Pollinator competition and the structure of floral resources

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ABSTRACT

The mutualism between plants and pollinators is built upon the trophic ecology of flowers and florivores. Yet the ecology of flowers-as-food is left implicit in most studies of plant-pollinator ecology, and it has been largely neglected in mainstream trophic ecology. This deficit is especially evident in an emerging issue of basic and applied significance: competition between pollinators for floral resources. In this synthesis, we start by exploring the notion of floral resource limitation upon which most studies concerning competition between pollinators are tacitly predicated. Both theoretical and empirical lines of evidence indicate that floral resource limitation must be understood as a complex ecological contingency; the question is not simply *whether* but *when*, *where*, and *in what regions of floral trait space* resources are limiting. Based on this premise, we propose a framework for understanding floral resource availability in terms of temporal, spatial, and functional structure. While this framework is conceptually intuitive, it is empirically and analytically demanding. We review existing methods for measuring and summarizing the multi-dimensional structure of floral resources, highlight their strengths and weaknesses, and identify opportunities for future methods development. We then discuss the causal relationships linking floral resource structure to species coexistence, plant-pollinator community dynamics, and exogenous drivers like climate, land use, and episodic disturbances. In its role as both cause and effect, floral resource structure mediates the relationship between behavioral ecology, landscape ecology, and coexistence theory with respect to flowers and florivores. Establishing floral resource structure as an object of study and application will both shed light on basic questions of coexistence and guide management decisions concerning contentious issues such as the compatibility of apiculture with wild pollinator conservation and the appropriate use of floral enhancements in agri-environment schemes.

Key words: nectar, pollen, coexistence, niche, landscape, foraging

1. Introduction

When flowering plants (Angiospermae) rose to prominence in the mid-Cretaceous (~100 million years ago), the relationship between insects and flowers was already ancient (Peris et al. 2017, Ollerton 2017). The key innovation of angiosperms was not that they bore flowers, for the homologous flowers (*sensu lato*) of gymnosperms not only existed but were already associated with insect pollinators when angiosperms arose (Frame 2003, Peris et al. 2017). Rather, it was their *edibility*, and especially that of their flowers, that distinguished angiosperms from their predecessors and paved the way for their rapid co-diversification with pollinating insects (Frame 2003). Angiosperms, more than any plant lineage before them, succeeded in harnessing florivory as a means of pollination **(Box 1)**, and this innovation established one of the chief foundations of global biodiversity (Benton et al. 2022). Today, the roughly 369,000 species of flowering plants (Willis 2017) and 352,000 species of flower-visiting insects (Wardhaugh 2015) together account for a third of all described extant species of eukaryotic life on Earth.

Box 1: Pollination and florivory

In the conceptual framework we present, we consider the consumption of pollen and/or nectar to be a special form of florivory, blurring the conventional distinction between pollinators and florivores (McCall and Irwin 2006). While nectar- and pollen-feeding animals often function as pollinators, describing their foraging behavior as "pollination" is misleading, not only because flower visitation does not necessarily result in pollen transfer, but because describing an animal trophism solely in terms of plant reproduction belies the herbivorous intent of even the most efficient pollinator **(Box 2)**. Nesting the specialized behavior of pollen- and nectar-feeding animals within the larger category of florivory emphasizes the trophic significance of flower visitation, irrespective of plant reproductive outcomes. This builds a bridge between the largely empirical field of pollination ecology and the rich theoretical tradition of trophic ecology.

Despite the ecological and evolutionary centrality of the trophic interface between flowers and florivores, the subject has been eclipsed by other forms of herbivory in the mainstream of ecological literature. When trophic ecology came to the fore in the 1960s, florivory was either completely ignored (e.g. Hairston et al. 1960) or given terse treatment as a special case to which general hypotheses might not apply (e.g. Murdoch 1966,

Slobodkin et al. 1967). In the landmark 1992 special issue of *Ecology* concerning the relative importance of bottom-up vs. top-down trophic processes (Matson and Hunter 1992), florivory was acknowledged only in a passing reference to nectarivorous birds (Hunter and Price 1992). Meanwhile, pollination ecology — a functional corollary of florivory — has risen to unprecedented prominence in the ecological literature, but largely without an appreciation of its trophic underpinnings.

The disconnect between trophic ecology and pollination ecology is particularly evident in the unsettled questions and increasing controversy regarding competition between pollinators for floral resources. Early studies of pollinator competition began in the 1970s, during the heyday of classical niche theory. In keeping with the research priorities of that time, pollinator communities were viewed as model systems for testing hypotheses concerning the coexistence of species with overlapping dietary niches (e.g. Johnson and Hubbell 1975, Inouye 1978, Hanski 1982). Following the lapse of classical niche theory in the 1980-90s (Chase and Leibold 2003), pollination ecology became a more applied and empirical science, but the topic of competition resurfaced in response to concerns about the impact of managed honey bees (*Apis mellifera* L.) on wild pollinators (Butz Huryn 1997, Steffan-Dewenter and Tscharntke 2000). In more recent years, this topic has intensified into a contentious debate about the place of honey bees and beekeeping in pollinator conservation (e.g. Geldmann and González-Varo 2018, González-Varo and Geldmann 2018, Kleijn et al. 2018, Saunders et al. 2018). Yet despite intense empirical scrutiny, consensus remains elusive. In the recent meta-analysis of Iwasaki and Hogendoorn (2022), 68% of studies involving resource competition between pollinators report "negative outcomes" (mostly in response to honey bees or bumble bees), and this equivocity is compounded by the fact that there is no common standard for what constitutes a "negative outcome" or what should be measured to infer one.

Meanwhile, and largely in parallel, coexistence theory has experienced a fresh wave of development (Chesson 2000, Chase and Leibold 2003) in which plants and pollinators feature prominently. Classical consumer-resource modeling (Tilman 1982), for example, has been extended to predict coexistence in plant-pollinator systems involving both competitive and mutualistic processes (Valdovinos and Marsland 2021, e.g. Hale and Valdovinos 2021, McPeek et al. 2022), and niche theory is being synthesized with network theory to clarify coexistence criteria in multi-species interaction networks (Valdovinos et al. 2016, Godoy et al. 2018). These theoretical advances have enormous potential to guide and interpret empirical studies of pollinator competition, but progress is hindered by the perennial challenge of reconciling the elegance of idealized models to the manifold complexity of real ecological systems. On the one hand, theoretical models achieve tractability by ignoring or highly simplifying the interplay of phenologies, distributions, and functional traits that, from an empirical perspective, are among the most salient characteristics of plant-pollinator interactions.

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Empirical studies, on the other hand — when disconnected from theory — accumulate descriptions and statistical associations without a clear sense of how they relate to causal processes and coexistence criteria.

When, however, plant-pollinator communities are viewed from a trophic-ecological perspective — as communities of flowers and florivores — theoretical and empirical approaches to pollinator competition are mediated by a clear question: are pollinator populations limited by floral resources? This question has, so to speak, a foot in each domain. On the theoretical side, consumer-resource models (e.g. Valdovinos and Marsland 2021) are predicated on the assumption of resource limitation. The validity of this assumption, however, is contingent upon the intersecting dimensions of temporal, spatial, and functional heterogeneity that can be elucidated only by empirical approaches.

