From Individuals to Networks: The Role of Variation in Plant-Pollinator Communities' Responses to Global Change

James DeWitt Crall[1], Marilia Palumbo Gaiarsa[2]

1. Department of Entomology
   College of Agricultural and Life Sciences
   University of Wisconsin-Madison
   1630 Linden Drive
   Madison, Wisconsin, USA, 53706
2. Life and Environmental Sciences Department
   School of Natural Sciences
   University of California, Merced
   5200 Lake Road
   Merced, California, USA, 95343

* Corresponding authors: e-mail: james.crall@wisc.edu; mgaiarsa@ucmerced.edu * ORCID Ids: JDC: 0000-0002-8981-3782; MPG: 0000-0003-4414-472X * Authors contributed equally to all components of this work *The authors have no conflicts of interest to declare

Abstract

1. Plant–pollinator communities are critical for biodiversity, ecosystem function, and human well-being. Yet our ability to predict divergent species responses to environmental change, the risk of abrupt collapse, or the potential for recovery in plant-pollinator systems remains limited.

2. Here, we argue that individual variation within species may play a critical but underappreciated role in shaping the sensitivity, robustness, and resilience of animal pollinators and plant-pollinator communities.

3. We explore processes by which individual variation may influence responses to perturbation, highlighting parallels with existing niche theory at the species level (e.g., the biodiversity-ecosystem function (BEF) literature). We suggest that individual variation—as a key but distinct component of total intraspecific variation—may generate more gradual (rather than abrupt) responses to environmental stress than predictions based on species means in many cases, but that these effects will depend on how traits underlying performance, interaction frequency, stress sensitivity, and pollination efficacy covary among individuals.

4. Finally, we highlight critical knowledge gaps and open questions in the structure and dynamics of plant-pollinator interactions at the individual scale and conclude by outlining a roadmap for integrating individual variation into studies of plant-pollinator communities under global change.

1 Introduction

"*No one supposes that all the individuals of the same species are cast in the same actual mould. These individual differences are of the highest importance for us, for they are often inherited, as must be familiar to every one; and they thus afford materials for natural selection to act on and accumulate.*" (Darwin, 1859)

Plant–pollinator interactions underpin the maintenance of terrestrial biodiversity and ecosystem function. Pollination mediates reproduction in most flowering plants and supports the stability and quality of yields for many crops important to human diets and livelihoods (Klein *et al.*, 2007; Ollerton *et al.*, 2011). Predicting if or when plant-pollinator communities might collapse in response to rapidly changing environmental conditions is crucial for conserving biodiversity and supporting human well-being (Potts *et al.*, 2010; Timberlake *et al.*, 2026). Despite the emergence of plant-pollinator systems as a model for the ecology of mutualistic networks in recent decades, our ability to predict the impacts of rapid environmental change on pollinators—and the consequences for ecological communities or ecosystem services—remains limited (Bascompte & Scheffer, 2023; Peralta *et al.*, 2024a). Among pollinators, closely related or apparently similar species show markedly divergent responses to environmental change, creating patterns of 'winners and losers' (Jackson *et al.*, 2022). Yet what makes some taxa resilient and others susceptible to different extinction drivers remains poorly understood. At the same time, understanding and possibly predicting the risk of collapse in plant–pollinator systems (e.g., 'tipping points' (Huang *et al.*, 2021)), the pace of decline after critical thresholds are exceeded, and the potential for recovery after disturbance are well-recognized challenges of paramount importance. However, empirical evidence for such critical thresholds remains largely theoretical (Burkle *et al.*, 2013; Lever *et al.*, 2014), and we have only a limited understanding of factors underlying tolerance to environmental change. Understanding the mechanisms underlying sensitivity and resilience to environmental change is key to accurately predicting and effectively mitigating the effects of global environmental change on biodiversity, while also identifying ‘safe operating spaces’ that maintain stable pollination services and human well-being (Steffen *et al.*, 2015; Timberlake *et al.*, 2026).

Individual variation within species can shape sensitivity to perturbation and capacity for rewiring and recovery (Cantwell-Jones *et al.*, 2024) and may be critical to addressing these knowledge gaps, yet has received limited attention in the literature on plant-pollinator interactions. More than 150 years ago, Darwin recognized the importance of within-species variation in driving evolution. This emphasis on variation among individuals marked a fundamental departure from the Linnaean focus on differences between discrete groups (i.e., species), but despite Darwin‘s early emphasis on variation, modern ecological theory has focused primarily on mean differences between species. Recent years, however, have reignited the emphasis on individual-level variation, recognizing its ubiquity (Bolnick *et al.*, 2003; Des Roches *et al.*, 2018; Sih *et al.*, 2004)—arising even in the absence of genotypic or environmental variation (Ayroles *et al.*, 2015; de Bivort, 2025)—and impact on ecological and evolutionary processes (Cantwell-Jones *et al.*, 2024; Gamelon *et al.*, 2025; Gomez & Perfectti, 2012; Violle *et al.*, 2012) from collective performance in social animals (Jolles *et al.*, 2020; Oster & Wilson, 1978) to species interactions (Bolnick *et al.*, 2003; Gaiarsa *et al.*, 2022; Guimarães, 2020). In parallel, the increasing dominance of global environmental change has shown the limits of the classical, static view of ecological systems under equilibrium conditions, shifting the emphasis toward understanding how species and communities respond to—and recover from—perturbations. A key challenge arising from this shift is identifying traits that promote robustness and resilience to environmental change, ranging from gene expression and regulatory networks (Vitousek *et al.*, 2025) to species and ecological communities (Bascompte & Scheffer, 2023; Hernández-Carrasco *et al.*, 2025; Inouye *et al.*, 2021). Here, we suggest that continued expansion of research on individual variation may help identify trait-based mechanisms that buffer sensitivity or promote resilience to environmental change, while also shedding light on the ecological and evolutionary forces that produce phenotypic variation within species in the first place (Des Roches *et al.*, 2018).

In pollinators, individuals vary substantially within species in key phenotypes including morphology (Couvillon & Dornhaus, 2010), physiology (Pimsler *et al.*, 2020), and behavior and cognition (Chittka *et al.*, 2003). Phenotypic variation underlies species' ecological niches and shapes plant-pollinator interactions (Junker *et al.*, 2013), such as tongue length driving visitation frequency in bees (Peat *et al.*, 2005) and moths (Haverkamp *et al.*, 2016) *via* trait matching (Klumpers *et al.*, 2019), and wing shape impacting dispersal in butterflies (Breuker *et al.*, 2007). While few studies have explicitly linked intraspecific variation to ecological resilience in plant-pollinator networks, the existing evidence suggests important potential effects. For example, across bumblebees (*Bombus* spp) species with higher variation in body size are more likely to have stable or increasing population size under anthropogenic environmental change (Austin & Dunlap, 2019). At the community level, the degree of niche complementarity and functional redundancy among individuals may influence species coexistence and community dynamics across different perturbation scenarios (Hart *et al.*, 2016; Poisot *et al.*, 2015; Tur *et al.*, 2014).

