants with different traits, the average conditions herbivores experience will not be the same as the average

plant phenotype. This is important because it means that the average plant within a habitat—and ecologists often characterize habitats by their average resource quality—may not be relevant for herbivore dynamics. Instead, the rare plant individuals that disproportionately support herbivores may drive herbivore dynamics (Helms & Hunter 2005, Valladares & Lawton 1991, Wetzel & Strong 2015). In some cases, aggregation helps herbivores overcome plant defenses by overwhelming individuals with high levels of attack (Fordyce 2003), while in others aggregation increases the importance of local density dependence (Mutz & Inouye 2023, Ray & Hastings 1996, Wetzel 2014). Indeed, variation in herbivory may be one answer to the conundrum of why the world is green despite the voracious appetite of its herbivores (Hairston et al. 1960). Perhaps herbivore damage is concentrated in spatiotemporal hotspots in a way that limits herbivore density and the ability of herbivores to exploit all theoretically available plant tissue.

The shapes of distributions of herbivory within plant populations are also likely to have major evolutionary consequences. Theory indicates that right skew in plant fecundity distributions speeds selection (Wilson & Levin 1986), suggesting that skewed effects of herbivores on plant fitness could influence plant defense evolution. Furthermore, theory suggests that the strength of selection (e.g., on plant resistance traits) is a concave-down, nonlinear function of interaction strength (e.g., amount of herbivory) at low mean interaction strengths (Benkman 2013). Given that mean herbivory is typically low (Turcotte et al. 2014), herbivory variability should generally reduce the strength of selection via Jensen's inequality (see the sidebar titled *Theoretical Mechanisms by Which Variability Can Influence Response Variables*), slowing plant evolutionary responses to herbivores. This implies that plant evolutionary responses to herbivores should be relatively slow in environments with low mean damage but high variability in herbivory, and relatively fast in environments with high mean and low variability in herbivory, such as might be found at low latitudes.

The shape of the distribution of herbivore attack could also influence the coexistence of alternative plant defense strategies within species. Higher variance or skew in herbivore attack could facilitate the coexistence of genotypes with resistance and tolerance strategies. If herbivores aggregate on tolerant genotypes (leading to high skew), they may spill over onto resistant genotypes, equalizing fitness differences and promoting coexistence (Tuomi & Augner 1993). The presence of tolerant plant genotypes with low resistance could even subsidize the herbivore population, increasing herbivore density and leading to further spillover onto resistant genotypes. Variance in herbivore pressure could also select for plant–plant communication among close relatives or eavesdropping among nonrelatives, as plants would benefit from information about herbivory on neighbors, if that information has some predictive value (Karban 2021, Karban et al. 2013).

## 5. VARIABILITY ACROSS POPULATIONS AND COMMUNITIES

Examining variability across populations and communities requires adopting a metapopulation or landscape perspective, and then quantifying variation among populations or communities within that broader context. Identifying the causes or consequences of variability means zooming out even more to examine how differences in the amount of variation among metapopulations influence ecology and evolution. In general, work at this scale has examined variation in single metapopulations or landscapes but has not asked what leads to higher or lower levels of among-population variability or revealed the consequences of variability at that scale.

### 5.1. Patterns and Causes of Variation Across Populations and Communities

The strength and characteristics of plant–herbivore interactions vary across populations and communities, with many systems exhibiting geographic mosaics of ecological and evolutionary outcomes (Muola et al. 2010, Thompson 2005). The geographic mosaic theory suggests that hot

spots and cold spots in the strength of interactions drive trait (co)evolution (Thompson 2005). This theory led to the prediction that plant defense traits and herbivore counter-defense traits should covary at landscape scales; multiple studies have uncovered such a pattern. For example, geographic variation across populations in production of furanocoumarins in wild parsnip (*Pastinaca sativa*) and detoxification ability by the parsnip webworm (*Depressaria pastinacella*) showed phenotypic matching [i.e., co-occurrence of plant toxin and insect detoxification traits (Zangerl & Berenbaum 2003)]. Another example found that the relative abundance of two aphid species that have different effects on *Arabidopsis thaliana* drove the evolution of a polymorphic defense gene among geographically separated populations (Zust et al. 2012).