We begin this review by exploring the question of floral resource limitation by analogy to the classical question of resource limitation among herbivores in general. We conclude that the proper question is not *whether* but *when, where*, and *in what regions of functional trait space* floral resources are limiting, and we refer to these joint temporal, spatial, and functional dynamics as *floral resource structure*. Guided by this conceptual model, we review existing methods for measuring and analyzing floral resource structure and identify opportunities for future methods development. We then discuss the causal relationships linking floral resource structure to pollinator coexistence and how these processes can be influenced by exogenous drivers like climate, land use, and episodic disturbances. Clarifying these relationships will facilitate the integration of empirical and theoretical approaches to pollinator coexistence, which will in turn provide a basis for sound management of plant-pollinator systems. In conclusion, we stress that this trophic-ecological perspective on plants and pollinators not only sheds light on the specific issue of pollinator competition but brings overdue attention to the trophic interface between flowers and florivores that generated and maintains so vast a share of global biodiversity.

Box 2: Floral resources

When an insect visits a flower, it does so in pursuit of one or more substances that can be referred to broadly as "floral resources." Chief among these resources are nectar and pollen. Nectar is an aqueous sugar solution, and its main function as a floral reward is to provide carbohydrate nutrition, though it also contains trace amounts of other substances that can be functionally significant (Nicolson and Thornburg 2007). Pollen, on the other hand, is first and foremost the angiosperm male gametophyte, and its function as a floral reward is secondary to its function in gene dispersal. As food for flower visitors, pollen complements the carbohydrate

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reward of nectar by supplying lipids and amino acids, along with a range of other substances (Roulston and Cane 2000). Aside from nectar and pollen, there are special cases in which fragrance (Vogel 1963), oil (Vogel 1974), or resin (Armbruster 1984) serve as floral rewards. The emphasis of our paper will be on nectar and pollen, since these are the most generalizable and well-studied floral resources, and their specific role as food matches the trophic-ecological framing of our discussion. Of the two, nectar is the more analytically tractable, since it can (with some caveats) be quantified neatly in terms of volume and sugar concentration. Pollen varies in multiple nutritional parameters, and its quantification is less straightforward (Lau et al. 2022). Nevertheless, the core concepts of temporal, spatial, and functional structure obtain, in principle, for any floral resource, and their application is limited only by the extent to which a given resource can be quantified.

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2. Is the world sweet? Examining the premise of floral resource limitation.

Hairston et al. (1960) famously proposed that herbivores — in contrast to predators and decomposers — are generally regulated not by food limitation but by the top-down pressure of predation and parasitism. This idea came to be known as the *green world hypothesis* because it began with the observation that the Earth is, by and large, replete with vegetation despite the ubiquitous presence of herbivores. While this hypothesis was formulated with foliage in mind (Slobodkin et al. 1967), it is worth examining its logic, together with that of competing hypotheses, in the context of floral resources and the peculiar herbivores that feed on them. Is the world as "sweet" as it is green, or are pollinators engaged in a Malthusian struggle for limiting supplies of nectar and pollen **(Box 3)**?

For Hairston et al. (1960), the conclusion that "the usual condition is for populations of herbivores *not* to be limited by their food supply" follows from the observations that "plants are abundant and largely intact" and "cases of mass destruction [of plants] by meteorological catastrophes are exceptional in most areas." Setting aside for now potential objections to this logic, we may ask whether floral resources can be regarded as generally "abundant", "intact", and robust to the vagaries of weather. Flowers certainly *can* be ostensibly abundant in a landscape, such as a maple forest or a rapeseed field at full bloom, but their abundance is not stable like that of foliage; the same forest and field could be almost flowerless a few weeks after peak bloom (Requier et al. 2015). The notion of intactness is also more nuanced for flowers than for foliage, since the

depletion of nectar and pollen is not visually apparent. A landscape dense with flowers could nevertheless be depauperate in nectar and pollen if the flowers have been heavily exploited (Heinrich 1976) or if their productivity has been stunted by drought (Waser and Price 2016, Phillips et al. 2018). As for robustness to weather events, flowers are presumably more sensitive than foliage (e.g. Papadopoulou et al. 2018), though the topic is not well-studied. Thus, the premises of the green world hypothesis, when extended to flowers and florivores, appear to be at best contingencies rather than givens.

The classical objections to green world hypothesis are, however, similarly problematic in the context of florivory. It is often argued that Hairston et al. (1960) overlook the role of plant defenses in regulating herbivory (e.g. Janzen 1977, Power 1992). While foliage may be abundant, herbivores nevertheless can be nutrition-limited either because *edible* plants are scarce or because even edible plants can be consumed only at a limiting rate due to the need for detoxification. This argument is less compelling, though, in the case of floral resources, which function as pollinator rewards and are not as strongly defended as other plant tissues (Rivest and Forrest 2020). In another line of reasoning, White (1978) advances the hypothesis that herbivores are generally limited not by the *abundance* of their food but by its *nitrogen content*; herbivores simply cannot eat available food fast enough to achieve a surplus of dietary nitrogen. In contrast to foliage, however, flowers are *not* nitrogen-poor. Indeed, the crude protein content of pollen ranges from 2.5 to 61% (Roulston et al. 2000), which covers a range similar to that of animal flesh (McCance and Widdowson 2014, Kouřimská and Adámková 2016), suggesting that pollen-feeders have more in common with carnivores than with folivores when it comes to nitrogen nutrition.

Considered over evolutionary time scales, it has been hypothesized that there should exist a positive feedback loop wherein food scarcity for pollinators entails visitation saturation for plants, resulting in selection pressure toward lower investment in nectar production, and thus more extreme nectar scarcity (Ratnieks and Balfour 2021). Indeed, precisely this evolutionary effect has been reported in the alpine lotus (*Saussurea nigrescens*) in response to high densities of managed honey bees, and the evolutionary process was rapid enough to be detected over the course of just three decades (Mu et al. 2014). Importantly, though, the logic of positive feedback works in both directions; when nectar is non-limiting, plants can be expected to compete for limited pollinator visitation, generating selection pressure toward *increased* nectar production (Ratnieks and Balfour 2021) and ultimately "sweet world" conditions. Indeed, the fact that mechanisms for nectar resorption are widespread in plants suggests that the phenomenon of nectar surplus is not uncommon (Nepi and Stpiczyńska 2008).

Thus, nectar- and pollen-feeding, while clearly special cases of herbivory, do not map neatly onto the classical debate concerning resource limitation in herbivores, and this uncertainty is exacerbated by the expectation

of destabilizing evolutionary feedback between the production and consumption of floral resources. Given this equivocity of theory, it is perhaps not surprising that empirical studies have reported both apparently limiting and apparently non-limiting conditions, often alternating through diel or seasonal time within a single locality (Hocking 1968, Mosquin 1971, Heinrich 1976, Roubik and Buchmann 1984, Bowers 1986, Williams 1989, Timberlake et al. 2021), though Roulston and Goodell (2011) argue that the weight of evidence indicates that floral resource limitation is the most common constraint on pollinator populations.

In light of these considerations, categorical notions of floral resource limitation must give way to questions of ecological contingency. *When*, *where*, and *to what degree* are floral resources limiting? Are resources limiting within certain regions of floral trait space (e.g. open, shallow flowers) but not in others (e.g. deep, restrictive flowers)? What processes govern the occurrence and severity of floral resource limitation or induce transitions between limiting and non-limiting states? All these questions stem from the recognition that the floral resources on which pollinators depend, and for which they potentially compete, are *structured in time, space, and functional traits* **(Figure 1)** (see also Timberlake 2019 pp. 9–15). In the sections that follow, we explore each of these dimensions of floral resource structure, synthesizing a scattered body of relevant literature into a coherent conceptual framework.

