

# The importance of competition between insect pollinators in the Anthropocene

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Resource competition likely plays an important role in some insect pollinator declines and in shaping effects of environmental change on pollination services. Past research supports that competition for floral resources affects bee foragers, but mostly with observational evidence and rarely linking foraging with population change. An increasing number of studies ask whether resources limit pollinator populations, using field measurements of reproductive success, time series and models. Findings generally support positive effects of floral resources, but also highlight the potential importance of nest site availability and parasitism. In parallel, recent experiments strengthen evidence that competition reduces access to floral resources. Developing common currencies for quantifying floral resources and integrating analyses of multiple limiting factors will further strengthen our understanding of competitive interactions and their effects in the Anthropocene.

## Addresses

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**Current Opinion in Insect Science** 2020, **38**:55–62

This review comes from a themed issue on **Ecology**

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Edited by **Thomas C Ings** and **Sarah EJ Arnold**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 6th February 2020

<https://doi.org/10.1016/j.cois.2019.11.001>

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## Introduction

Interspecific competitive interactions are crucial to understanding and managing pollinator communities and pollination services in the Anthropocene. First, competition from non-native and managed pollinators may be an important contributor to native pollinator declines [1,2]. In addition, competitive interactions among both native and non-native species can play a major role in mediating responses to other environmental changes. Species persistence and pollination services under habitat loss and climate change both likely are shaped by competition and niche partitioning [3–5].

Many studies going back to the 1970s test for competition in pollinator communities, primarily with bees competing for floral resources (nectar and pollen) [6]. Much of this work focuses on potential negative effects of species widely introduced outside their historic ranges, such as *Apis mellifera* and *Bombus terrestris*. This now substantial literature supports that competition often changes bee forager abundances and behavior, although with mixed results across systems [2].

Yet, fundamental gaps remain. The majority of studies observe pollinators at a small spatial scale, for only part of a single flight season (Figure 1). We know much less about how short-term, local changes in forager numbers or plant use relate to fitness and population dynamics. This crucial link between foraging and populations depends on temporal variation in floral resources, as well as how limited pollinators are by less well-studied factors such as survival during diapause, nest site availability and parasites (Figure 1). Further, most studies are observational, measuring niche overlap or negative correlations between species abundances. Experiments remain rare, given logistical challenges of manipulating pollinators and floral resources in the field. This makes untangling the effects of competition from other factors very difficult, a crucial problem given the diversity of threats facing pollinators [7].

The last several years have seen an exciting surge in research addressing these two key issues. While many recent studies do not directly test for competition, they represent an important step forward in beginning to shed light on the mechanistic links that connect resources to populations and communities (Figure 1). This work also highlights novel approaches and continuing challenges for studying insect pollinator competition.

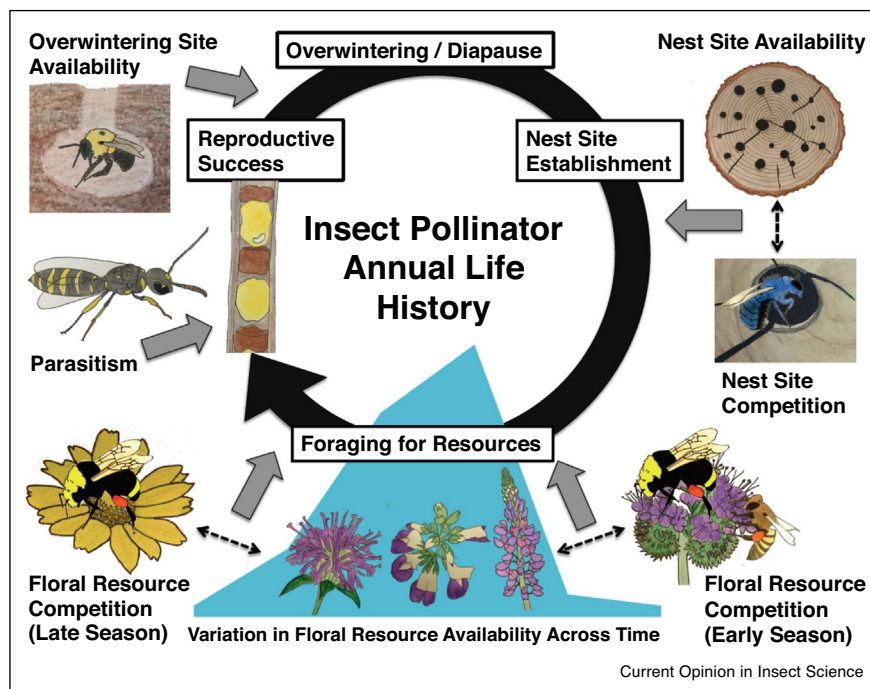
## Linking resources to populations

For competition to strongly influence pollinator communities, resources such as nectar, pollen or nest sites must limit population growth. To predict how competition interacts with global change, we also need to know what resources are limiting and when they are limited, both within and across years. Recent, novel work addressing this crucial link between resources and population growth takes three broad approaches.