One important feature of spatial variability not considered by geographic mosaic theory is that herbivory often varies predictably across populations along environmental gradients (Hahn & Maron 2016, Moreira et al. 2018). For example, plant populations in more productive sites (e.g., fertile soil or longer growing seasons) tend to accrue higher amounts of herbivore damage (Hahn & Maron 2016). Seed and flower herbivory on the shrub *Haplopappus squarrosus* declines from 70% along California's productive, coastal region to 40% in its mountain populations (Louda 1982). Low herbivory translates into greater plant abundance at high elevations, compared to coastal sites, despite better plant performance at coastal sites when herbivores were excluded (Louda 1982). Similarly, across populations of the plant *Monarda fistulosa*, predispersal seed predation varied from as low as 10% in dry intermountain grassland populations to more than 75% damage in mesic tallgrass prairie populations (Hahn et al. 2021). Numerous additional studies clearly document strong variation in mean herbivory across populations distributed along environmental gradients (Anstett et al. 2016, Hahn & Maron 2016). Given the substantial variation in mean herbivory documented across environmental gradients, it stands to reason that variability and other features of among-population distributions could vary too, though empirical data are lacking.

Beyond geographic mosaics, one of the best-documented dimensions of variability at the metapopulation scale is synchrony of population dynamics (Peltonen et al. 2002). Ecologists have long been fascinated by species and metapopulations with high temporal variability—such as population cycles or outbreak dynamics—and high synchrony in those dynamics across subpopulations (i.e., low spatial variability) even across thousands of kilometers (Liebhold et al. 2004). General causes of this pattern of variability have been difficult to establish, but empirical examples of synchrony and differences in synchrony abound. For example, Liebhold et al. (2012) contrast the spongy moth (*Lymantria dispar*), which synchronously defoliates thousands of hectares of eastern US forests in outbreak years, with the fall webworm moth (*Hyphantria cunea*), which only ever defoliates locally, minimizing the spatial scale of its damage. The autumnal moth (*Epirrita autumnata*) exhibits variation in synchrony, cycling from low densities to outbreaks that can cause total defoliation and significant mortality of birch forests over hundreds of kilometers in the Arctic, but not farther south (Ruohomäki et al. 2000). From the plant perspective, masting—synchrony in seed production—leads to substantial variation across years with large consequences for animal populations and plant–herbivore interactions (Pearse et al. 2016). One well-studied example is the California blue oak (*Quercus douglasii*), which can produce from zero to more than 100,000 acorns per tree, with production correlated at distances at least up to 800 km within years (Koenig & Knops 2005). Escaping herbivory through herbivore satiation is thought to be a key cause of masting (Crawley & Long 1995, Koenig & Knops 2005, Pearse et al. 2016).

## 5.2. Consequences of Differing Levels of Variation Among Populations and Communities

The substantial differences in interpopulation variability that have been documented across many systems are likely to have major ecological and evolutionary consequences. Applying distributional

thinking to the geographic mosaic framework, we hypothesize that plant–herbivore systems in landscapes with short growing seasons (e.g., high latitude systems) will have more variation among populations because herbivores with short time horizons will concentrate their feeding on the first acceptable populations they find. In contrast, herbivores in systems with longer seasons (e.g., many tropical systems), and potentially more generations per year, will have more time for dispersal and invest more in searching, leading to more even damage distributions across populations. The diversity, abundance, and specialization of herbivores in the tropics compared to temperate regions (Dyer et al. 2007, Endara et al. 2023, Forister et al. 2015) could reinforce this pattern of tropical evenness by increasing the probability that every plant population is colonized by at least one of its herbivore species. In temperate systems, a less diverse community may result in increased probability of a single population harboring high insect abundance and damage. Similarly, high synchrony in population dynamics, combined with dispersal and gene flow (hypothesized to be a main driver of synchrony), should lead to consistent herbivore selection regimes across populations and potentially a lack of herbivore-mediated divergence in defense traits among plant populations. Indeed, Endara et al. (2023) argue that herbivore specialization and diversity in the tropics lead to divergence in plant defense traits among co-occurring close relatives, whereas herbivore generalism (and preference for rare plants) at higher latitudes leads communities to be dominated by plants with more similar defense phenotypes, leading to lower community trait variability within a site.