Box 3: Defining food limitation

It can be said that an organism is "food-limited" if an increase in food availability — either due to increased food supply or the release of food from competition — would increase the organism's fitness (i.e. its reproductive success). By extension, a food-limited population is one whose rate of growth would increase with increased food availability. Importantly, this definition does not require the exhaustion of food resources or the actual starvation of individuals. Since time spent foraging entails energy expenditure, risk of predation, and the delay of other vital activities (e.g. mating, oviposition, nest construction and defense), it can be expected that fitness will generally increase with the temporal *rate* of food acquisition — indeed, this expectation is a key premise of optimal foraging theory (Fretwell and Lucas 1969) and its application to insect pollinators (Goulson 1999). Food acquisition rate will, in turn, increase with resource availability (i.e. "standing crop") (Dreisig 1995), since sparse resources require more travel and searching time to exploit than dense resources. Finally, it can be assumed that there exists some threshold of standing crop above which foraging efficiency becomes effectively saturated and further increases in resource availability have a negligible effect on fitness. Below this threshold, food is limiting and, to the extent that food is shared, com-

petition can occur within and/or between co-occurring species. Note, however, that food limitation is not just a binary state (limiting vs. nonlimiting) but a continuous gradient, quantifiable in terms of the fitness deficit under actual food availability relative to saturating food availability. The realization of competition, moreover, can be modulated by processes other than food limitation, such as positive interactions (e.g. mutualism, facilitation) within or between species and cyclic networks of intransitive competition (Soliveres and Allan 2018), potentially obscuring the relationship between food limitation *per se* and fitness outcomes attributable to competition.
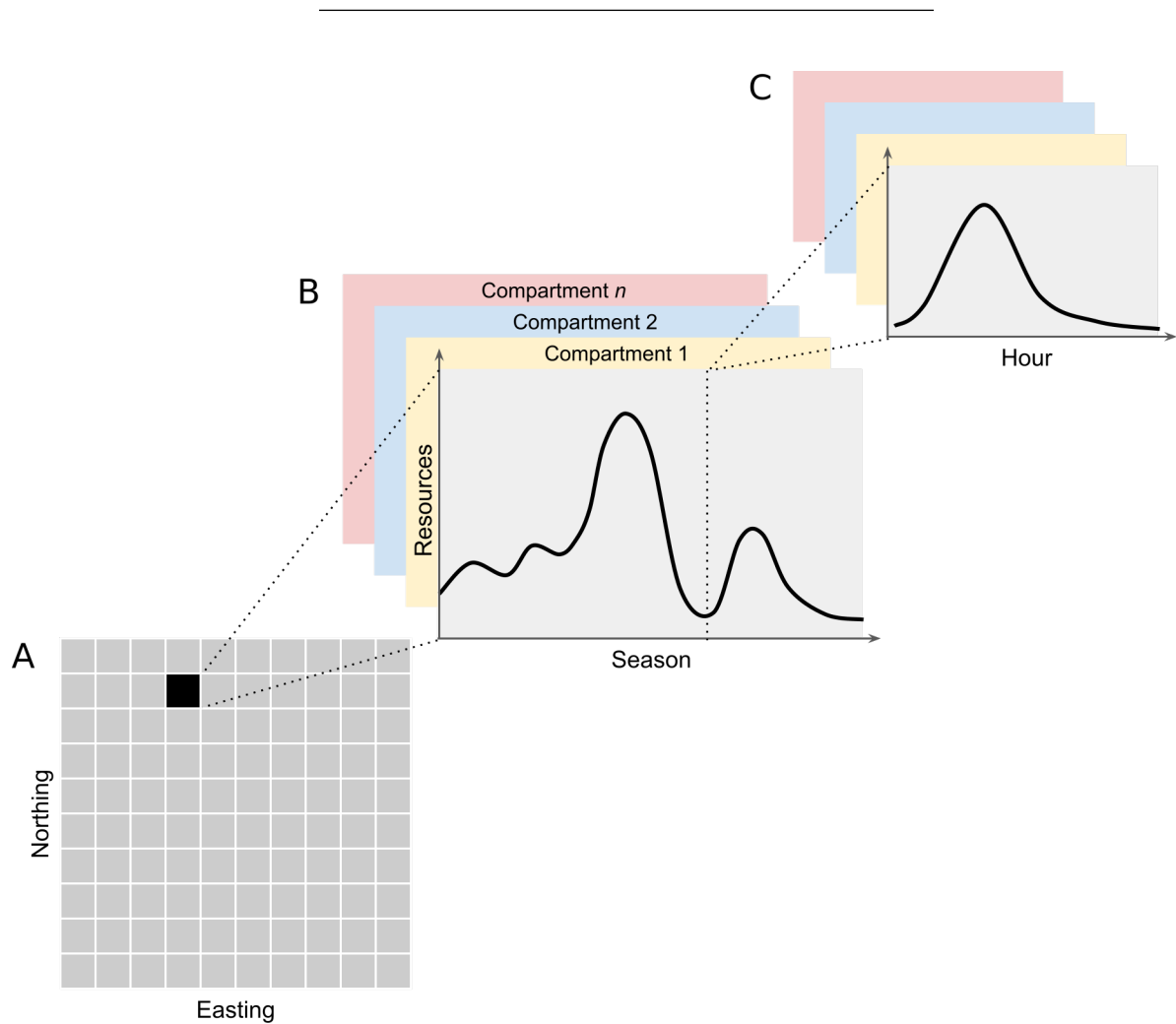

Figure 1: Spatial, temporal, and functional dimensions of floral resource structure. For any spatial unit (A), floral resource availability varies through time at both seasonal (B) and diel scales (C). These patterns, in turn, vary through space, and aggregate floral resource availability at any given time and place is distributed across the functional variation of the floral community (e.g. flower shape, corolla depth, color), which can be represented in discrete form as functional compartments (e.g. zygomorphic flowers, deep flowers, violet flowers).

3. Production, consumption, standing crop, and depletion

Before elaborating the dimensions of time, space, and functional traits in which floral resources are structured, it is important to distinguish four interlocking senses in which floral resource conditions can be understood: production, consumption, standing crop, and depletion. Floral resource *production*, the rate at which resources are released by plants, can be understood loosely as a property of the floral community *per se*, though in fact it is not wholly independent of resource consumers, since flowers can increase nectar production in response to nectar removal (Luo et al. 2014). While the rate of floral resource production can be understood as a rough indication of pollinator carrying capacity, it cannot be used to infer resource limitation or competition unless complemented by rates of floral resource *consumption* (e.g. Timberlake et al. 2019). The *standing crop* is the pool of resources actually available to foragers. For a given time interval, the standing crop is determined by the difference between the rates of production and consumption (adjusted, when relevant, for other processes of resource reduction, such as nectar resorption or flower senescence). Standing crop determines the rate of reward experienced by foragers (Dreisig 1995) and can be interpreted, therefore, as an index of fitness **(Box 3)**. While standing crop is likely to be strongly correlated with resource limitation, it is not a direct indicator of competition; a low standing crop could be the result of low resource production even in the absence of resource exploitation, such as on a day when weather conditions suppress pollinator foraging. Estimates of standing crop can be complemented, however, by estimates of resource consumption to infer resource *depletion*, i.e. the proportion of the potential standing crop actually consumed to yield the realized standing crop (Heinrich 1976). Interpreted jointly, estimates of standing crop and depletion rate reveal both the rate of reward an individual forager experiences and the degree to which that rate of reward would increase in the absence of other foragers, the former serving as an index of fitness and latter as an index of competition.