Despite its potential to influence ecological sensitivity and resilience (Fig. 1; Cantwell-Jones *et al.* 2024; Guimarães 2020), few studies to date have explored the role of individual variation in shaping the responses of plant-pollinator communities to anthropogenic change, let alone identified underlying mechanisms. Here, we explore the growing empirical evidence for individual variation in plant-pollinator communities (Arroyo-Correa *et al.*, 2025; Cantwell-Jones *et al.*, 2024; Gaiarsa *et al.*, 2022; Guimarães, 2020; Peralta *et al.*, 2024b) and consequences for ecological sensitivity and resilience. We focus on pollinators because of robust emerging empirical evidence for individual variation, but include plant examples where appropriate to highlight that these patterns and processes are not restricted to pollinators; our intention is to provide illustrative examples of how and why individual variation matters, rather than provide a comprehensive review. We first synthesize perspectives on how individual variation may influence higher-order characteristics (such as sensitivity, robustness, and resilience) at the population, species, and community scales, drawing parallels with the role of species diversity and niche heterogeneity in ecosystem functioning. We next explore illustrative examples of mechanisms by which individual variation affects the sensitivity, robustness, and resilience of plant-pollinator communities under perturbation. Finally, we identify critical open questions and practical future directions that we hope will spur new focus on understanding the role of individual variation in the resilience of plant-pollinator networks. While we focus here on the effect of niche-based, phenotypic variation on communities' responses to global change as a starting point, plant-pollinator interactions arise from both niche (e.g., trait matching) and neutral processes (e.g., variation in interaction rates driven by population abundance or stochastic fluctuations) (Peralta *et al.*, 2020), and similar dynamics likely occur for neutral processes. We specifically highlight the need to (a) quantify individual variation in empirical systems, (b) identify correlations between phenotypic traits underlying performance at the organismal scale and interaction patterns at the community scale, and (c) leverage emerging technologies and theoretical models to address these urgent knowledge gaps.

2 A framework for linking individual variation to community dynamics

We focus here on how individual variation affects sensitivity, robustness, and resilience at higher levels of biological organization (see Box 1 for operational term definitions used here; (Fig. 2)) (e.g., colonies, populations, species, or communities). This framework parallels the biodiversity–ecosystem function literature, where well-established theoretical and empirical work has demonstrated links between species diversity and the productivity and stability of ecological communities. More species-rich plant communities generally show greater productivity (e.g., biomass production), which may arise through several mechanisms, including niche complementarity (Tilman *et al.*, 2001) or (perhaps more often) sampling effects (diverse communities are more likely to con-

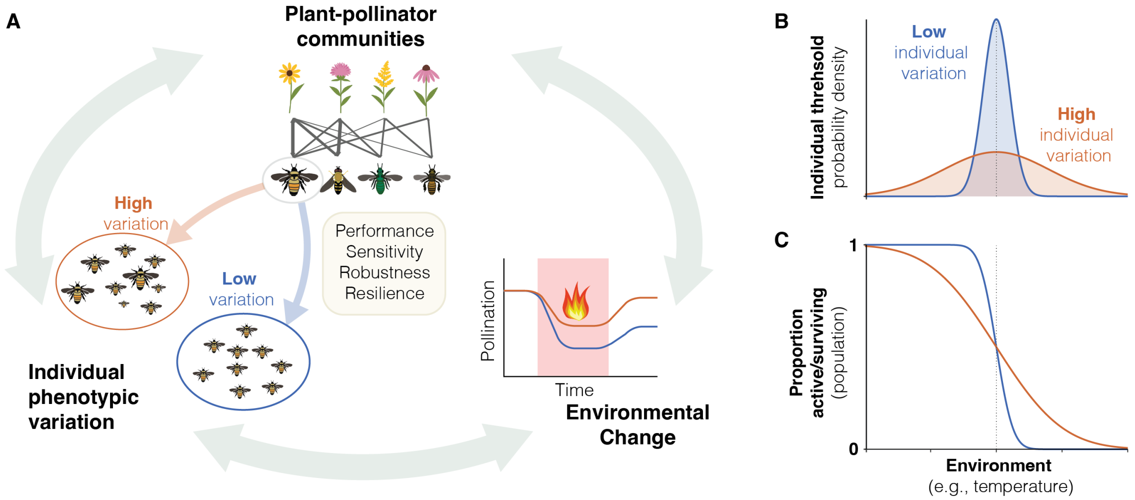

Figure 1: **Linking individual phenotypic variation in plant–pollinator communities to environmental change**. (A) Individual variation in traits affects the performance, sensitivity, robustness, and resilience of plant and pollinator species, ultimately driving population and community responses to environmental change. (B-C) Schematic representation of how trait distributions influence physiological thresholds (e.g., upper thermal limits). (B) Population-scale sensitivity to environmental conditions (e.g., temperature) may have high (orange) or low (blue) individual trait variation. This, in turn, may result in (C) an abrupt cutoff when the threshold is reached in populations with low individual variation (in blue), and a slow decay in populations with high individual variation, suggesting that these populations can withstand greater environmental variation. While here we focus on pollination and population dynamics, this framework can be applied to other scales and aspects of performance. Graphic art of pollinators by Jeremy Hemberger

tain highly productive species; Cardinale *et al.* 2006). Species diversity can also promote stability of ecosystem function (e.g., through biological insurance effects and response diversity; Loreau *et al.* 2021), akin to widening the stability basin (or 'robustness' in our terminology) in Holling's 'ball-and-cup' analogy (Holling *et al.*, 1973).

Analogous to niche variation across species, individual niche complementarity (e.g., the extent to which individuals differ in dietary breadth) and sampling effects (e.g., the probability that a local population contains highly active foragers) may have comparable effects on performance, sensitivity, and resilience at the population scale, opening the potential for 'downscaling' species niche theory to individuals. However, individual variation may also reflect distinct patterns and processes. For example, physiological or phenotypic trade-offs may exist only at the level of individuals and not at higher levels (i.e., colony, population, or species); while foraging bees exhibit trade-offs between speed and accuracy in learning that reflect fundamental neurobiological constraints at the individual level (Chittka *et al.*, 2003), colonies of social species benefit from a diversity of cognitive strategies among workers (Burns & Dyer, 2008). As a result, trade-offs observed at the individual level do not necessarily scale to colonies, populations, or species, and *vice versa*. Thus, diversity-performance relationships established at one scale (such as performance-tolerance tradeoffs that support biodiversity-stability relationships across species (Loreau *et al.*, 2001; Mariotte *et al.*, 2013)) will not necessarily translate down to lower scales (e.g., individuals or colonies). It is thus critical to draw on biodiversity–ecosystem function theory while recognizing potential limitations of directly applying species-level effects to the individual level.

Box 1. Definitions of key terms

The use of key terms varies across the literature and between fields; here, we adopt the following definitions. We define ***individual variation*** as the component of intraspecific variation attributable to differences between individuals (i.e., ***inter-individual variation***, equivalent to the between-individual component of niche variation in Bolnick *et al.* 2003). Total intraspecific variation is thus a summation of ***intra-individual variation*** (e.g., niche breadth within individuals arising from ontogeny, plasticity, or other factors) and *inter-individual variation*. ***Performance*** is the ability of individuals, species, or communities to carry out key ecological functions (such as pollination) under given conditions. ***Sensitivity*** describes the degree to which performance shifts in response to changes in the environment (biotic or abiotic), and can be interpreted as the local slope in a performance vs. environment curve. ***Robustness*** refers to the ability of individuals (or communities) to sustain ecological functions under a range of environmental conditions or stress. ***Resilience*** is the capacity to recover functional performance after disturbance, whether through phenotypic plasticity, reorganization (e.g., interaction rewiring), or compensatory dynamics.