Incorporating variability into plant defense hypotheses may improve our understanding of how herbivory shapes the evolution of plant defense. For example, the resource availability hypothesis, one of the most well-supported plant defense hypotheses, predicts that species growing in resource-poor habitats should evolve slow growth rates and high levels of defense to protect their valuable leaf tissue from herbivores. Species growing in high-resource environments, in contrast, should evolve fast growth rates but low defenses because they can rapidly replace (i.e., tolerate) tissue lost to herbivores (Coley et al. 1985, Endara & Coley 2011). The hypothesis was originally conceived assuming that herbivore pressure is solely a function of plant defense and does not vary among habitats for other reasons. It also assumed a linear relationship between tissue lost to herbivores and growth rate; empirical studies contradict both these assumptions. As described above, herbivory is highly variable across populations and the relationship between herbivory and plant fitness is often nonlinear, with some species displaying concave-up and others concave-down relationships (Islam & Crawley 1983, Marquis 1984). Variation in herbivore pressure among populations, either in mosaics or across gradients, could lead to a new optimal defense level for each resource availability level. Additionally, relaxing the assumption of a linear relationship between damage and plant fitness could capture how herbivory variability alters the optimal defense level via nonlinear averaging (see the sidebar titled Theoretical Mechanisms by Which Variability Can Influence Response Variables). For example, locations with predictably low levels of herbivory should favor plant species that allocate more toward growth and reproductive capacity. However, in locations with low average herbivory but high variability, the evolutionary responses of plants may depend on how tolerant of damage a plant is. A highly tolerant species would not need to allocate energy to resistance, whereas a highly intolerant species should err on the side of allocating to resistance to protect itself in the rare but costly event of herbivory (Orrock et al. 2015). Given the empirical evidence of nonlinear fitness–herbivory relationships and the prevalence of tolerance (in which plants experience no fitness effects of low levels of herbivory, thus creating a nonlinearity), this suggests an important but underappreciated role for herbivory variability in determining optimal levels of defense across resource gradients.

## 6. FUTURE DIRECTIONS

Our consideration of variability in plant–herbivore interactions highlights four suggested future directions. First, we invite researchers to consider more explicitly the complex sources of variability in plant–herbivore interactions, including both deterministic and stochastic processes. The study of herbivory has focused a great deal on how and why plant defense traits differ at many scales, and how these traits can affect and respond to herbivores. Most foundational hypotheses attempting to explain differences in herbivory—among biomes, species, individuals, or plant parts—have focused on trade-offs between the benefits and costs of defense allocation, and assumed for the most part that herbivore pressure is a constant. However, we know that herbivory is a dynamic—and inherently variable—process shaped by plants, herbivores, and their environments. We also need more information on the structure of stochastic sources of variation in herbivory, including environmental and demographic stochasticity (Shoemaker et al. 2020). Considering which sources of variation are most important for the herbivores in a given system will be essential to better predict the dynamic nature of plant–herbivore interactions and is likely to lead to a next generation of foundational plant–herbivore hypotheses that explicitly incorporate variability.

Second, to understand the consequence of variability, it is essential that we acknowledge and capture the nonlinear nature of relevant biological relationships. For example, the relationships between herbivore damage levels and plant fitness, and between plant defense levels and herbivore population growth, are surprisingly poorly characterized, despite being central to plant–herbivore biology. Measuring the shapes of these functions can be logistically challenging but is not impossible (Underwood 2010, Wetzel et al. 2016). These data are essential because the extent to which variability matters for ecology and evolution depends strongly on the extent of nonlinearity in these functions (Bolnick et al. 2011) (see the sidebar titled *Theoretical Mechanisms by Which Variability Can Influence Response Variables*).

