

Bringing population ecology back to wild bees

Nicholas Dorian¹ and Elizabeth Crone¹

¹Tufts University

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Abstract

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Nicholas N. Dorian^{1*} (nicholas.dorian@tufts.edu)

Elizabeth E. Crone¹ (elizabeth.crone@tufts.edu)

¹Tufts University, Department of Biology, 200 College Avenue, Medford, Massachusetts United

***Corresponding author:** Nicholas N. Dorian

Phone: +1 (203) 561-0280

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Abstract: In recent years, ecologists have focused on describing patterns of change in wild bee communities, but we know little about the population-level mechanisms driving those changes. We believe this emphasis on community-level patterns stems from two misconceptions: the perceptions that population-level studies are too conceptually narrow to provide rigorous inference, and that studying bees throughout their life cycles is prohibitively challenging without pinned specimens. Here, we combat these ideas. First, when population-level studies are couched in ecological theory, they can also have a broad scope of inference. And second, studies of wild bees throughout their life cycles are possible because dozens of species can be identified to species in the field. More generally, we emphasize the need to link data-rich pattern-oriented approaches in ecology with an understanding of the basic biology and mechanisms that generate those patterns.

Problem Statement: In recent years, it has become popular for ecologists to analyze patterns of biodiversity in relation to ongoing climate and land use change. An implicit assumption underlying these studies is that the places and times at which a species is most conspicuous are the most important for its persistence. However, ecologists have long known that this relationship is not necessarily true (e.g. Crouse, Crowder, & Caswell, 1987). If our goals are to predict future dynamics, mitigate population declines, or manage invasive species, we also need to understand the population-level processes behind large-scale patterns.

Context: The mismatch between our knowledge of large-scale patterns and population-level processes is especially evident in research about wild bees. In North America, there are nearly 4000 species of wild bees. Over the past 20 years, in response to concerns over declining wild bee populations (Potts *et al.* 2010), ecologists have generated enormous volumes of data at the community level. To characterize this trend, we read all papers about wild bees from 2020 published in 19 representative ecology journals (95 articles; Table S1). More than half of these papers (51/95 articles) described bee communities in relation to an environmental factor (Figure S1). Studies typically collected data via lethal sampling of adult bees during foraging and characterized community composition by identifying pinned specimens.

These community-level studies have taught us many things about wild bees: where and when adults occur (Carril *et al.* 2018), how biodiversity metrics vary across land-use types (Harrison *et al.* 2018), and changes in abundance of target taxa (LeCroy *et al.* 2020). At the same time, we have learned very little about the mechanisms driving those patterns. For nearly all wild bees, we have glaring knowledge gaps about basic biology throughout the life cycle, including overwintering and nesting habitat. Therefore, we cannot fully contextualize and interpret community-level patterns. For example, what do we learn from knowing that bee communities differ by two or ten species of metallic sweat bees (*Dialictus* spp.) if we do not know how these species differ from each other ecologically?

Our viewpoint: We are at an impasse in which ecologists keep generating community-level data on wild bees without collecting the life history and population-level knowledge needed to fully understand, contextualize, and interpret those data. Investing in research mainly at the community level is a missed opportunity to understand processes about wild bees across scales of biological organization. In addition, our lack of understanding of wild bee life cycles limits our ability to prescribe management to address declines (see, e.g., U.S. Fish and Wildlife Service 2020).

We believe that an emphasis on community-level studies stems from two misconceptions. First, population-level studies are perceived as too conceptually narrow, i.e. a “sample size of one” in the context of bee communities at landscape scales. And second, studying wild bees is perceived as prohibitively challenging without pinned specimens.

We believe that population-level studies of wild bees can be done in a way that leads to general inference (not a sample size of one). We also believe that, if we overcome the misconception that studies of bee populations are too narrow in scope, it will be straightforward to overcome the technical limitations to doing field work with wild bees. Rather than being an especially striking example of the focus on process over pattern, wild bees could become an example of balancing breadth with depth to understand how local processes determine landscape-level patterns.

Overcoming the perception of narrowness: Population-level studies can have a broad scope of inference

if they are grounded in testable ecological theory. In this framework, generalization comes from studies that test general hypotheses and theoretical predications using single species. Generalization also comes from comparative approaches that leverage each of these cases as building blocks to construct “rules of thumb” about ecological processes (Grainger *et al.* 2022). As a result, population-level studies throughout the life cycle can simultaneously teach us rules for how populations operate and communities assemble, and generate quantitative guidelines for species-specific conservation.