To illustrate the importance of variation among individuals in a population—and how it differs from total intraspecific variation—consider a simple plant-pollinator community composed of three plants and two pollinators, which are highly generalist at the species level (i.e., all pollinator species interact with all plant species; Fig. 3A). Both pollinator species interact similarly with the same plant species, resulting in identical species-level interaction patterns. Yet these similar patterns arise from different individual-level strategies. One pollinator species is composed of individual 'specialists', with low overlap in resource use among individuals, leading to high inter-individual variation, high floral fidelity, and low intra-individual variation. In contrast, the other pollinator species is composed of individual 'generalists', with high overlap in resource use among individuals, leading to low inter-individual variation, low floral fidelity, and high intra-

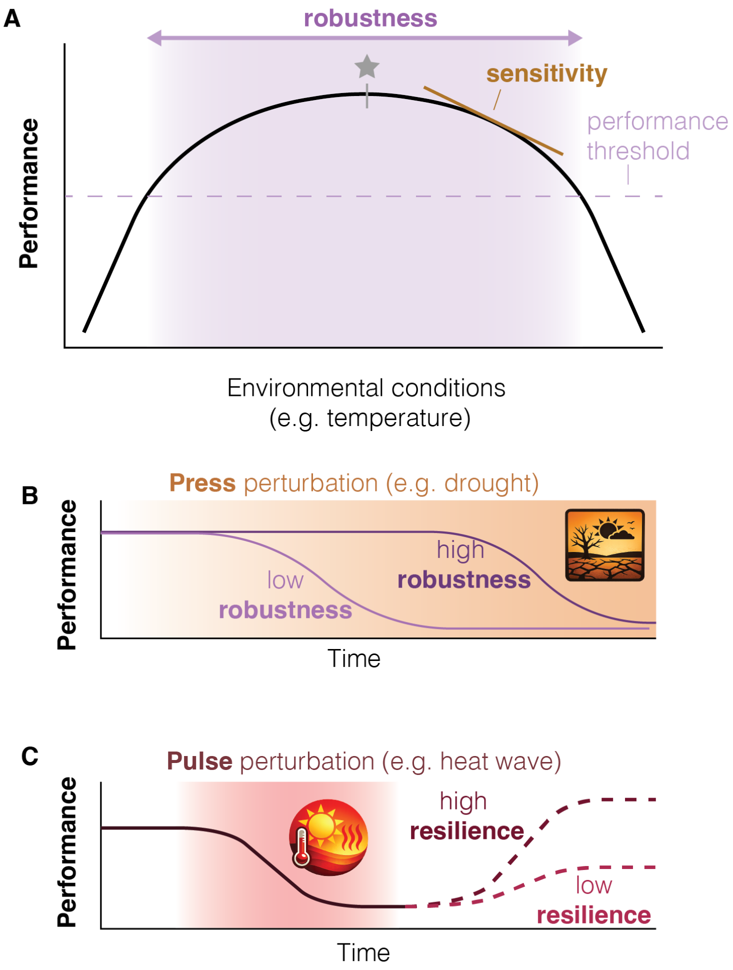

Figure 2: **Conceptual framework for key terms**. (A) Environmental conditions, such as temperature, can affect pollinator performance, including flight capacity and pollination efficiency. Sensitivity is defined as the rate of change in performance with respect to environmental conditions (i.e., the local slope). Robustness is defined as the range of conditions under which performance remains above a relevant threshold, such as the critical thermal minimum and maximum, with more robust populations exhibiting greater tolerance to a wider range of conditions than less robust populations (B). (C) Resilience is defined as the capacity to recover performance after a perturbation. For example, after the critical thermal maximum is temporarily exceeded, populations with high resilience will return to (or potentially exceed) their pre-perturbation performance level more quickly, whereas populations with low resilience will take longer—or may never fully recover. Schematic illustrations in (B) and (C) were generated with OpenAI's DALL-E model.

individual variation (Fig. 3B). These differences in individual-level interaction structure may lead to substantial differences in pollination services (‘performance’). Highly specialized individuals will repeatedly visit flowers of the same plant species, exhibiting high floral fidelity and thereby leading to greater conspecific pollen transfer relative to generalized individuals (Fig. 3C). In this context, perturbations, such as individual mortality, will also have different effects on the two pollinator species. In populations or species composed of individual specialists, interactions could be completely lost, leading to greater sensitivity and potentially lower resilience if dietary preferences are genetically encoded. In contrast, populations composed of individual generalists would show a proportional decrease in interactions until all individuals were lost, reflecting high robustness (potentially at the cost of lower performance; Fig. 3D). These patterns would also translate to key aspects of network structure. For example, networks with species containing individual generalists would retain high connectance (the proportion of all potential species links that are filled in a network) until a rapid collapse of connectance at high population loss (Lever *et al.*, 2014). In contrast, in networks with species containing individual specialists, network-level connectance would be predicted to decline gradually as pollinator populations decline.

3 Individual variation as a driver of plant-pollinator responses to global change

Plant–pollinator communities often show divergent responses to similar environmental perturbations. Here, we build on the framework above to explore how individual variation may help explain this heterogeneity in sensitivity, robustness, and resilience.

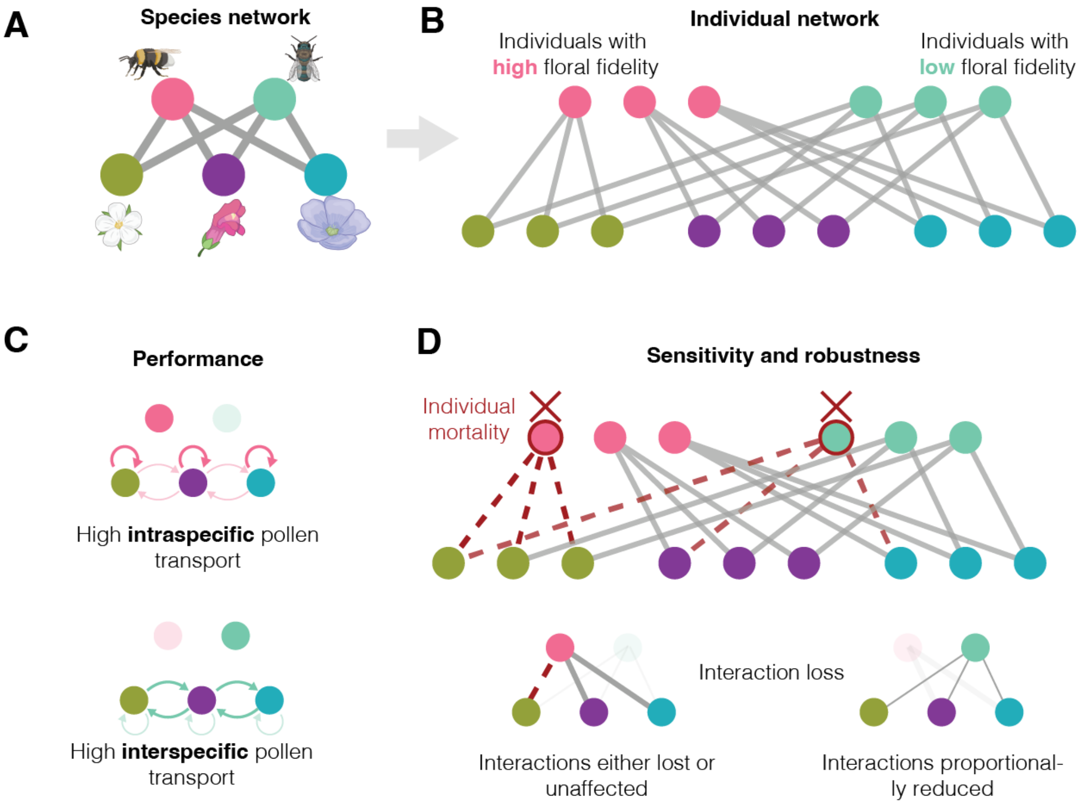

Figure 3: **Linking individual variation to species interactions**. (A) Representative plant-pollinator community and underlying (B) individual-level interactions, reflecting two pollinator species composed of 'specialist' (high floral fidelity) or 'generalist' (low floral fidelity) individuals, and how the resulting (C) pollination service changes based on the predicted pollen transport from different individuals. (D) Individual variation in interaction patterns also affects population responses to the loss of an individual in species-level interactions. Pollinator and flower illustrations in (A) were generated with BioRender.