Third, theory indicates that the consequences of variation become increasingly important as processes transition across scales, from individuals to communities (Chesson 2012), but hypotheses in plant–herbivore interactions rarely tackle the issue of scale directly. For example, researchers have often assumed that what is optimal for a plant individual will tell us about macroevolutionary patterns, yet we know little about the complexity that arises when biological processes scale from interactions over a growing season to lifetime fitness to natural selection to macroecological and macroevolutionary patterns. Accounting for this complexity will require biologists to embrace and extend statistical approaches that can account for the nonindependence of processes across scales. We should also work to extend mathematical models of plant–herbivore interactions to explicitly address links across multiple scales. Linking data collected at smaller scales to hypotheses about interactions and dynamics at larger scales remains an important, and challenging, goal for ecology.

Finally, we urge researchers to record and report measures of variation in herbivory over a range of spatial and temporal scales. Large sample sizes from randomly selected units are essential to adequately understand the extent of variability and estimate distributions. Distributions of herbivory are often likely to be skewed, and adequately capturing the extremes of a skewed distribution requires larger sample sizes compared to estimates of means. Repeated sampling through time is also essential, given that herbivores and plants are dynamic, and the distribution measured at one time might not be representative of their interactions across their lifetimes. Our searching of the literature revealed many cases where researchers report differences in means, without sufficient information to reconstruct full distributions of interactions, traits, or densities. As public archiving of data becomes the norm, it will become easier to recalculate metrics of variation. However, simply including full distributions in plots (i.e., histograms and density plots) or reporting distribution parameters such as variance, skew, and kurtosis within the main text of a paper



will increase opportunities for distributional thinking and foster opportunities for novel insights in plant–herbivore interactions.

## 7. CONCLUSIONS

The key role of variability in shaping biological outcomes has become increasingly apparent across broad subfields in ecology and evolutionary biology. For example, in physiological ecology, variability in abiotic factors interacts with nonlinear fitness functions to shape performance (Ruel & Ayres 1999); in disease ecology, variability in pathogen transmission influences outbreak dynamics (Lloyd-Smith et al. 2005, Paull et al. 2012); and in population ecology, variability in local densities interacts with nonlinear population growth to determine local and regional dynamics (Abbott & Nolting 2017, Inouye 2005a, Melbourne & Chesson 2005, Underwood 2004). However, our understanding of the role of variability in shaping plant–herbivore interactions and their consequences has lagged. We hope this overview will stimulate expanded efforts to describe patterns of variation in herbivory through data collected across scales from leaf-to-leaf to biome-to-biome and an iterative interaction between data and theory that will refine our understanding of the drivers and consequences of variability for ecology and evolution. Considering the foundational importance of plants and herbivores for ecosystems (Schmitz 2008), embracing variability and distributional thinking should provide a fresh perspective that greatly enhances the explanatory power of highly variable and context-dependent species interactions.

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# Contents

## I. Integrative Themes and Emerging Concerns

- 30×30 for Climate: The History and Future of Climate  
Change–Integrated Conservation Strategies  
*L. Hannab and G.F. Midgley* ..... 1
- Exploring Alternative Futures in the Anthropocene  
*Steven Cork, Carla Alexandra, Jorge G. Alvarez–Romero, Elena M. Bennett,  
Marta Berbés–Blázquez, Erin Bohensky, Barbara Bok, Robert Costanza,  
Shizuka Hashimoto, Rosemary Hill, Sohail Inayatullah, Kasper Kok,  
Jan J. Kuiper, Magnus Moglia, Laura Pereira, Garry Peterson, Rebecca Weeks,  
and Carina Wyborn* ..... 25
- Plastics and the Environment  
*I.E. Napper and R.C. Thompson* ..... 55
- Toward Zero–Carbon Urban Transitions with Health, Climate  
Resilience, and Equity Co–Benefits: Assessing Nexus Linkages  
*Anu Ramaswami, Bhartendu Pandey, Qingchun Li, Kirti Das, and Ajay Nagpure* ..... 81