In many other fields of ecology, there is a long tradition of leveraging single-species studies to learn rules about how populations operate. For example, herbaceous perennial plants are model systems for testing life history theory. By the 1990s, ecologists had generated enough population-level data to conduct comparative studies across dozens of taxa (Silvertown *et al.* 1996; Salguero-Gómez *et al.* 2017). Similarly, butterfly populations are longstanding model systems for movement (Kareiva & Shigesada 1983; Schultz & Crone 2001) and metapopulation dynamics (Baguette *et al.* 2003; Matter *et al.* 2004). And, bumble bees have been foundational in our understanding of foraging ecology (Thomson *et al.* 1987; Harder 1990) and pollination biology (Waser & Price 1981; Ogilvie & Thomson 2016). Studies with bumble bees in these areas represented about one-quarter of our literature search (21/95 articles).

However, the idea of grounding population-level studies in theory is not widespread among bee ecologists interested in conservation or other responses to environmental change. From our literature survey, one quarter of articles (23/95) investigated bee populations, but half of these (11/23 articles) were largely descriptive, e.g., describing the range of a species, characterizing diet breadth, or reporting fecundities. Describing patterns at the population level is not a fix to describing patterns at the community level. The kinds of population-level studies that provide broad inference about wild bees are those that test theoretically-motivated predictions.

Wild bees as model systems for ecological theory: In this context, wild bees could be excellent systems for testing several areas of ecological theory. The second half of population-level studies in our sample (12/23 articles) exemplify this viewpoint, mainly testing theory about 1) nutritional ecology and 2) drivers of vital rates (Fig. 1). Studies in these two areas help us interpret findings from landscape-level studies as follows:

Nutritional ecology : Wild bees are elegant systems for asking questions about nutritional ecology because offspring are fed discrete amounts of pollen, and diet contents can be inferred from foraging females or nest contents (Cane & Sipes 2006). Past work has focused on the use of novel pollen sources, dietary mixing, and nutritional needs across life stages (Praz *et al.* 2008; Filipiak 2019; McAulay *et al.* 2020). From this work, we learn how patterns of bee biodiversity are shaped by landscape features like floral resources.

Drivers of vital rates: Vital rates are the demographic parameters like survival and reproduction that govern progression through the life cycle. Knowing how environmental factors like resource availability and natural enemies influence bee vital rates (Roulston & Goodell 2011; Crone & Williams 2016) is key for contextualizing and forecasting patterns of bee abundance across on the landscape.

We think wild bees would be excellent model systems in at least three additional areas, none of which came up in our 95-article sample (Fig.1). While these areas have a rich tradition in many fields of ecology, they have generally received less attention in bees, and so could be especially valuable for future research:

1. *Voltinism and phenology* (e.g. *timing of life cycle events*): Standing variation in bee voltinism—the number of generations occurring within a year—makes it straightforward to study mechanisms underpinning widespread changes in phenology (Bartomeus *et al.* 2011; Duchenne *et al.* 2020). For instance, some wild bees produce offspring that emerge after one or two years (Forrest *et al.* 2019), and ecological theory predicts that producing offspring with mixed emergence times can act as a bet-hedging strategy in variable environments. Wild bees could be used to test bet-hedging theory and also to understand how phenological variation confers resilience to bee populations in general.
2. *Habitat selection at multiple spatial scales* : Bees are central-place foragers, meaning nesting habitat is not necessarily the same as foraging habitat. This contrast makes bees well suited for teasing apart drivers of habitat selection. Mechanistic studies in bees could build habitat selection theory by testing whether predictions for long-lived vertebrates (Mayor *et al.* 2009) hold for short-lived invertebrates.

For conservation, these studies would teach us explicitly about both foraging and nesting habitat needs (Antoine & Forrest 2020).

3. *Movement ecology* : Adult bees make two kinds of movements during their lives: daily foraging to flowers and less frequent dispersal to new nesting sites. One general question is whether the same rules determine movement during these two behavioral modes. For conservation, understanding the interplay between foraging and dispersal is key to contextualizing range shifts (Marshall *et al.* 2020) and identifying future reserve placement (Hannah *et al.* 2007).