3.1 Individual variation and sensitivity

Among both plants and pollinators, closely related and ecologically similar taxa are showing strongly divergent responses to global environmental change. For example, in North America, populations of several bumble bee species are stable or increasing, while others are in decline (Jackson *et al.*, 2022). This pattern appears to be linked to morphological variation within species (Austin & Dunlap, 2019), suggesting that individual phenotypic variation may affect the sensitivity of populations and species to environmental change (Des Roches *et al.*, 2018) through distinct mechanisms. Generally, when individual variation in stress susceptibility is low (e.g., in thermotolerance), performance at the population scale is expected to show a strongly nonlinear decline near the population mean tolerance (Fig. 1B, C). In contrast, greater individual variation in susceptibility would yield a consistent decline in performance on either side of the population mean (Fig. 1B). As a result, greater individual variation may 'smooth' population-level sensitivity curves, whereas limited variation could promote more threshold-like responses. Thus, populations with limited individual variation may exhibit a greater tendency toward rapid, threshold-like responses to environmental perturbations, leading to rapid declines in pollination when critical stress levels are reached. This is consistent with recent work showing that low variation in heat sensitivity within insects *(Drosophila)* leads to more abrupt, threshold-like declines in survival near the population-mean tolerance (Bullard *et al.*, 2026).

Individual variation in sensitivity within pollinator species is increasingly well documented; individual pollinators differ markedly in their susceptibility and sensitivity to stressors such as disease (Decanini *et al.*, 2007), temperature variations (Feuerborn *et al.*, 2023), and pesticide exposure (Easton-Calabria *et al.*, 2023). Moreover, variation in body size is widespread and can influence sensitivity to stressors, such as starvation (Couvillon & Dornhaus, 2010) and habitat loss (Bommarco *et al.*, 2010). Intraspecific variation in thermal tolerance also varies across populations (Pimsler *et al.*, 2020) and reproductive caste (Feuerborn *et al.*, 2023). While these patterns highlight the ubiquity of intraspecific variation in stress susceptibility, the links between individual-level variation in susceptibility and tolerance thresholds or sensitivity at the population or species level have not, to our knowledge, been directly tested.

Beyond effects of individual variation on population or species sensitivity, individual variation among pollinators may also influence the sensitivity of communities and species interactions to perturbations (Fig. 3). For example, in social and semi-social bees, division of labor may allow individual foragers to specialize (*via* high floral fidelity) on particular floral resources (Brosi, 2016; Yourstone *et al.*, 2023), while maintaining dietary diversity at the colony scale within species. In contrast, individual solitary bees must acquire the full range of nutrients for their offspring (Filipiak, 2019). Consequently, they often exhibit low flower fidelity, regardless of resource abundance (Bosch & Vicens, 2005; Torchio & Tepedino, 1980; Williams & Tepedino, 2003). As a result, interactions with individual specialists (e.g., in social species) may yield higher mean pollination efficacy but greater sensitivity (Gomez & Perfectti, 2012; Lopes *et al.*, 2022), echoing productivity-stability trade-offs in ecosystem services (Montoya *et al.*, 2019).

3.2 Individual variation and robustness

Predictions that environmental perturbations could drive the rapid collapse of plant–pollinator communities through cascading loss of interactions and coextinction have become a central theme in pollination ecology (Lever *et al.*, 2014; Memmott *et al.*, 2004). Even though the distribution of individual phenotypes within populations has major implications for robustness and coexistence at the species and community scales (Baruah, 2022; Hart *et al.*, 2016, Fig. 4A), empirical evidence for abrupt community-level collapse or the mechanisms shaping robustness across whole plant–pollinator systems remains surprisingly limited. When individual variation is low, and individuals strongly overlap in traits such as thermal optima or dietary breadth, the loss of individuals can lead to proportional declines in population-level performance (Figs. 1B, 4A). In contrast, when trait distribution is highly variable, even random losses can trigger nonlinear, unstable outcomes in population-level pollination performance (Figs. 1C, 4B). Such effects are conceptually similar to ‘sampling effects’ described at the species scale (Cardinale *et al.*, 2006; Lepš *et al.*, 2006). When individual trait variation is high, performance (e.g., pollination) at the population scale may depend disproportionally on a small subset of highly active individuals, a pattern supported by empirical studies of individual bees (Crall *et al.*, 2018; Tenczar *et al.*, 2014).

However, the extent to which individual loss propagates to the community scale depends not only on how performance varies across individuals, but also on how interactions are organized within networks (Fig. 3D). For example, when an individual is removed (Fig. 3D), the consequences for community-level performance depend both on that individual’s interaction pattern and complementarity with other individuals. In our hypothetical community shown in Fig. 3, individual-scale network connectance increases after the loss of individuals (0.33 before individual loss vs. 0.38 after; Figs. 3B and 3D, respectively). Superficially, this increase in connectance could suggest greater redundancy in pollination function and increased robustness (Lever *et al.*, 2014). However, explicitly accounting for the interaction patterns of the removed individuals reveals a disproportionate decline in pollination services for some species (e.g., the green plant in Fig. 3) not only through reduced visitation but also because the remaining (generalist) pollinators predominantly transport large amounts of heterospecific pollen. Thus, although network-level metrics may suggest improved system performance, individual-level contributions to pollination can decline sharply when specialized individuals are lost (Fig. 3B).

Generalization at the individual level may buffer interaction loss at the population and species scales (Fig. 3D), thereby maintaining temporal patterns in network structure and population-level performance, and increasing the robustness and persistence of ecological networks (Gaiarsa *et al.*, 2021; Guimarães, 2020; Ponisio *et al.*, 2017). The limited empirical data that exist suggest that indeed intraspecific variation in interaction frequency may promote community robustness: plant population persistence is greater when pollinated by a combination of specialized and generalized individuals (Arroyo-Correa *et al.*, 2025), and variation in individual phenotypes and in pollinator attraction may increase the feasibility of plant populations (i.e., range of environmental conditions where a community may persist, consistent with ‘robustness’ here; Arroyo-Correa *et al.* 2023). A key unresolved question is whether interaction performance covaries with sensitivity: robustness may increase if high-performance individuals are more stress-resistant, but decrease if they are disproportionately vulnerable.

Networks of ecological interactions typically exhibit highly skewed distributions, in which most species (and likely most individuals; Bolnick *et al.* 2003) interact with only a few interaction partners (specialists), while the remainder interact with many partners (generalists). As a result, individual-level network metrics, such as connectance, nestedness, or modularity, may diverge strongly from species-level averages. While the distribution of interactions has important consequences for network dynamics at the species scale (Bascompte & Jordano, 2007; Gaiarsa & Guimarães, 2019), understanding whether these findings scale down to individual-level interaction networks can help identify individuals of high functional importance that sustain these critical interactions.

3.3 Individual variation and resilience

Plant-pollinator communities show a remarkable capacity to recover following disturbance (Kaiser-Bunbury *et al.*, 2017), yet these responses are highly variable (Dzekashu *et al.*, 2024), and there is evidence of persistent, long-term degradation in many systems (Burkle *et al.*, 2013). Individual variation may promote the recovery of populations and species interactions after perturbation through several mechanisms. In the short term, rare behavioral phenotypes (including those that may be suboptimal under normal conditions) and stress-tolerant individuals can sustain low-density populations and avert local extinctions through ecological bet-hedging (Kain *et al.*, 2015).