## Drivers of reproductive success

One valuable and growing area of research moves away from measuring forager abundances on flowers to measuring reproductive success, using trap nests or

Figure 1



Conceptual diagram illustrating different limiting factors (grey arrows) that potentially determine reproductive success and population growth in insect pollinators over annual flight seasons (black circular arrow). Competition can change availability of nest site, nectar and pollen resources; in turn, the intensity of competition depends on resource abundance (dashed arrows). Short-term competition among foragers may not affect reproductive success, depending on timing relative to variation in floral resources across the flight season. Other potential limiting factors such as parasitism (middle left) or pesticide exposure (not shown) also mediate the influence of nesting and forage resources on reproduction. Whether differences in reproductive success translate into population change in the next year depends on survival during diapause and after spring emergence. Artwork by M. L. Page.

lab-initiated colonies introduced to the field [8–10,11<sup>\*\*</sup>,12–22]. Associations between reproductive success and potential causal drivers such as floral resource availability can then be tested, connecting fitness metrics such as solitary bee brood cell numbers or *Bombus* colony male and queen production to proxies of resource abundance (Table 1).

The majority of these studies show positive relationships between floral resources and at least some measures of reproductive success (Table 1), strengthening the case that changes in resource availability due to competition are likely to affect fitness. However, important uncertainties remain. Sometimes floral resources predict *Bombus* early season colony weight gain or worker numbers, but not whether or how many new queens are produced [20,21]. Counterintuitive or even seemingly contradictory results can emerge when multiple habitat or resource variables are tested, and these different metrics likely correlate in complex ways (Table 1). Few studies consider more than one potential limiting factor, and those that do find weaker relationships between reproductive success and floral resources than for parasitism [11<sup>\*\*</sup>] or nest site availability [18].

A key limitation to drawing general conclusions is that approaches for quantifying floral resources are widely variable and generally very coarse in scale. Common proxies of resource availability include total flower cover or density combined across all species, amount of land with a given crop, or habitat categories (Table 1). Most competition research focuses on foraging at the scale of flower patches, for specific plants and even resources (nectar or pollen). This mismatch in how resources are measured in different studies is a significant barrier to connecting recent findings with the existing competition literature. Further, different habitat types almost certainly vary not only in floral resources but also in other potential limiting factors such as nest site availability or pesticide exposure [16,23]. While valuable for addressing questions about land-use practices, large-scale metrics of resource availability do not provide fine-scale resolution to ask whether nectar limitation, pollen limitation [24] or both [19] matter for particular pollinators.

Some interesting recent findings nevertheless are highly relevant to our understanding of competitive interactions. For example, pollinators often narrow their diet breadth in response to competitors [25<sup>\*</sup>]. Floral resource diversity

Table 1

**Studies testing relationships between floral resources and bee reproductive success, summarized by: Habitat, including continent (NA = North America, SA = South America); focal species; metrics of floral resources; measures of reproductive success that showed a positive (+) or no (0) response to floral resources; and other variables that showed negative, no or positive (-/0/+) relationships with reproductive success**