## II. Earth’s Life Support Systems

- Harmful Cyanobacterial Blooms: Biological Traits, Mechanisms, Risks,  
and Control Strategies  
*Lirong Song, Yunlu Jia, Boqiang Qin, Renhui Li, Wayne W. Carmichael,  
Nanqin Gan, Hai Xu, Kun Shan, and Assaf Sukenik* ..... 123
- Pushing the Frontiers of Biodiversity Research: Unveiling the Global  
Diversity, Distribution, and Conservation of Fungi  
*Tuula Niskanen, Robert Lücking, Anders Dahlberg, Ester Gaya,  
Laura M. Suz, Vladimir Mikryukov, Kare Liimatainen, Irina Druzhinina,  
James R.S. Westrip, Gregory M. Mueller, Kelmer Martins–Cunha, Paul Kirk,  
Lebo Tederso, and Alexandre Antonelli* ..... 149
- Soils as Carbon Stores and Sinks: Expectations, Patterns, Processes,  
and Prospects of Transitions  
*Meine van Noordwijk, Ermias Aynekulu, Renske Hijbeek, Eleanor Milne,  
Budiman Minasny, and Danny Dwi Saputra* ..... 177

Understanding Fire Regimes for a Better Anthropocene <i>Luke T. Kelly, Michael-Shawn Fletcher, Imma Oliveras Menor, Adam F.A. Pellegrini, Ella S. Plumanns-Pouton, Pere Pons, Grant J. Williamson, and David M.J.S. Bowman</i> .....	207
---	-----

### III. Human Use of the Environment and Resources

Deforestation-Free Commodity Supply Chains: Myth or Reality? <i>Eric F. Lambin and Paul R. Furumo</i> .....	237
Great Green Walls: Hype, Myth, and Science <i>Matthew D. Turner, Diana K. Davis, Emily T. Yeh, Pierre Hiernaux, Emma R. Loizeaux, Emily M. Fornof, Anika M. Rice, and Aaron K. Suiter</i> .....	263
Mapping Industrial Influences on Earth's Ecology <i>James E.M. Watson, Erle C. Ellis, Rajeev Pillay, Brooke A. Williams, and Oscar Venter</i> .....	289
Mitigation of Concurrent Flood and Drought Risks Through Land Modifications: Potential and Perspectives of Land Users <i>Lenka Slavíková and Anita Milman</i> .....	319
Surveying the Evidence on Sustainable Intensification Strategies for Smallholder Agricultural Systems <i>Meha Jain, Christopher B. Barrett, Divya Solomon, and Kate Gbezzi-Kopel</i> .....	347
Brine: Genesis and Sustainable Resource Recovery Worldwide <i>Chenglin Liu, Tim K. Lowenstein, Anjian Wang, Chunmiao Zheng, and Jianguo Yu</i> .....	371
Groundwater Quality and Public Health <i>Xianjun Xie, Jianbo Shi, Kunfu Pi, Yamin Deng, Bing Yan, Lei Tong, Linlin Yao, Yiran Dong, Junxia Li, Liyuan Ma, Chunmiao Zheng, and Guibin Jiang</i> .....	395
The Global Technical, Economic, and Feasible Potential of Renewable Electricity <i>Nils Angliviél de La Beaumelle, Kornelis Blok, Jacques A. de Chalendar, Leon Clarke, Andrea N. Habmann, Jonathan Huster, Gregory F. Nemet, Dhruv Suri, Thomas B. Wild, and Inês M.L. Azevedo</i> .....	419
The State of the World's Arable Land <i>Lennart Olsson, Francesca Cotrufo, Timothy Crews, Janet Franklin, Alison King, Alisher Mirzabaeov, Murray Scown, Anna Tengberg, Sebastian Villarino, and Yafei Wang</i> .....	451