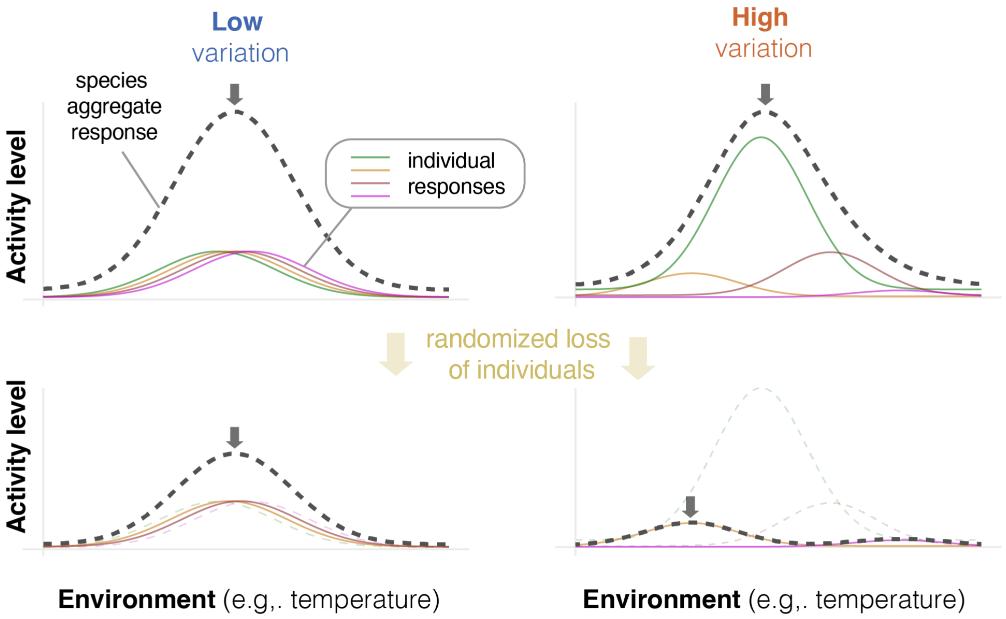

Figure 4: **Impacts of individual variation on robustness to the loss of individuals**. (A) When individuals have overlapping optima and functional roles (i.e., low individual variation), losses translate into proportional reductions in performance. (B) By contrast, when individuals vary widely in optima or amplitudes, random losses can lead to nonlinear declines and instability in population- or community-level performance. Solid lines show theoretical individual responses, and dashed lines show species aggregate responses. Dark grey arrows indicate peak activity level in each scenario.

.

For example, in seed-dispersal communities, a few plant individuals can attract disproportionately high vertebrate partner diversity, highlighting how rare or specialized individuals can buffer populations against perturbations (Quintero *et al.*, 2025). Individual variation may thus promote (short-term) resilience by improving population growth at low densities (Chesson, 2000). Over longer timescales (i.e., generations), individual variation may promote evolutionary rescue in response to environmental change and perturbation (Bell, 2013).

High individual variation may also promote population and species persistence and recovery under long-term, press disturbances (e.g., phenological or range shifts under climate change) by allowing species to fill new (or extirpated) niche space or exploit novel spatio-temporal overlaps with potential interaction partners by expanding individual variation (Fig. 2). For example, species with high trait variance may access a broader set of resources (Peat *et al.*, 2005; Peralta *et al.*, 2024b), thereby reducing dependence on any single resource and increasing population-level resilience (and robustness). Indeed, increased individual niche variation was proposed more than half a century ago as a primary mechanism for species-level niche expansion (Van Valen, 1965). Individual-niche heterogeneity underlying species-level niche expansion could provide a plausible mechanism for why some species with higher intraspecific morphological variation exhibit stronger population growth in response to environmental change (Austin & Dunlap, 2019).

4 Open questions

Together, the patterns we outline above suggest that plant–pollinator communities with similar species-level composition or network structure may nevertheless exhibit dramatic differences in sensitivity, robustness, and resilience due to the distribution of phenotypic variation among individuals. Yet many open questions remain, and resolving them will require moving beyond species averages to understand how individual-level heterogeneity shapes ecological responses to perturbation.

- **What is the empirical distribution of individual trait variation in interactions?** While it is often implicitly assumed that individuals have similar functional efficacy (Gomez & Perfectti, 2012; Herrera, 1987; Lopes *et al.*, 2022; Vázquez *et al.*, 2005), it is likely that individual phenotypic variation (e.g., in behavior and morphology) may influence pollen deposition (e.g., Fig. 3 and section 3.2 above) *via* differential visitation frequency and interaction efficacy (e.g., pollen deposition). As a result, observed species-level interaction networks may substantially misestimate functional robustness if interaction frequency and interaction efficacy are unevenly distributed among individuals. For example, communities in which a small subset of individuals disproportionately contribute to pollen deposition may be far more vulnerable to perturbation than species-level network structure alone would predict. The handful of empirical studies that have directly quantified individual-level variation in interaction frequency and network position (Arroyo-Correa *et al.*, 2021; Gaiarsa *et al.*, 2022; Peralta *et al.*, 2024b) show strong variation in interaction patterns and functional outcomes for both plants and pollinators. However, empirical studies quantifying individual interactions—especially linking them to other phenotypic traits associated with performance and stress susceptibility—remain quite sparse. Recent technological advances—particularly in computer vision and metabarcoding (see Future Directions)—could enable unprecedented resolution to quantify how individual variation in interaction frequency (and potentially efficacy) shapes the dynamics and robustness of ecological communities.

- **How do trait correlations shape performance, sensitivity, and resilience?** A second critical gap our framework highlights is how traits underlying performance and interaction frequency correlate with sensitivity at the organismal scale. For example, how does tolerance to environmental stressors (e.g., pesticide exposure) vary between low- and high-performing individuals? In social and semi-social bees, a small number of individual workers perform the vast majority of foraging bouts (Crall *et al.*, 2018) and floral visits (Thomson & Chittka, 2001). If highly connected or high-performing individuals are also comparatively stress-tolerant, ecological function may remain stable despite substantial environmental change. In contrast, if the individuals contributing most strongly to pollination are also the most stress-sensitive, perturbations could generate abrupt declines in pollination despite limited population loss. Quantifying trait correlation structures may reveal trade-offs between performance and tolerance, analogous to species-level trade-offs underlying diversity–stability relationships (Loreau *et al.*, 2021). For example, in plant communities under drought stress, tradeoffs between productivity and drought tolerance across species may promote community stability under fluctuating conditions (Mariotte *et al.*, 2013) (although such tradeoffs are not universal; Jung *et al.* 2020). However, it remains largely unknown whether similar trade-offs occur among individuals within populations. Thus, quantifying individual-level trait covariance is critical and will require integrative studies spanning multiple trait axes—such as disease susceptibility, morphology, and cognition. Variation across species in natural history may play an important role in structuring these tradeoffs: for example, sociality in pollinators may affect interaction patterns (see section 3.1, Fig. 3) as well as stress sensitivity (Crall & Raine, 2023). Critically, this will also require moving beyond static morphology to dynamic, multi-metric measures of performance that link sensitivity-relevant traits (e.g., disease or thermal susceptibility) to population- and community-level consequences, including interaction structure, functional outcomes, and the consistency of organisms' roles in interaction networks (Gaiarsa *et al.*, 2025). These correlations can reveal how selection within species cascades to shape the structure and dynamics of mutualistic interactions.