Reference	Habitat	Species	Floral measures	Response (+)	Response (0)	Other factors (-/0/+)
[8]	Agricultural (Europe)	<i>Osmia bicornis</i>	Distance to key forage plants		Total brood cells Mean nest size	Habitat type (+) Nesting habitat (0)
[9]	Agricultural (Europe)	trap-nesting bees	Total cover	Total brood cells		Parasitism (0)
[10]	Desert (SA)	trap-nesting bees	Total density Diversity Stability		Total brood cells Mean nest size	
[11**]	Subalpine (NA)	<i>Osmia iridis</i>	Density of two host plants	Rate brood cell production	Total per capita reproduction	Parasitism (-) Temperature (+)
[12]	Agricultural (Europe)	<i>Bombus terrestris</i>	Late spring cover Crop type	Diversity collected pollen Colony weight gain		Habitat heterogeneity (0)
[13]	Mixed (Australia)	<i>Tetragonula carbonaria</i>	Diversity Habitat type	Brood, queen production Population growth		Total floral abundance (0) Diversity pollen loads (+)
[14]	Grassland (Europe)	<i>Bombus terrestris</i>	Woody pollen collected	Colony growth rate		Amount semi-natural habitat (-) Pollen quality (-)
[15]	Reclaimed (NA)	<i>Bombus impatiens</i>	Diversity Turnover	Colony size Male, queen production	Queen weight	Site area (-) Local floral abundance (-)
[16]	Mixed (Europe)	<i>Bombus terrestris</i>	Habitat urbanization	Maximum colony size Food stores Male, queen production		Amount flower-rich habitat (0)
[17]	Grassland (NA)	<i>Bombus impatiens</i>	Dominance Amount natural habitat	Colony growth rate Queen production		Relative floral abundance (0) Floral diversity (0)
[18]	Orchards (Europe)	<i>Osmia rufa</i>	Habitat area	Brood cells/site		Parasitism (-) Nest site addition (+)
[19]	Mixed (NA)	<i>Bombus impatiens</i>	Habitat type	Foraging rate Total food intake Colony mass Number reproductives	Pollen nutritional quality	
[20]	Agricultural (Europe)	<i>Bombus impatiens</i>	Crop area	Early colony weight gain	Probability male, queen production	
[21]	Mixed (NA)	<i>Bombus vosnesenskii</i>	Total density visited plant species	Worker, male production	Queen production	
[22]	Agricultural (Europe)	<i>Bombus</i> spp.	Habitat type	Nest density		

is among the strongest predictors of solitary or social bee reproductive success, potentially more so than food quantity or quality [12,13,15]. Interestingly, patch selection by *Bombus* foragers likewise may respond more to floral diversity than density [26]. Multiple studies support that sustained access to floral resources also matters. Shorter flowering seasons [27\*] and periods of resource scarcity either early [21,28] or late [14,29,30] in the flight season have been linked to lower bee abundances and colony growth, as well as risk of population decline. This suggests that even intermittent or short-term periods of intense competition can affect fitness. Research to date concentrates in agricultural landscapes, so caution may be

needed in extrapolating these patterns to other habitats; changes in continuity or diversity of floral resources could arguably matter more in simplified communities.

### Time series

A second strategy for linking floral resources or competitors with populations is time series analysis. Negative within-year correlations between pollinator species do not necessarily indicate population effects, but could result from changes in foraging behavior that minimize competitive effects on reproductive success. Time-lagged correlations in abundance can provide stronger evidence for population effects, for example, when the abundance

of a competitor last year predicts forager numbers this year. Use of multivariate analyses that include other potential drivers of population dynamics can help reduce noise and control for confounding factors. Time series are also useful for validating whether reproductive success measured with lab-initiated colonies or trap nests provides good predictions of population change. Reproduction at the end of a flight season does not necessarily drive subsequent population size, if substantial mortality occurs during diapause or spring nest establishment.

Only a handful of studies have monitored bee populations and tested for links with resource availability, while also accounting for at least some other factors such as weather variation. Over 14 years, *Bombus* numbers in coastal California associated positively with abundances of key forage plants and negatively with density of competing *Apis* in the previous year [31]. Abundances of alpine *Bombus* in Colorado over eight years varied with length of flowering season, linked to date of snow melt [27\*]. In contrast, tropical bees foraged for less diverse pollen but showed no evidence of population decline over four years after invasion of *Apis mellifera scutellata*, compared to the four years before invasion [32]. Pollen availability predicted patch occupancy but not fluctuations in nest abundance of a rare European solitary bee, over four and nine years, respectively [33,34].

Testing for lagged effects over shorter time spans is a less data-intensive alternative. Native solitary bees showed stronger year-lag than within-year effects of proximity to large commercial apiaries [35] and mass-flowering crop cover [36], suggesting changes either in reproductive success or nest site selection. Genetic tracking of lineages is an especially promising way to separate within and between-year resource and competitive effects. Carvell *et al.* [37\*\*] connected spring queens with offspring queens emerging in the following year; spring floral resources proved strongly predictive of lineage success, with summer forage for workers also a factor.