In the sections below, our primary interest is in the structure of the standing crop and the depletion rate of floral resources, since these concepts bear the most direct relation to pollinator coexistence, though we will also touch on the underlying processes of floral resource production and consumption. We emphasize that each of these patterns and processes can be mapped onto the dimensions of time, space, and functional traits presented in our conceptual framework. We will revisit the distinction between production, consumption, standing crop, and depletion in section 5, where it becomes crucial for guiding and interpreting empirical approaches to floral resource structure.

4. Floral resource structure: time, space, and functional traits

4.1 Time

At the species-level, seasonal flowering phenology can be described in terms of several archetypal patterns (Gentry 1974, Willmer 2011). At one extreme, "steady-state" species produce a small number of flowers over an extended period of weeks or months. At the opposite extreme, "big bang" species produce flowers gratuitously for a period of only a few days, and the timing of this mass-bloom can vary from year to year or even skip years. "Multiple-bang" species follow a similar pattern, but individuals within a population are not synchronized, resulting in multiple mass-blooming events per year (or potentially none at all). Between the extremes of steady-state and big-bang, the "cornucopia" pattern describes species that bloom approximately synchronously at the population level, at a consistent time of year, and produce a moderate number of flowers over a period of more than several days and up to several weeks. The steady-state, big-bang, and multiple-bang patterns occur mostly in the tropics, while the cornucopia pattern prevails in temperate areas.

Species-level flowering phenology plays out in a community context (Robertson 1895), generating community-level patterns of floral resource production through time. Conceiving of floral resources as a dynamic curve through seasonal time rather than as a static trait of a given habitat reframes the question of resource limitation and pollinator competition in explicitly temporal terms (Ogilvie and Forrest 2017). The question of *whether* competition occurs gives way to questions of how the temporal dynamics of resource production interact with those of resource consumption and whether there exist periods of mismatch between supply and demand in which competition between pollinators intensifies (Schellhorn et al. 2015). Timberlake et al. (2019), for example, found that seasonal patterns of nectar availability in agricultural landscapes in England include marked dearth periods in early spring and late summer during which nectar production falls well below the estimated requirements of local bumble bee populations.

The temporal structure of floral resources also obtains at the diel scale, where within-day floral phenology interacts with within-day patterns of pollinator foraging activity. At the species level, diel patterns of nectar production typically follow a three-phase pattern consisting of periods of (1) secretion, (2) cessation, and (3) resorption (Torres and Galetto 1998, Amorim et al. 2013), resulting in a unimodal pattern of nectar availability (usually peaking in the morning) often mirrored by a corresponding pattern of pollinator visitation (e.g. Cavalcante et al. 2018, Ballarin et al. 2022). Notably, however, descriptions of diel patterns of nectar production and pollinator visitation come almost exclusively from single-species case studies; it remains an open question how species-level patterns combine to produce the community-level patterns of nectar availability experienced by generalist pollinators. In one of the only studies of its kind, Percival (1955)

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recorded diel patterns of pollen presentation in a community of 60 species of flowering plants in Wales. At the species level, the timing of peak pollen presentation varied broadly, ranging from early morning (before 9:00) to late afternoon (16:00), and in rare cases even during the night. Aggregated across plant species, though, community-level pollen presentation was generally unimodal and peaked between 8:00 and 11:00, with seasonal variation. Notably, Percival (1955) also recorded concomitant pollen foraging by honey bees, and she found that it tended to be shifted later in the day by roughly two hours relative to the start and peak of pollen presentation, likely due to the sensitivity of honey bees to cool air temperatures. The concentration of honey bee foraging activity at midday could provide a competition refuge in diel time for pollinator species that can forage under cooler conditions (Tepedino 1981, Araújo et al. 2022).

These seasonal and diel dynamics of floral resources raise questions about an assumption built into even the most sophisticated consumer-resource models of pollinator coexistence (e.g. Valdovinos and Marsland 2021), namely that resource production rate can be treated as a constant, with variation in standing crop driven only by the adaptive allocation of pollinator foraging effort. Even if consumer-resource models can be made robust to the temporal structure of floral resources, though, their core premise of floral resource limitation might prove to be temporally contingent over both season and diel time scales.

Behind seasonal and diel patterns of floral resources there also exist processes that influence floral resources over supra-annual time scales. We will revisit this topic in Section 5.3.

4.2 Space

Just as community-level floral phenology interacts with pollinator foraging to structure floral resources in time, so the non-uniform *spatial* distribution of flowers and florivores can generate spatial heterogeneity in floral resources, a phenomenon that Pleasants and Zimmerman (1979) aptly describe as a fluctuating "nectar topography."

Before exploring the spatial structure of floral resources, though, it is worth considering a process that might be expected to negate it, namely *optimal foraging*. Optimal foraging theory (OFT) predicts that spatial heterogeneity in floral resource production should be dampened by the tendency of foragers to distribute themselves across flower patches in proportion to the rate of reward experienced by individual foragers at each patch, thus equalizing individual rate of reward across all co-exploited patches (Fretwell and Lucas 1969, Goulson 1999). So, from the perspective of a given species at a given time and place, spatial structure in floral resource production is, in a sense, behaviorally averaged out into a more or less uniform standing crop. This effect is perhaps most intuitive in the colony-level foraging behavior of eusocial species like honey bees

and bumble bees, which have indeed been shown to allocate foraging effort in a manner that approximates the predictions of OFT (Bartholdi et al. 1993, Dreisig 1995). In principle, though, the theory applies also to solitary species at the population level.

OFT depends on idealizing assumptions that never obtain perfectly in real systems, including that foragers have perfect knowledge of their environment and that there exist no constraints (e.g. interference competition) on their selection or exploitation of patches. Even in cases when the assumptions of OFT are well-approximated, though, the spatial structure of floral resources remains important. Since pollinator species vary in foraging range (Gathmann and Tscharntke 2002, Greenleaf et al. 2007) and pollinator nest sites are distributed in space, neighboring colonies or individuals optimize their foraging over non-identical (but potentially overlapping) subsets of their shared landscape (Westphal et al. 2006), and therefore experience different rates of reward (Olsson et al. 2015).

With respect to competition and coexistence, the outcome of these underlying mechanisms by which pollinators interact with spatially heterogeneous floral resources can be expected to be mediated by the behavioral and physiological traits of the species involved. For example, Bolin et al. (2018) demonstrate that a tradeoff between foraging range and metabolic rate can allow two species with different foraging ranges to coexist stably. Moreover, while we have assumed the approximation of OFT, with its tendency to negate spatial heterogeneity in floral resources, it is important to remember that the spatial structure of floral resources interacts with the temporal dynamics described above, which may prevent the equilibrium conditions of OFT from being realized. When temporal dynamics are considered in conjunction with spatial heterogeneity, the process of patch *discovery* can be decisive in determining foraging efficiency (Visscher and Seeley 1982, Schürch and Grüter 2014), invoking the classical concept of "fugitive species" and the potential for a stabilizing tradeoff between colonization (in this case, patch discovery) and dominance (Hutchinson 1951, Hanski 1995).