- **How do temporal changes in individual variation shape responses to environmental conditions?** Phenotypic plasticity can rapidly reshape trait distributions across short ecological scales—from hours to seasons. The effect of plasticity will depend on how individual plants and animals differ in their responses (e.g., developmental or behavioral) to environmental change (i.e., 'reaction norms'; Cabirol *et al.*, 2023; Dingemanse *et al.*, 2010; Suter & Widmer, 2013), and may play a critical role in buffering higher levels of organization (e.g., colonies, populations, or communities). For example, within social bee colonies, individual mortality may trigger compensatory upregulation of activity among other workers, providing colony-level buffering. Individual pollinators can also shift their floral visitation patterns (and degree of 'specialization', or floral fidelity) in response to local resource availability and weather (Brosi, 2016; Rose-Person *et al.*, 2025; Slominski & Burkle, 2021; Spiesman & Gratton, 2016). Thus, the existence of individual variation in behavioral compensation (i.e., 'behavioral reaction norms') may buffer pollination function at the population level, even in the absence of colony-level coordination, functionally equivalent to 'response diversity' across species. Alternatively, the loss of individuals may amplify effects at higher levels (e.g., colony or population); in social insect colonies, the loss of specialized workers may drive collective colony collapse (Perry *et al.*, 2015). These examples emphasize how individual variation may drive community-level compensation and regulation across scales (Vitousek *et al.*, 2025), but also underscore that individuals' plastic behavioral responses across space and time remain poorly understood.

5 Future directions

Despite growing recognition that individual variation can shape the sensitivity, robustness, and resilience of plant–pollinator communities under global change, key gaps remain in our ability to both measure individual phenotypes and interactions at scale and link those data to predictive theory. We suggest that future work should emphasize two complementary priorities: (1) scalable approaches for characterizing individual variation, and (2) tighter integration of theory, data, and experimentation.

5.1 Scale up measurements of individuals in the lab and field

A persistent bottleneck lies in the difficulty of repeatedly monitoring large numbers of individuals under ecologically relevant conditions. Emerging tools now facilitate the quantification of individual behavior and interaction patterns at unprecedented scales. In particular, the convergence of low-cost camera systems, robust image and video analysis, and deep learning algorithms for behavioral quantification could enable high-throughput monitoring of individual-scale interactions and activity (e.g., Arroyo-Correa *et al.* 2021; Sittinger *et al.* 2024; Smith *et al.* 2026; Spiesman *et al.* 2021). Integrating deep-learning-based detection with classical computer vision can further support automated tracking of floral preferences and visitation dynamics for uniquely identified individuals (e.g., Jain *et al.* 2025; Ulrich *et al.* 2024), enabling repeated-measures estimates of specialization, foraging activity, interaction turnover, and behavioral plasticity.

In addition, molecular tools such as DNA metabarcoding can complement visual observations by resolving resource use and cryptic interactions, revealing individual-level dietary patterns and interaction networks (e.g., Argueta-Guzmán *et al.* 2026; Gaiarsa *et al.* 2022). These scalable approaches should support—not replace—the need for natural history and data collection on basic information on trait distributions, phenology, and trait covariances, which remain missing for most plant and pollinator species. A promising direction would be to leverage image data from field collections and citizen-science repositories to quantify phenotypic variation within and across populations and species (e.g., Ostwald *et al.* 2025).

5.2 Integrate theory and data through prediction-focused synthesis and experimentation

Although theoretical models incorporating individual variation have advanced substantially (e.g., Arroyo-Correa *et al.* 2025; Baruah 2022), they remain constrained by limited empirical estimates of trait distributions, trait covariances, and the structure of individual-level interactions. A critical next step is to bridge species-scale frameworks—such as BEF and ecological network theory—to the individual level. Central concepts at the species-level—complementarity, response diversity, and sampling effects—have clear analogs at the individual level, but their consequences for community function and dynamics may differ when variation is structured within species rather than among species (e.g., Fig. 3). For example, two plant–pollinator communities with identical species richness and similar connectance may differ dramatically in robustness if interaction frequency and pollination efficacy are broadly distributed across individuals in one community but concentrated among a few highly connected or highly effective individuals in another. Understanding when species-level expectations scale down to the individual level would shed light on how population-level trait variation affects network stability, persistence, and pollination function under environmental change.

Critically, as with the BEF literature, expanding beyond observation to experiments that manipulate the distribution of individual phenotypes within populations could provide causal tests of how environmental perturbations propagate to affect interaction networks and community dynamics. Manipulating the distribution of individual phenotypes within populations may provide an experimentally tractable route to testing collapse thresholds, buffering capacity, and resilience mechanisms that are otherwise difficult to study through species-level diversity manipulations.

In summary, the convergence of scalable monitoring, molecular and image-based phenotyping, and increasingly mature individual-based theory creates an opportunity to understand, quantify, and ultimately predict the effects of individual variation on plant–pollinator community responses to global change. Integrating these advances can help address current central gaps: why apparently similar species diverge in their responses to environmental change, what determines tolerance limits and the potential for abrupt declines, and which mechanisms allow populations and communities to persist or recover following disturbance. By linking individual trait distributions to interaction structure and pollination function, the framework we propose here can move us toward a predictive ecology of plant-pollinator communities under global change, advancing fundamental ecological understanding while informing conservation strategies that protect not only species richness, but also functional diversity down to the scale of individuals.

References

Argueta-Guzmán, M., González, B., Van Pelt, N. *et al.* (2026) Distinct foraging goals shape floral resource use in a generalist solitary bee. Preprint.

Arroyo-Correa, B., Bartomeus, I. & Jordano, P. (2021) Individual-based plant–pollinator networks are structured by phenotypic and microsite plant traits. *Journal of Ecology* **109**, 2832–2844.

Arroyo-Correa, B., Bartomeus, I., Jordano, P., Cagua, E.F. & Stouffer, D.B. (2025) Bridging the gap between individual specialization and species persistence in mutualistic communities. *Ecological Monographs* **95**, e70031.

Arroyo-Correa, B., Jordano, P. & Bartomeus, I. (2023) Intraspecific variation in species interactions promotes the feasibility of mutualistic assemblages. *Ecology Letters* **26**, 448–459.

Austin, M.W. & Dunlap, A.S. (2019) Intraspecific variation in worker body size makes north american bumble bees (bombus spp.) less susceptible to decline. *The American Naturalist* **194**, 381–394.

Ayroles, J.F., Buchanan, S.M., O'Leary, C., Skutt-Kakaria, K., Grenier, J.K., Clark, A.G., Hartl, D.L. & De Bivort, B.L. (2015) Behavioral idiosyncrasy reveals genetic control of phenotypic variability. *Proceedings of the National Academy of Sciences* **112**, 6706–6711.

Baruah, G. (2022) The impact of individual variation on abrupt collapses in mutualistic networks. *Ecology Letters* **25**, 26–37.

Bascompte, J. & Jordano, P. (2007) Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **38**, 567–593.

Bascompte, J. & Scheffer, M. (2023) The resilience of plant–pollinator networks. *Annual Review of Entomology* **68**, 363–380.

Bell, G. (2013) Evolutionary rescue and the limits of adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120080.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1–28.

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P., Steffan-Dewenter, I. & Öckinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2075–2082.

Bosch, J. & Vicens, N. (2005) Sex allocation in the solitary bee osmia cornuta: do females behave in agreement with fisher's theory? *Behavioral Ecology and Sociobiology* **59**, 124–132.

Breuker, C.J., Brakefield, P.M. & Gibbs, M. (2007) The association between wing morphology and dispersal is sex-specific in the glanville fritillary butterfly melitaea cinxia (lepidoptera: Nymphalidae). *European Journal of Entomology* **104**.

Brosi, B.J. (2016) Pollinator specialization: from the individual to the community. *New Phytol.* **210**, 1190–1194.