Monitoring also creates opportunities for natural experiments, by tracking changes before and after introduction of a non-native competitor. A convincing mechanistic explanation strengthens the case for competitive effects. For example, disappearance of several native solitary bee pollinators in Utah corresponded with arrival of *Apis mellifera scutellata* and also changes in the timing and amount of pollen removal from a key forage plant [38]. Similarly, declines in native Japanese *Bombus* after *B. terrestris* introduction correlated with nest usurpation by the non-native [39], a process that may be ongoing with other recent pollinator introductions [40].

### Modeling

Mathematical models can be a powerful tool for evaluating the effects of species interactions and abiotic factors on fitness and population growth. Yet these methods have

been underused for insect pollinators. Recently, *Bombus* colony and population growth have been modeled mechanistically using a diversity of frameworks, including statistical [41], individual-based [42], delay differential [43], demographic [44,45\*], spatial [45\*,46] and community [47] models.

Modeling holds great promise for exploring how competition interacts with other limiting factors to affect population growth [44]. For example, modeling predicts that both length of flowering season and nest site competition mediated by emergence phenology will affect *Bombus* species persistence in alpine meadows, under different scenarios of climate and habitat change [47]. In a simulated agricultural landscape, supplementing late-season floral resources with wildflower strips increased populations more than additional nesting habitat [46]. Crone and Williams [41] found that colony growth and queen production increased with total flower cover; yet per-flower colony growth rates were even more strongly associated with reproduction, suggesting a major role for other, unknown limiting factors.

A continuing challenge is that many published model structures are complex and come with heavy data requirements [43]. Few field data are available for some crucial parts of insect pollinator life history, such as survival through diapause and nest establishment success (Figure 1). Sensitivity analysis can be an effective way to assess how parameter uncertainty affects model predictions [41], but there are important tradeoffs between the additional biological realism of complicated models and the costs of including more parameters with high uncertainty [48].

### Experimental evidence for competition

Experimental evidence is crucial if we are to move beyond correlations and demonstrate causal effects of competition on pollinator populations. Field studies manipulating competitor or resource density remain rare, and come with important caveats [1]. Still, this work contributes an important part of the picture emerging from recent research.

Competitor densities can be increased with experimental additions, most commonly using managed *Apis* colonies [49–51,52\*,53] (Table 2). Addition experiments go beyond comparing habitats at different distances from established apiaries [54], although fully randomizing colony placement in a managed landscape can be challenging. Recent experimental *Apis* additions consistently changed local abundances of non-*Apis* foragers, although effects often interact with landscape characteristics (Table 2). Cage experiments enable tighter control of competitor density and can facilitate measuring both foraging behavior and reproductive success (Table 2). Most *Apis* addition experiments come from Europe; if anything research in the native range of managed

Table 2

**Recent experimental studies testing for competition between insect pollinators, summarized by: Habitat, including continent (NA = North America); Focal species; Competing species, including type of population (M = managed, NN = non-native, N = native); Type of experiment (Competitor addition, food addition, competitor removal); and Results**

Reference	Habitat	Focal species	Competitor	Type experiment	Result
[49]	Agricultural (Europe)	<i>Bombus</i> spp.	<i>Apis mellifera</i> (M)	Addition	Reduced <i>Bombus</i> foragers only in homogeneous landscapes
[50]	Agricultural (Europe)	Flying insects	<i>Apis mellifera</i> (M)	Addition	Reduced wild insect density, more strongly in large fields
[51]	Scrubland (Asia)	Native bees	<i>Apis mellifera</i> (M)	Addition	Lower native visitation in 3 of 4 years, but not for all plant species
[52*]	Scrubland (Europe)	All pollinators	<i>Apis mellifera</i> (M)	Addition	Fewer pollinator species and interaction links
[53]	(Europe)	<i>Osmia bicornis</i>	<i>Apis mellifera</i> (M)	Cage	Reduced visitation, niche breadth, nests and brood cells
[58]	Subalpine (NA)	trap-nesting bees	None	Nectar addition	Increased larval mass but not survival
[60]	Subalpine (NA)	<i>Bombus appositus</i>	None	Nectar + pollen addition	Increased queen production
[59]	Mixed (NA)	<i>Bombus impatiens</i>	None	Nectar + pollen addition	Increased colony weight gain only in non-urban sites; no change reproduction
[61]	Meadow (NA)	<i>Bombus</i> spp.	None	Nectar + pollen addition	Increased worker numbers, reproductive success
[55]	Forest (Asia)	<i>Bombus</i> spp.	<i>Bombus terrestris</i> (NN)	Removal (2 years)	Increased worker, queen abundances
[25*]	Subalpine (NA)	<i>Bombus</i> spp.	<i>Bombus</i> spp. (N)	Removal (single days)	Increased niche overlap
[56]	Subalpine (NA)	<i>Bombus</i> spp.	<i>Bombus</i> spp. (N)	Removal (single days)	Reduced floral fidelity

pollinators may underestimate competitive effects where they are non-native [2].