Finally, it is important to note that our discussion thus far has assumed central place foraging. For non-central-place foragers, like butterflies and hover flies, the spatial component of floral resource structure becomes difficult to define. Nevertheless, spatial patterns of floral resources still matter for non-central-place foragers, and while their activity area is not determined by nest site locations, it is constrained by the occurrence of host organisms for oviposition. The latter consideration could provide a basis for extending some aspects of central-place foraging theory to non-central-place foragers.

4.3 Functional traits

The temporal and spatial patterns discussed above interact to determine the floral resource conditions at any given time, place, and spatiotemporal scale. The flowers of a floral community are not, however, merely interchangeable packages for uniform commodities. Both flowers and the resources they contain vary in a suite of functional traits that interact with the functional traits of pollinators to determine the degree to which a given pollinator species uses a given floral species and, consequently, the degree to which different pollinator species overlap in their dietary niches (Junker and Parachnowitsch 2015, Cappellari et al. 2022).

Popular accounts of plant-pollinator co-evolution tend to emphasize the selection pressure on plants and pollinators toward mutual *compatibility*. On the part of plants, however, this process is balanced by selection pressure toward *incompatibility* with potential visitors that would exploit floral resources without increasing plant fitness (e.g. due to nectar robbing, floral damage, or heterospecific pollen deposition) (Junker and Parachnowitsch 2015). Similarly, coexisting plant species may diverge in functional traits as a means of partitioning the pool of potential visitors and minimizing competition for pollinators (e.g. Armbruster et al. 1994).

For a thorough treatment of floral traits and their mediation of plant-pollinator interactions, we refer the reader to Junker and Parachnowitsch (2015). Briefly, visual and olfactory traits filter the potential visitor community by attracting (or "advertising" to) some species and repelling (or "hiding" from) others. When, on the basis of vision and olfaction, a pollinator selects a flower, it must then interact with the morphology of the flower to obtain the reward, which can be variously obstructed or concealed by structures such as deep corollas, nectar spurs, viscin-threaded pollen, or appressed keel petals. Finally, the traits of the reward itself — e.g. the volume and concentration of nectar (Balfour et al. 2021), the protein and lipid content of pollen (Vaudo et al. 2016), the presence of stimulating or toxic secondary compounds (Adler 2000, Wright et al. 2013, Rivest and Forrest 2020) — function to reinforce or deter further visitation. Thus, the interaction between floral functional traits and insect visitors involves the interplay of attraction and repulsion, accessibility and preclusion, reward and penalization.

The net effect of the functional structure of floral resources is to distribute the resource consumption of each pollinator species — and the overlap of resource consumption *between* pollinator species — non-uniformly across the spectrum of floral resources produced in the landscape. Any claims, therefore, about floral resource limitation have to be "located" in functional space. Moreover, the functional heterogeneity of floral resources, interwoven with that of the pollinators that feed on them, raises an important distinction that has thus far remained latent in our discussion of competition, namely the crucial difference between *inter-* and *intra-*

specific competition. It is this distinction that defines the relationship between competition and *coexistence*, since the fundamental condition for coexistence is not the absence of competition but rather that competition *within* species exceed competition *between* species, such that each species limits its own population density more than it limits that of other species (Hanski 1995). Whether this condition is met depends on the degree of realized niche overlap within and between species, which in turn depends on the functional trait interactions that determine flower selection by pollinators. Thus, just as floral resource limitation is structured in functional trait space, so also are the *consequences* of floral resource limitation: given resource limitation, whether a set of species coexist stably or tend toward competitive exclusion is contingent on the functional structure of the floral resource pool. This has important implications for understanding the impacts of land use change — including conservation management — on pollinator diversity, a topic we will revisit in section 5.

5. A research agenda

As we have shown above, the heterogeneity of floral resources in time, space, and functional traits has deep theoretical roots and is a common thread running through a broad empirical corpus. Nevertheless, studies explicitly focused on floral resource structure are rare, likely due both to methodological limitations and a lack of clearly formulated questions.

To motivate and facilitate the study of floral resource structure and its relevance to pollinator coexistence, we propose a research agenda consisting of three domains (**Figure 2**). First, it is necessary to develop empirical and analytical techniques for measuring floral resource structure in the field and summarizing its high-dimensionality with appropriate metrics. Once measured and summarized, floral resource structure can be studied as both a cause and effect of other ecological phenomena. As a cause, floral resource structure influences processes of competition and coexistence that ultimately shape pollinator communities. Pollinator community composition, in turn, feeds back into floral resource structure through immediate effects on patterns of resource consumption and long-term effects on plant reproduction. In addition to this causal dialectic between plant and pollinator communities, both are susceptible to exogenous influences — biotic and abiotic, acute and chronic — that are often related to human activity.
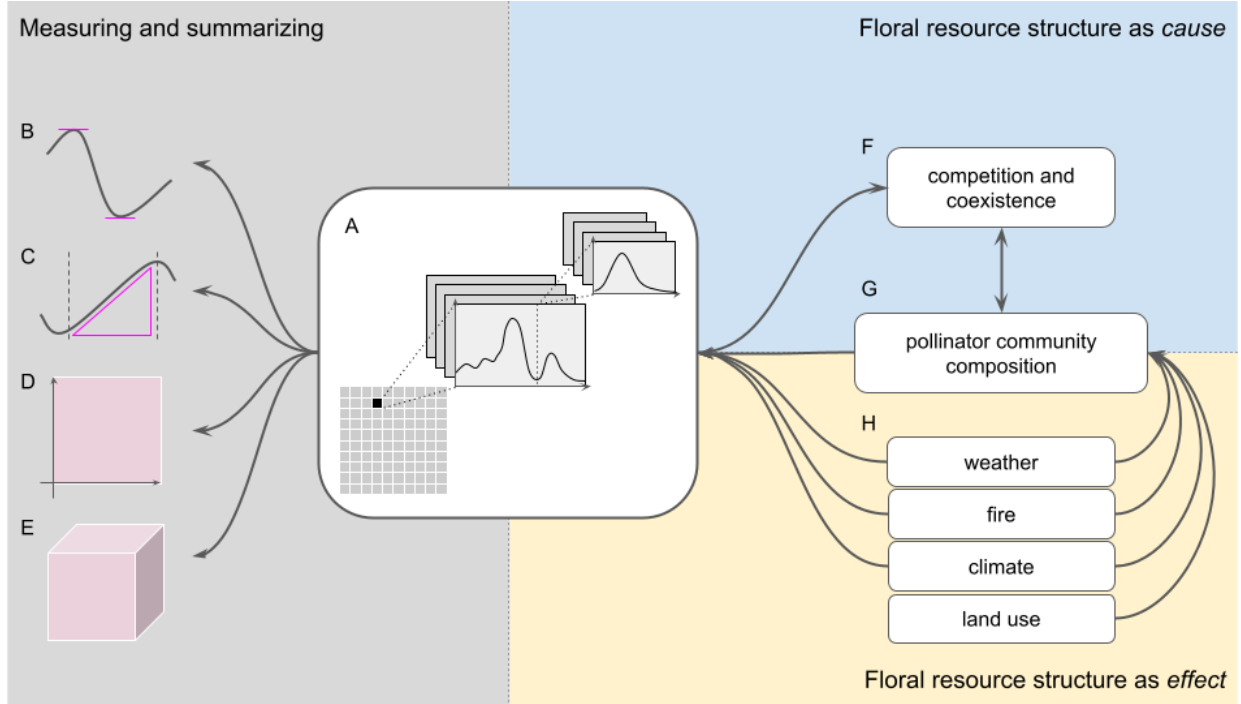
Figure 2: A three-domain research agenda for the study of floral resource structure. Empirical and analytical techniques are needed for measuring floral resource structure (A) and deriving meaningful summary metrics, such as temporal maxima and minima (B), slopes over discrete time frames (C), dimensionality reduction via ordination (D), and full-dimensional analysis using hypervolumes (E). When appropriately measured and summarized, floral resource structure can be studied inferentially as a modulator of competition and coexistence (F) and ultimately a driver of pollinator community composition (G). Conversely, floral resource structure is also an effect of pollinator community composition, together with a suite of exogenous drivers (H).