#### IV. Management and Governance of Resources and Environment

Environmental Decision-Making in Times of Polarization <i>Madeline Judge, Yoshibisa Kashima, Linda Steg, and Thomas Dietz</i> .....	477
Implications of Green Technologies for Environmental Justice <i>Parth Vaishnav</i> .....	505
The Commons <i>Arun Agrawal, James Erbaugh, and Nabin Pradhan</i> .....	531
Governance and Conservation Effectiveness in Protected Areas and Indigenous and Locally Managed Areas <i>Yin Zhang, Paige West, Lerato Thakholi, Kulbushansingh Suryawanshi, Miriam Supuma, Dakota Straub, Samantha S. Sithole, Roshan Sharma, Judith Schleicher, Ben Ruli, David Rodríguez-Rodríguez, Mattias Borg Rasmussen, Victoria C. Ramenzoni, Siyu Qin, Deborah Delgado Pugley, Rachel Palfrey, Johan Oldekop, Emmanuel O. Nuesiri, Van Hai Thi Nguyen, Noubou Ndam, Catherine Mungai, Sarah Milne, Mathew Bukhi Mabele, Sadie Lucitante, Hugo Lucitante, Jonathan Liljeblad, Wilhelm Andrew Kiwango, Alfred Kik, Nikoleta Jones, Melissa Johnson, Christopher Jarrett, Rachel Sapery James, George Holmes, Lydia N. Gibson, Arash Ghoddousi, Jonas Geldmann, Maria Fernanda Gebara, Thera Edwards, Wolfram H. Dressler, Leo R. Douglas, Panayiotis G. Dimitrakopoulos, Veronica Davidov, Eveline M.F.W. Compaoré-Sawadogo, Yolanda Ariadne Collins, Michael Cepek, Paul Berne Burow, Dan Brockington, Michael Philippe Bessike Balinga, Beau J. Austin, Rini Astuti, Christine Ampumuza, and Frank Kwaku Agyei</i> .....	559
Sustainability Careers <i>Christopher G. Boone, Erin Bromaghim, and Anne R. Kapuscinski</i> .....	589
Three Decades of Climate Mitigation Policy: What Has It Delivered? <i>Janna Hoppe, Ben Hinder, Ryan Rafaty, Anthony Patt, and Michael Grubb</i> .....	615
Overheating of Cities: Magnitude, Characteristics, Impact, Mitigation and Adaptation, and Future Challenges <i>Jie Feng, Kai Gao, H. Khan, G. Ulpiani, K. Vasilakopoulou, G. Young Yun, and M. Santamouris</i> .....	651
Risks to Coastal Critical Infrastructure from Climate Change <i>Indrajit Pal, Anil Kumar, and Anirban Mukhopadhyay</i> .....	681
US Legal and Regulatory Framework for Nuclear Waste from Present and Future Reactors and Their Fuel Cycles <i>Sulgiye Park and Rodney C. Ewing</i> .....	713

## V. Methods and Indicators

### Metrics for Decision-Making in Energy Justice

*Erin Baker, Sanya Carley, Sergio Castellanos, Destenie Nock,  
Joe F. Bozeman III, David Konisky, Chukwuka G. Monyei,  
Monisha Shah, and Benjamin Sovacool* ..... 737

### Modeling Low Energy Demand Futures for Buildings: Current State and Research Needs

*Alessio Mastrucci, Leila Niamir, Benigna Boza-Kiss, Nuno Bento,  
Dominik Wiedenhofer, Jan Streeck, Shonali Pachauri, Charlie Wilson,  
Souran Chatterjee, Felix Creutzig, Srihari Dukkupati, Wei Feng,  
Arnulf Grubler, Joni Jupesta, Poornima Kumar, Giacomo Marangoni,  
Yamina Sabeel, Yoshiyuki Shimoda, Bianka Shoai-Tebrani, Yobei Yamaguchi,  
and Bas van Ruijven* ..... 761

### Advances in Qualitative Methods in Environmental Research

*Holly Caggiano and Elke U. Weber* ..... 793

### Attribution of Extreme Events to Climate Change

*Friederike E.L. Otto* ..... 813

## Indexes

Cumulative Index of Contributing Authors, Volumes 39–48 ..... 829

Cumulative Index of Article Titles, Volumes 39–48 ..... 838

## Errata

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