Alternatively, competitor density can be reduced experimentally [25\*,55,56]. Achieving long-term removal can be very difficult; Nagamitsu *et al.* [55] only lowered non-native *B. terrestris* abundances successfully in one of two years, but documented corresponding increases in queen numbers for the two native *Bombus* that overlap most with *B. terrestris* in tongue length. Most removal experiments are short (Table 2). These methods echo early research on bee competition [6], but are being applied to more species with the goal of analyzing whole pollination networks. Single species removal can increase niche overlap and reduce complementarity in plant use, providing an experimental confirmation of correlational patterns from many observational studies (Table 2). Non-experimental work on spillover effects from managed *Apis* in crops onto nearby natural habitat shows similar patterns; increased *Apis* numbers correlate with other pollinators foraging on less-abundant plant species and narrowing their diet breadth [57].

Experiments manipulating food availability to nests or colonies support positive relationships between floral resources and reproductive success consistent with observational work [58–61] (Table 2). Resource supplementation with experimental hedgerow and wildflower plantings in agricultural systems can produce similar effects [62]. Still, most studies of forage plantings measure pollinator visitor numbers or species richness rather than

reproductive success; these effects could be explained by concentration of foragers in dense resource patches rather than population changes [63,64]. For example, hedgerow plantings in central California did not increase the number of bees captured emerging from ground nests, and the species composition of nesters differed from that of foragers [65]. Pollinator diversity responds to some of the same factors as within-species reproductive success, but likely with different mechanistic explanations. For example, increased floral diversity after hedgerow planting raised pollinator species richness, but by enabling persistence of floral specialists [66]. Habitat improvement strategies likely also affect factors such as pesticide exposure, nest site availability, and parasite abundances, although these differences to some extent can be quantified and included in analyses [64].

New survey and analysis methods show promise for separating local effects of florally rich habitat on foraging patch selection from population changes [67]. Genetic approaches offer another exciting avenue, allowing for estimation of *Bombus* nest densities. Abundances of both foragers and nests for some *Bombus* species increased on British farms with enhanced floral resources [22]. Surveys of male and queen numbers along transects could also serve as a coarse proxy of reproductive success, if the spatial scale is large enough to reduce potentially confounding effects of foraging behavior. For example, more *Bombus* reproductives were found in 2 km radius Swedish farm patches if they had early flowering red clover fields in the center [29].



## Conclusions and future directions

As previous reviews summarize, many studies extending back over decades show correlational evidence of competition between insect pollinators, particularly with introduced species [1,2]. Yet past reviews also agree: this large body of research still does not answer the crucial questions of when and why such effects change pollinator populations and communities. Promisingly, an increasing number of more recent studies are testing relationships between resource availability and reproductive success or population change. The majority support positive effects, especially for floral resources, but also to some extent nesting habitat. In parallel, recent experimental work strengthens evidence for competitive effects on access to floral resources. Findings generated with a diversity of methods encouragingly converge in a number of respects.

Population modeling offers potentially powerful approaches for testing the importance of resource competition, but gaps in data availability remain a major challenge. Arguably, the best path forward is not more research on forager competition, but studies on factors such as overwinter survival, nest establishment and parasitism that contextualize resource competition in the life history of pollinators (Figure 1). Genetic methods offer exciting new opportunities, enabling estimation of nest density and tracking of lineages across years [22,26,37\*\*]. A second key need is development of more common currencies and methodologies for quantifying floral and other resources, so that research at local and landscape scales can be bridged effectively [68]. In particular, using habitat type as a proxy for resources makes untangling the effects of different limiting factors very difficult [23]. Finally, we need more studies that integrate multiple limiting factors or environmental changes, including not just floral resources but pesticides, nest sites, climate change and parasites [11\*\*].

## Conflict of interest statement

Nothing declared.

## Acknowledgements

M.L. Page was partially supported by a Department of Defense National Defense Science and Engineering Graduate Fellowship. We thank the editor for thoughtful comments on our MS.

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