5.1 Measuring and summarizing floral resource structure

Measuring floral resources at spatial and temporal scales relevant to pollinator foraging is a long-standing methodological problem (Frankl et al. 2005) involving the perennial tradeoff between data quality and scalability. Moreover, different empirical approaches capture different aspects of floral resource structure (production, consumption, standing crop, and depletion), and the selection of what to measure must be aligned carefully with research questions.

The most basic approach to quantifying floral resources is simply counting flowers or summing flower cover (e.g. Tepedino and Stanton 1980). The obvious limitation of this approach it does not measure nectar or pollen directly (Zimmerman and Pleasants 1982), but in some cases flower density can be strongly correlated with nectar and pollen density (Hicks et al. 2016).

A more sophisticated approach that has enjoyed popularity in recent studies is to generate species-level

estimates of resource production by sampling flowers from which pollinators have been excluded (Pleasants 1981); then, these species-level estimates are propagated to the level of landscapes via floristic surveys and projected through time via phenological models (e.g. Baude et al. 2016, Hicks et al. 2016, Tew et al. 2021). The strengths of this approach are that it relies on established field methods and can (with caveats) yield floral resource estimates over large scales of time and space with relatively modest empirical work. One drawback to this approach is the potential for errors or biases in a small set of direct measurements to be propagated to whole populations and landscapes, particularly when values are imputed outside the ecological context in which they were measured. Emergent remote sensing techniques could potentially mitigate errors stemming from field surveys (Barnsley et al. 2022), but the application of remote sensing to floral surveying is still in its infancy. More importantly, though, this approach—like simple flower counting—only provides estimates of floral resource *production*. While estimates of floral resource production can be interpreted as indicators of pollinator carrying capacity, they are of little relevance to questions of competition and coexistence unless complemented by estimates of resource *consumption*, e.g. by modeling the energy requirements of a local pollinator community (Timberlake et al. 2019, Jachuła et al. 2021).

Instead of focusing on floral resource *production*, one can measure directly the *standing crop* of floral resources by sampling flowers open to pollinator visitation (e.g. Heinrich 1976). Combined with concomitant sampling of flowers from which pollinators have been excluded, this approach enables the calculation of resource *depletion* rate (Heinrich 1976). Joint inference from standing crop and depletion rate is richly informative, since the standing crop can be interpreted as an index of pollinator fitness (all else held equal — see **Box 3**) and the depletion rate can be interpreted as an index of competition intensity (Heinrich 1976). Estimates of standing crop and depletion rate, however, scale poorly; they cannot be imputed beyond the time and place in which they are measured, since they depend not only on (putatively) generalizable rates of resource production but also on idiosyncratic local rates of resource consumption.

Another approach that has gained traction in recent years is to infer floral resource conditions through the use of an indicator organism. Honey bee colonies have been recommended for this purpose because they are generalist foragers and furnish several readily obtained indices of floral resource conditions, including colony weight dynamics, foraging distances encoded in waggle dances, responsiveness to artificial feeders, and conflict levels at the nest due to robbing behavior (Couvillon and Ratnieks 2015, Danner et al. 2016, Sponsler et al. 2020, Garbuzov et al. 2020) **(Figure 3)**. In principle, though, other indicator organisms, such as bumble bee colonies or trap-nesting solitary bees, could be used to obtain measures of nest weight or foraging rate that could be interpreted as proxies of floral resource conditions (Requier et al. 2020). Inferences based on an indicator organism represent the *standing crop* of floral resources and, therefore,

provide an attractive compromise between scalability and relevance to competition. These inferences could also be complemented by spot checks of floral resource depletion rates to determine whether periods of low standing crop are also periods of high depletion (indicating strong competition). Drawbacks of this approach, however, include the extraneous influence of the life history, activity patterns, and floral selection biases of the indicator organism. Careful consideration must also be given to the spatial scale at which an indicator organism can be understood to represent floral resource conditions.
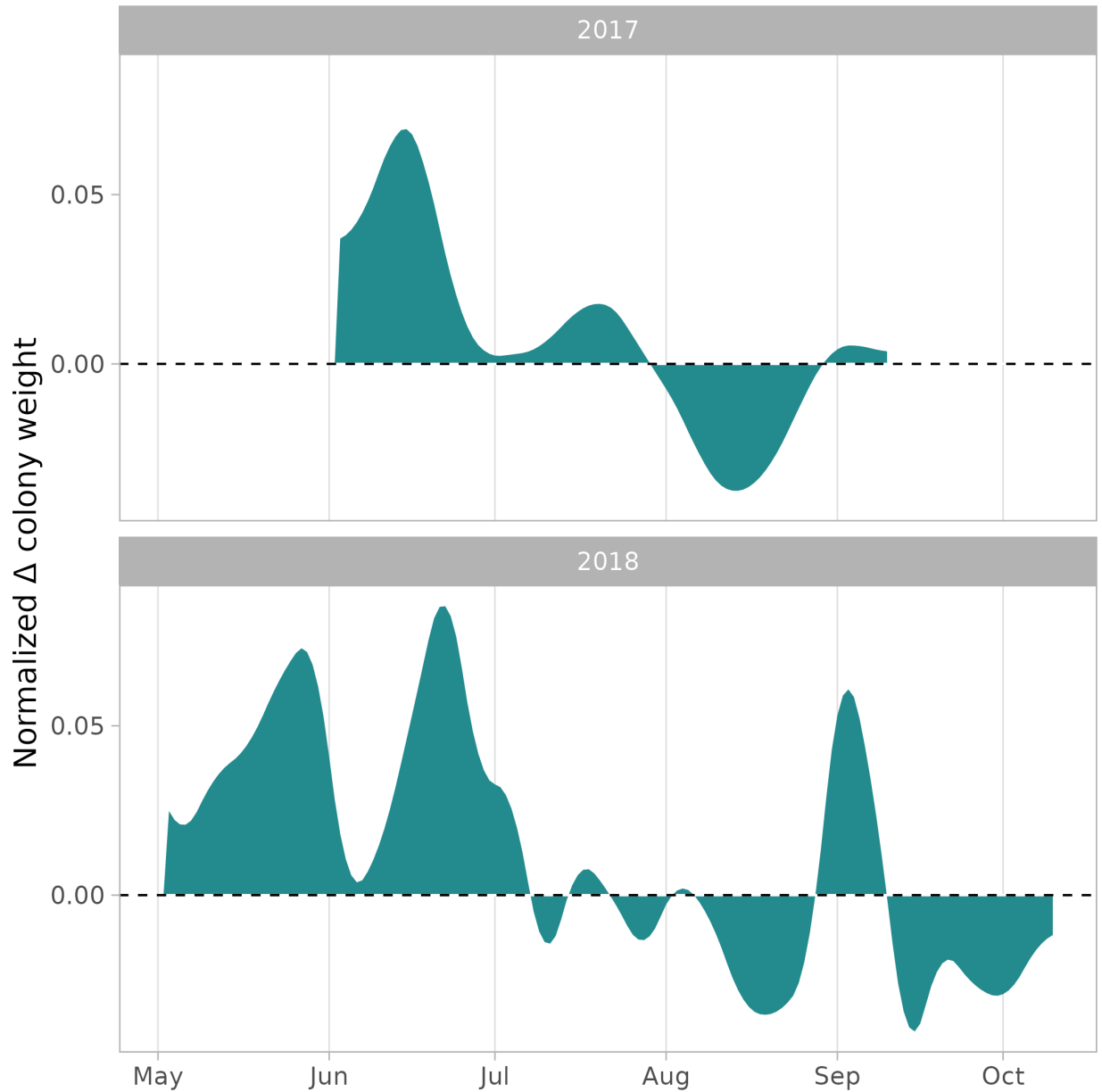
Figure 3: Honey bee colony weight dynamics as an indicator of seasonal patterns of floral resource availability. Portions of the curve above zero (dotted line) indicate weight gain while portions below zero indicate weight loss. This study system (Philadelphia, PA) exhibits the classic pattern of summer dearth (mid-August) that has been described in many temperate systems. Two strong pulses of floral resource abundance are evident in the spring, and a brief late pulse occurs after the summer dearth. Figure redrawn from Sponsler et al. (2020).