Bullard, G.W., Buckley, L.B. & Kingsolver, J.G. (2026) Incorporating variation in death times improves predictions of ectotherm responses to stressful temperatures. *PLoS biology* **24**, e3003623.

Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013) Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* **339**, 1611–1615.

Burns, J.G. & Dyer, A.G. (2008) Diversity of speed-accuracy strategies benefits social insects. *Current biology* **18**, R953–R954.

Cabirol, A. *et al.* (2023) Considering variation in bee responses to stressors can reveal potential for resilience. *Journal of Applied Ecology* **60**, 1435–1445.

Cantwell-Jones, A. *et al.* (2024) Using individual-based trait frequency distributions to forecast plant-pollinator network responses to environmental change. *Ecology Letters* **27**, e14368.

Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**, 989–992.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual review of Ecology and*

Systematics **31**, 343–366.

Chittka, L., Dyer, A.G., Bock, F. & Dornhaus, A. (2003) Bees trade off foraging speed for accuracy. *Nature* **424**, 388–388.

Couvillon, M.J. & Dornhaus, A. (2010) Small worker bumble bees (bombus impatiens) are hardier against starvation than their larger sisters. *Insectes sociaux* **57**, 193–197.

Crall, J.D., Gravish, N., Mountcastle, A.M., Kocher, S.D., Oppenheimer, R.L., Pierce, N.E. & Combes, S.A. (2018) Spatial fidelity of workers predicts collective response to disturbance in a social insect. *Nature communications* **9**, 1201.

Crall, J.D. & Raine, N.E. (2023) How do neonicotinoids affect social bees? linking proximate mechanisms to ecological impacts. *Advances in insect physiology*, vol. 64, pp. 191–253, Elsevier.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*. John Murray, London, project Gutenberg edition, https://www.gutenberg.org/files/2009/2009-h/2009-h.htm.

de Bivort, B.L. (2025) The developmental origins of behavioral individuality. *Annual Review of Cell and Developmental Biology* **41**.

Decanini, L.I., Collins, A.M. & Evans, J.D. (2007) Variation and heritability in immune gene expression by diseased honeybees. *Journal of Heredity* **98**, 195–201.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., Schweitzer, J.A. & Palkovacs, E.P. (2018) The ecological importance of intraspecific variation. *Nature ecology & evolution* **2**, 57–64.

Dingemanse, N.J., Kazem, A.J., Réale, D. & Wright, J. (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends in ecology & evolution* **25**, 81–89.

Dzekashu, F.F., Yusuf, A.A., Takemoto, K., Peters, M.K., Lattorff, H.M.G., Steffan-Dewenter, I. & Pirk, C.W. (2024) Network resilience of plant-bee interactions in the eastern afromontane biodiversity hotspot. *Ecological Indicators* **166**, 112415.

Easton-Calabria, A.C. *et al.* (2023) Colony size buffers interactions between neonicotinoid exposure and cold stress in bumblebees. *Proceedings of the Royal Society B* **290**, 20230555.

Feuerborn, C., Quinlan, G., Shippee, R., Strausser, T.L., Terranova, T., Grozinger, C.M. & Hines, H.M. (2023) Variance in heat tolerance in bumble bees correlates with species geographic range and is associated with several environmental and biological factors. *Ecology and evolution* **13**, e10730.

Filipiak, M. (2019) Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. *Journal of Applied Ecology* **56**, 1410–1418.

Gaiarsa, M.P., Bramon Mora, B., Kremen, C. & Ponisio, L.C. (2025) Changes in species composition and community structure during plant–pollinator community assembly. *Ecology* **106**, e70119.

Gaiarsa, M.P. & Guimarães, P.R. (2019) Interaction strength promotes robustness against cascading effects in mutualistic networks. *Scientific reports* **9**, 676.

Gaiarsa, M.P., Kremen, C. & Ponisio, L.C. (2021) Pollinator interaction flexibility across scales affects patch colonization and occupancy. *Nature Ecology & Evolution* **5**, 787–793.

Gaiarsa, M.P. *et al.* (2022) Individual dietary specialization in a generalist bee varies across populations but has no effect on the richness of associated microbial communities. *The American Naturalist* **200**, 730–737.

Gamelon, M., Morimoto, J. & White, H.J. (2025) Special feature: Intraspecific variation in ecology and evolution. *Journal of Animal Ecology* **94**, 262–267.

Gomez, J.M. & Perfectti, F. (2012) Fitness consequences of centrality in mutualistic individual-based networks. *Proceedings of the Royal Society B: Biological Sciences* **279**, 1754–1760.

Guimarães, P.R. (2020) The structure of ecological networks across levels of organization. *Annual Review of Ecology, Evolution, and Systematics* **51**, 433–460.

Hart, S.P., Schreiber, S.J. & Levine, J.M. (2016) How variation between individuals affects species coexistence. *Ecology letters* **19**, 825–838.

Haverkamp, A., Bing, J., Badeke, E., Hansson, B.S. & Knaden, M. (2016) Innate olfactory preferences for flowers matching proboscis length ensure optimal energy gain in a hawkmoth. *Nature Communications* **7**, 11644.

Hernández-Carrasco, D., Tylianakis, J.M., Lytle, D.A. & Tonkin, J.D. (2025) Ecological and evolutionary consequences of changing seasonality. *Science* **388**, eads4880.

Herrera, C.M. (1987) Components of pollinator" quality": comparative analysis of a diverse insect assemblage. *Oikos* pp. 79–90.

Holling, C.S. *et al.* (1973) Resilience and stability of ecological systems.

Huang, H., Tu, C. & D'Odorico, P. (2021) Ecosystem complexity enhances the resilience of plant-pollinator systems. *One Earth* **4**, 1286–1296.

Inouye, B.D. *et al.* (2021) Trade-offs among resilience, robustness, stability, and performance and how we might study them. *Integrative and Comparative Biology* **61**, 2180–2189.

Jackson, H.M. *et al.* (2022) Climate change winners and losers among north american bumblebees. *Biology Letters* **18**, 20210551.

Jain, A., Tang, A.T.S. & Crall, J. (2025) Ethomics for ecotoxicology: Automated tracking reveals diverse effects of insecticides on bumble bee foraging and in-nest behavior. *Integrative And Comparative Biology* p. icaf118.

Jolles, J.W., King, A.J. & Killen, S.S. (2020) The role of individual heterogeneity in collective animal behaviour. *Trends in ecology & evolution* **35**, 278–291.

Jung, E.Y., Gaviria, J., Sun, S. & Engelbrecht, B.M. (2020) Comparative drought resistance of temperate grassland species: testing performance trade-offs and the relation to distribution. *Oecologia* **192**, 1023–1036.

Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H. & Stang, M. (2013) Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional ecology* **27**, 329–341.

Kain, J.S., Zhang, S., Akhund-Zade, J., Samuel, A.D., Klein, M. & de Bivort, B.L. (2015) Variability in thermal and phototactic preferences in drosophila may reflect an adaptive bet-hedging strategy. *Evolution* **69**, 3171–3185.

Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M. &

Blüthgen, N. (2017) Ecosystem restoration strengthens pollination network resilience and function. *Nature* **542**, 223–227.

Klein, A., Vaissière, B., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* **274**, 303–313.

Klumpers, S.G., Stang, M. & Klinkhamer, P.G. (2019) Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length. *Ecology letters* **22**, 469–479.

Lepš, J., Bello, F.d., Lavorel, S. & Berman, S. (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* **78**, 481–501.

Lever, J.J., Nes, E.H., Scheffer, M. & Bascompte, J. (2014) The sudden collapse of pollinator communities. *Ecology Letters* **17**, 350–359.