Overcoming limitations of fieldwork with wild bees : Studying wild bee populations requires working with living specimens in the field. In the 20th century, it was not uncommon for entomologists to study wild bees throughout their life cycle (e.g., Linsley *et al.* 1952; Eickwort 1975; Batra 1980). However, recent population-level studies of wild bees are quite taxonomically restricted. In our sample, the theory-motivated population-level studies worked with just three genera of wild bees: *Bombus* (5 papers), *Osmia* (6 papers), and *Ceratina* (1 paper). Although these genera are valuable model systems, they limit our potential scope of inference compared to the enormous taxonomic and ecological diversity found within wild bees.

We believe that one reason why studies of bees are taxonomically restricted is the perception that wild bee species can only be identified with a microscope. While this perception is true for many species, it is also true that many wild bee species can be identified while alive using field marks—features like coarse morphology, phenology, behavior, and habitat associations unique to each species. Radical as it may sound, this is not a new idea for insects. Butterfly and dragonfly watchers have transitioned over the past 25 years from nets and kill jars to field marks and binoculars. We can do the same for bees.

To illustrate this possibility, we have compiled a starting list of field-identifiable bee species in eastern North America. Out of ~400 candidate species, at least 70 can be recognized from field marks, and they are distributed across the bee phylogeny (Fig. 2; see Table S2 for list). If we extrapolate across North America, this means that, conservatively, about 20% of 4000 bee species could be studied at the population level.

Once we recognize that bees can be identified in the field, we can use old-school methods to study them throughout their life cycles. Methods like mark-recapture, nest excavations, and trap nests, which were commonplace in 20th century natural history studies of bees (Linsley *et al.* 1952), are still some of the best suited tools for studying wild bee populations (Iles *et al.* 2019; Williams *et al.* 2019; Wong & Forrest 2021)(Fig. 1).

An ecologist looking for a study species might carefully select one from our field-identifiable list that typifies a theoretical question of interest—for example, variation in voltinism, use of habitat types sensitive to climate or land use change, or spatial scales of foraging (see examples in Figure 1). Choosing a species that can be used to test theory is a classic approach in ecology, however, based on our conversations with early-career ecologists interested in pollinator conservation, this approach seems to be lost from the current paradigms of studying wild bees.

Conclusions: Although an emphasis on studying large-scale patterns over population-level processes is particularly striking in wild bees, it is currently a widespread trend across ecology. We want to remind ecologists that relying only on large-scale studies to understand large-scale processes is unnecessarily restrictive. Population-level studies at smaller scales can help us interpret and contextualize large-scale patterns by testing theory-motivated mechanisms. Studies throughout the life cycle are also especially urgent for filling knowledge gaps for taxa (like bees) that are of conservation importance but whose basic biology is poorly understood. We are not saying this is easy—it is always challenging to balance theory with natural history in a meaningful way. However, such studies are far more feasible than ecologists studying wild bees tend to assume. For all taxonomic groups, we need to remember to balance breadth with depth to meaningfully understand and address the biological impacts of global change.

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- Figure 1.** Areas of theory for which wild bees are excellent systems at the population level. Two areas came up in our sample of recent papers in bee ecology (blue panels). Three other areas represent promising avenues for future research (yellow panels). I. Nutritional ecology: McAulay *et al.* 2020 used egg transfer experiments in mason bees *Osmia* spp. to examine factors influencing pollen specialization; II. Drivers of vital rates: Stuligross *et al.* 2020 used cage experiments to tease apart the combined effects of pesticide and resource availability on blue orchard bee *Osmia lignaria* demography; III. Voltinism and phenology: *Colletes validus* could be studied by locating nests and excavating brood cells to track life cycle timing; IV.

Habitat selection: *Eucera pruinosa* could be studied by comparing nesting vs. foraging habitat; V. Movement ecology: *Agapostemon virescens* could be studied through spatially explicit mark-recapture of females.

Figure 2. Field-identifiable bees in eastern North America are spread across the bee tree of life, with 70 species from 28 genera across 5 families. Circle size is proportional to the number of species in each genus on our list. Phylogeny reproduced from Hedtke et al. 2013. Fig. 1



Fig. 2