Alternatively, similar inferences might be achieved via a *floral* indicator species. As discussed earlier, optimal foraging theory (OFT) predicts that foragers will distribute themselves so as to equalize individual rate of reward across resource patches, and there is some evidence that flower-visiting insects approximate this pattern (Bartholdi et al. 1993, Dreisig 1995). Individual rate of reward for a given patch is, with certain

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qualifications (e.g. Possingham 1989), proportional to its standing crop of resources (Dreisig 1995). Thus, the standing crop of a floral indicator patch (i.e. a "phytometer") could be monitored as a proxy for the standing crop encountered across all floral patches in the landscape that are simultaneously exploited by the pollinator species visiting the phytometer. This approach is, however, not yet well established, and baseline empirical work is needed to validate it (though see Steffan-Dewenter et al. 2001, Garbuzov et al. 2020).

Regardless of the method used to measure the components of floral resource structure, the inferential use of floral resource structure as either a predictor or a response generally will require some means of summarization. For example, seasonal time series of floral resources often exhibit consistent oscillations between relative abundance and scarcity (e.g. Sponsler et al. 2020), and the maxima, minima, or slopes associated with such motifs can be expressed as single values and modeled as predictors or responses. Functional traits of floral communities can be summarized with metrics of functional diversity (Magneville et al. 2022) or mapped onto lower-dimensional space via ordination (Junker and Parachnowitsch 2015). Beyond these more conventional techniques, Junker and Larue-Kontić (2018) demonstrated that floral functional traits can be treated as an n-dimensional hypervolume, an approach that furnishes a growing number of analytical options, including methods for estimating the size and overlap of hypervolumes (Blonder 2018). In principle, this approach could be extended to incorporate the temporal and spatial dimensions of floral resource structure. Nevertheless, Blonder (2018) warns against using hypervolumes when dimensions can be expected to interact with each other, as floral functional traits are known to do even without incorporating time and space (Junker and Parachnowitsch 2015).

5.2 Floral resource structure as *cause*

We have framed our discussion of floral resource structure around the issue of pollinator competition, arguing that the latter can be understood only in light of the former. The causal processes that link these phenomena, however, are complex, and they lie on the frontier of both theoretical and empirical research. These processes also occur over both ecological and evolutionary time scales, and research questions should be formulated accordingly.

One of the central themes emerging from our discussion is the temporal dynamism of floral resources, manifest at multiple scales. This implies that floral resource limitation, and hence competition, are similarly dynamic in time. Biological fitness, however, is defined at discrete generational time steps, each of which can be understood as an integration of all the continuous processes that determine the number of surviving offspring an organism can produce. Thus, two species can be said to compete only if the presence of one species has a

net negative effect on the population growth of the other. This raises a very difficult but motivating question: how, and under what conditions, does spatiotemporally transient resource limitation (operationally defined in terms of foraging rate; see **Box 3**) translate into net fitness effects across generations? For example, consider a bumble bee colony and a neighboring honey bee colony. Does a one-week period of resource scarcity in late spring, during which the foraging rate of the bumble bee colony is diminished by exploitative competition from the honey bee colony, lead to the production of fewer bumble bee gynes and males in late summer? Or, inversely, can transient floral resource surplus buffer a species against the effect of food-limited baseline conditions? While a thorough treatment of these questions is beyond the scope of our paper, we would point out they lead in the direction of a rich theoretical literature concerning resource pulses (e.g. Holt 2008) and species coexistence in variable environments (e.g. Chesson 1994). In particular, an organism's capacity for food storage (e.g. honey or pollen hoarding) can be expected to be instrumental in determining its response to temporal variation in floral resource availability (Holt 2008).

Theoretical uncertainties notwithstanding, the conceptual framework of floral resource structure as a driver of pollinator community assembly can serve as a guide for more nuanced empirical studies. Traditionally, community-ecological approaches to plants and pollinators have focused on correlations between pollinator communities and coarse floristic summaries, such as species richness or aggregate flower cover. Approaching plant-pollinator community ecology with an appreciation for floral resource structure enables the formulation of more causally explicit questions and the more targeted collection of data. For example, floral *functional* diversity may better explain pollinator diversity than mere floral species richness, and patterns of peaks and troughs of floral abundance through seasonal time may furnish a richer account of pollinator abundance than temporal snapshots or averages of flower cover. These considerations are especially important in studies concerning competition between pollinators. Before measuring putative indicators of competition (e.g. inversely correlated abundance patterns), available knowledge of the study system and species involved should be used to identify times, places, and regions of trait space where food is likely to be limiting, and findings should be interpreted in a way that acknowledges the temporal, spatial, and functional contingency of competition. If insufficient prior knowledge exists, measurement of floral resource structure — particularly floral resource depletion rates — should precede or accompany the measurement of other competition indices.

5.3 Floral resource structure as *effect*

Thus far we have focused on floral resource structure as a *cause* of pollinator communities, but causation also flows in the opposite direction. Over short time scales, the consumption of floral resources by pollinators yields patterns of standing crop and depletion rate (Heinrich 1976, Dupont et al. 2004), potentially

with cascading effects on the structure of interaction networks and pollination services (Brosi and Briggs 2013). These impacts can be especially pronounced when a new pollinator species invades an existing plant-pollinator network, a scenario epitomized by the massive introduction of managed honey bees into habitats previously comprised of wild pollinator species (Valido et al. 2019). Over longer time scales pollinator visitation influences plant traits and community assembly via competition between plants for pollination services (Robertson 1895, Mitchell et al. 2009). Importantly, floral resource structure is also sensitive to the invasion of exotic plant species, directly via their effects on floral resource production and indirectly via the redistribution of floral resource consumption by the pollinator community (Hachuy-Filho et al. 2020).