Lopes, S.A., Bergamo, P.J., Najara Pinho Queiroz, S., Ollerton, J., Santos, T. & Rech, A.R. (2022) Heterospecific pollen deposition is positively associated with reproductive success in a diverse hummingbird-pollinated plant community. *Oikos* **2022**.

Loreau, M., Barbier, M., Filotas, E., Gravel, D., Isbell, F., Miller, S.J., Montoya, J.M., Wang, S., Aussenac, R., Germain, R. *et al.* (2021) Biodiversity as insurance: from concept to measurement and application. *Biological Reviews* **96**, 2333–2354.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper, D., Huston, M., Raffaelli, D., Schmid, B. *et al.* (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808.

Mariotte, P., Vandenberghe, C., Kardol, P., Hagedorn, F. & Buttler, A. (2013) Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *Journal of Ecology* **101**, 763–773.

Memmott, J., Waser, N.M. & Price, M.V. (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 2605–2611.

Montoya, D., Haegeman, B., Gaba, S., De Mazancourt, C., Bretagnolle, V. & Loreau, M. (2019) Trade-offs in the provisioning and stability of ecosystem services in agroecosystems. *Ecological Applications* **29**, e01853.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326.

Oster, G.F. & Wilson, E.O. (1978) *Caste and ecology in the social insects*. Princeton University Press.

Ostwald, M.M., Chen, K., Alexander, N., Ding, L., Gonzalez, V.H. & Seltmann, K.C. (2025) Climate explains global functional trait variation in bees. *Functional Ecology* **39**, 1748–1760.

Peat, J., Tucker, J. & Goulson, D. (2005) Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? *Ecological Entomology* **30**, 176–181.

Peralta, G., CaraDonna, P.J., Rakosy, D., Fründ, J., Tudanca, M.P.P., Dormann, C.F., Burkle, L.A., Kaiser-Bunbury, C.N., Knight, T.M., Resasco, J. *et al.* (2024a) Predicting plant–pollinator interactions: concepts, methods, and challenges. *Trends in ecology & evolution* **39**, 494–505.

Peralta, G., Perry, G.L., Vázquez, D.P., Dehling, D.M. & Tylianakis, J.M. (2020) Strength of niche processes for species interactions is lower for generalists and exotic species. *Journal of Animal Ecology* **89**, 2145–2155.

Peralta, G., Resasco, J., Worthy, S., Frost, C.M., Guevara, A.T., Manning, I., Cagnolo, L. & Burkle, L.A. (2024b) Pollinator intraspecific body size variation and sociality influence their interactions with plants. *Functional Ecology* **38**, 875–882.

Perry, C.J., Søvik, E., Myerscough, M.R. & Barron, A.B. (2015) Rapid behavioral maturation accelerates failure of stressed honey bee colonies. *Proceedings of the National Academy of Sciences* **112**, 3427–3432.

Pimsler, M.L., Oyen, K.J., Herndon, J.D., Jackson, J.M., Strange, J.P., Dillon, M.E. & Lozier, J.D. (2020) Biogeographic parallels in thermal tolerance and gene expression variation under temperature stress in a widespread bumble bee. *Scientific reports* **10**, 17063.

Poisot, T., Stouffer, D.B. & Gravel, D. (2015) Beyond species: why ecological interaction networks vary through space and time. *Oikos* **124**, 243–251.

Ponisio, L.C., Gaiarsa, M.P. & Kremen, C. (2017) Opportunistic attachment assembles plant-pollinator networks. *Ecology Letters* **48**.

Potts, S., Biesmeijer, J., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W. (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **24**, 345–353.

Quintero, E. *et al.* (2025) Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations. *Proceedings of the National Academy of Sciences* **122**, e2402342122.

Rose-Person, A., Santiago, L.S. & Rafferty, N.E. (2025) Drought stress influences foraging preference of a solitary bee on two wildflowers. *Annals of Botany* **135**, 153–164.

Sih, A., Bell, A. & Johnson, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in ecology & evolution* **19**, 372–378.

Sittinger, M., Uhler, J., Pink, M. & Herz, A. (2024) Insect detect: An open-source diy camera trap for automated insect monitoring. *Plos one* **19**, e0295474.

Slominski, A.H. & Burkle, L.A. (2021) Asynchrony between solitary bee emergence and flower availability reduces flower visitation rate and may affect offspring size. *Basic and Applied Ecology* **56**, 345–357.

Smith, M.A.Y., Bernauer, O.M., Melone, G., Graham, B., Wiessing, J., Salas, R., Hemberger, J., Bhattacharyya, A., Tang, A.T., Rojas, E. *et al.* (2026) Autopolls: A tool for automated monitoring of pollinators using deep learning. *Methods in Ecology and Evolution* .

Spiesman, B.J. & Gratton, C. (2016) Flexible foraging shapes the topology of plant–pollinator interaction networks. *Ecology* **97**, 1431–1441.

Spiesman, B.J., Gratton, C., Hatfield, R.G., Hsu, W.H., Jepsen, S., McCornack, B., Patel, K. & Wang, G. (2021) Assessing the potential for deep learning and computer vision to identify bumble bee species from images. *Scientific reports* **11**, 7580.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., De Vries, W., De Wit, C.A. *et al.* (2015) Planetary boundaries: Guiding human development on a changing planet. *science* **347**, 1259855.

Suter, L. & Widmer, A. (2013) Phenotypic effects of salt and heat stress over three generations in arabidopsis thaliana. *PloS one* **8**, e80819.

Tenczar, P., Lutz, C.C., Rao, V.D., Goldenfeld, N. & Robinson, G.E. (2014) Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels. *Animal Behaviour* **95**, 41–48.

Thomson, J.D. & Chittka, L. (2001) Pollinator individuality: when does it matter. *Cognitive ecology of pollination* pp. 191–213.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845.

Timberlake, T., Sapkota, S., Saville, N., Cirtwill, A., Baral, S., Bhusal, D., Devkota, K., Giri, S., Harris-Fry, H., Joshi, D. *et al.* (2026) Pollinators support the nutrition and income of vulnerable communities. *Nature* pp. 1–6.

Torchio, P.F. & Tepedino, V.J. (1980) Sex ratio, body size and seasonality in a solitary bee, osmia lignaria propinqua cresson (hymenoptera: Megachilidae). *Evolution* pp. 993–1003.

Tur, C., Olesen, J.M. & Traveset, A. (2014) Increasing modularity when downscaling networks from species to individuals. *Oikos* **123**, 1317–1326.

Ulrich, J., Stefanec, M., Rekabi-Bana, F., Fedotoff, L.A., Rouček, T., Gündeğer, B.Y., Saadat, M., Blaha, J., Janota, J., Hofstadler, D.N. *et al.* (2024) Autonomous tracking of honey bee behaviors over long-term periods with cooperating robots. *Science Robotics* **9**, eadn6848.

Van Valen, L. (1965) Morphological variation and width of ecological niche. *The American Naturalist* **99**, 377–390.

Vázquez, D.P., Morris, W.F. & Jordano, P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology letters* **8**, 1088–1094.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**, 244–252.

Vitousek, M.N., Taff, C.C. & Williamson, J.L. (2025) Resilience and robustness: from sub-organismal responses to communities. *Trends in Ecology & Evolution* .

Williams, N.M. & Tepedino, V.J. (2003) Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee osmia lignaria. *Behavioral Ecology* **14**, 141–149.

Yourstone, J., Varadarajan, V. & Olsson, O. (2023) Bumblebee flower constancy and pollen diversity over time. *Behavioral Ecology* **34**, 602–612.