Floral resource structure is also influenced by exogenous drivers such as climate and land use change, fire, and weather events, both via the effect of these forces on plant-pollinator community composition and by their direct influence on the physiology and behavior of species already present. Thus, floral resource structure *as an ecological effect* mediates the response of plant-pollinator communities to local disturbances and global change processes.

Directed processes occurring over large spatial and temporal time frames, such as climate and land use change, can induce systematic shifts in floral resource structure. One of the most pronounced effects is the alteration of seasonal patterns of floral resource availability. In the Rocky Mountains, for example, climate-driven shifts in air temperature and the timing of snowmelt have generated an early season shift in floral abundance, a net expansion of the flowering season, and the emergence of a mid-season gap in floral abundance (Aldridge et al. 2011, CaraDonna et al. 2014, Ogilvie et al. 2017). In addition to influencing seasonal patterns of aggregate floral resource availability, climate shifts can affect individual plant species in different ways, resulting in altered patterns of co-flowering among species (e.g. CaraDonna et al. 2014, Theobald et al. 2017), with corresponding effects on the distribution of floral availability across functional space. There is even evidence that rising carbon dioxide levels can alter pollen protein content via effects on plant metabolism (Ziska et al. 2016). Similarly, land use processes such as urbanization, agricultural intensification, and agricultural abandonment can drive shifts in floral resource availability via their effects on the distribution, composition, and local climate of plant species (Baude et al. 2016, Walcher et al. 2017, Ganuza et al. 2022, Cabon et al. 2022).

Stochastic and episodic events can also shape floral resource structure in both transient and persistent ways. Fire is one of the most powerful episodic processes in nature, and it is a defining feature of many ecosystems. While the acute effect of fire on floral resource availability is the obliteration of virtually all flowers, the successional process initiated by fire can dramatically increase floral resource abundance and diversity in recently burned sites relative to older plant communities (Potts et al. 2003). While typically

less dramatic than fire, the vagaries of weather are increasingly appreciated as drivers of plant-pollinator relationships via their effects on both the production of floral rewards by plants and the collection of floral rewards by pollinators. Drought, for example, can suppress both pollen and nectar production (Waser and Price 2016, Phillips et al. 2018) and even cause shifts in functional traits by altering the composition of floral volatiles (Rering et al. 2020). Conversely, heavy rains can both suppress pollinator foraging activity and cause mechanical damage to delicate flowers, such as those of the black locust *Robinia pseudoacacia* (Papadopoulou et al. 2018). A study of the buff-tailed bumble bee (*Bombus terrestris*, L.) found that the ratio of pollen to nectar foraging increased under drier weather conditions, indicating that weather can not only regulate the rate of pollinator activity but induce qualitative shifts in pollinator foraging behavior (Peat and Goulson 2005). With respect to episodic modulators of floral resource availability, one must remember MacArthur's (1984 p. 21) insight that even transient competition can have lasting effects on species coexistence.

Alongside these natural or inadvertent drivers, it is important to consider from an explicitly structural perspective the consequences of human interventions *intended* to affect floral resources. Many efforts to conserve pollinators — including some folded into formal government programs like Agri-Environment Schemes in the EU or the Conservation Reserve Program in the US — are based on the simple reasoning that more flowers will equal more bees (Scheper et al. 2013, Cole et al. 2020). But simply boosting the aggregate volume of floral resources without considering seasonal dynamics of availability may result in amplified oscillations between abundance and scarcity rather than the desired effect of relieving floral resource limitation during dearth periods (Ogilvie and Forrest 2017, Timberlake et al. 2019, Ogilvie and CaraDonna 2022). Moreover, increasing floral resource abundance without aligning floral functional traits to the needs of vulnerable pollinator species could simply increase the dominance of already-abundant species (Sutter et al. 2017). Similarly, it is notable that, in both scientific literature and popular discourse, it is often simultaneously assumed that pollinators are generally limited by floral resources *and* plants are generally limited by pollinator visitation. This pair of assumptions is implicit, for example, whenever the enhancement of local pollination services is invoked as a reason to augment floral habitat for pollinators. While scenarios in which pollinators compete for floral resources without satisfying the visitation requirements of their hosts are theoretically possible (e.g. due to nectar robbing or heterospecific pollen deposition), it is more likely that resource-limitation for pollinators implies pollen-saturation for plants, and a sweet world for pollinators is one in which plants compete for visitation (Mosquin 1971, Roubik and Buchmann 1984, Ratnieks and Balfour 2021).

6. Conclusion

Floral resource structure, we have argued, mediates potential competitive interactions between pollinators by determining when, where, and in which functional compartments floral resources are limiting. Whether "sweet world" conditions — those in which pollinator populations are *not* limited (or weakly limited) by floral resources — are the exception or the rule in plant-pollinator communities remains poorly understood, but theoretical and empirical lines of evidence indicate that both limiting and non-limiting conditions are possible, and understanding the causes of such conditions and of transitions between them should be a priority in future research. Such research will require the development of versatile techniques for measuring and summarizing floral resource structure, but a strong methodological foundation already exists, ready to be refined and aligned to clear research questions.

Descriptive approaches to floral resource structure should ultimately be directed toward the integration of empirical and theoretical strains of plant-pollinator community ecology. The trophic-ecological perspective on floral resources that we present complements consumer-resource modeling approaches to pollinator co-existence (e.g. Valdovinos and Marsland 2021), since the former elucidates the patterns of floral resource limitation on which the latter is predicated. Understanding floral resources in terms of temporal, spatial, and functional structure also harmonizes with the recent move in ecological network analysis toward spatially and temporally explicit approaches (Burkle and Alarcón 2011, Bramon Mora et al. 2020, CaraDonna et al. 2021).

Uniting pattern and process is the crux of *application*. Clarifying the causal relationships between floral resource structure, pollinator coexistence, and plant-pollinator interactions — as well as the sensitivity of each to exogenous drivers — will provide a coherent basis for addressing contentious management issues, such as the compatibility of apiculture with wild pollinator conservation and the appropriate use of floral enhancements in agri-environment schemes.

With regard to the specific issue of potential competition between managed honey bees and wild pollinators, one very practical implication of our discussion is that it would be prudent to evaluate floral resource standing crop and depletion rate (see Section 5.1), at relevant times of year, when considering the introduction of honey bees to a given locality. This kind of site assessment protocol could complement other approaches to apicultural regulation (e.g. Henry and Rodet 2020), and the information gained would be as useful to beekeepers as to conservationists, since neither party benefits from the addition of colonies to an already resource-scarce situation (e.g. Alton and Ratnieks 2016). Ideally, pre-introduction site assessment should be complemented by post-introduction assessment to evaluate the impact of added honey bee colonies on floral

resource conditions.

While our discussion has focused on the role of food in regulating pollinator populations, it is important to remember that all populations are limited by *something*, and the possibility of non-limiting floral resource conditions implies the operation of other constraints, such as nest site limitation, predation, disease, or even intrinsic physiological limits on reproductive rate (Roulston and Goodell 2011).

If plant-animal mutualisms are the "architecture of biodiversity" (Bascompte and Jordano 2007), floral resource structure is one of its chief foundations (Hale et al. 2020). Its significance extends beyond the mutualism between plants and pollinators *sensu stricto* to embrace all forms of flower-florivore interactions, together with the myriad dependents on fruit and seed production, among which humans stand as notable examples.

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