

# Bumble bee communities are structured by a spatiotemporal mosaic of competitive processes

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## Introduction

Bumble bees (Hymenoptera: *Bombus* spp.) are classic model organisms for the study of resource competition in biological communities. Nevertheless, the role of resource competition in structuring bumble bee communities has proven difficult to generalize. It is evident that sympatric bumble bees *can* compete for floral resources, and strongly so. Heinrich (1976) found that a bumble bee community can deplete the daily standing nectar pool of a given locality by more than 90%, and starvation has been implicated in the demise of colonies in isolated subalpine meadows (Bowers 1985), leaving little room to doubt the potential for resource limitation. Other studies have found local bumble bee communities to be over-dispersed in terms of tongue length (e.g. Inouye 1977), a matching trait (sensu Schleuning et al. 2020) corresponding to floral corolla depth, and phylogeny (Pellissier et al. 2013), which can be interpreted as a catch-all for unmeasured trait variation. Nevertheless, it is equally evident that sympatric bumble bee species do not *always* compete for floral resources to the point of competitive exclusion, since bumble bee communities with an apparent excess of species richness and deficit of trait dispersion are commonly observed (Goulson, Lye, and Darvill 2008).

To account for both the importance and variability of competitive processes in bumble bee communities, it is helpful to distinguish three processes that could obtain to varying degrees: no competition, interspecific competition, and intraspecific competition (**Table 1**). We will refer to these processes as hypotheses, since their realization in any given community is matter of inference. Below, we elaborate each and formulate corresponding empirical predictions.

Hypothesis	Prediction
H1: No competition	<ol style="list-style-type: none"><li>1. BB density <math>\nmid</math> FL density</li><li>2. BB trait dispersion = null expectation</li><li>3. BB-FL trait-matching &gt; null expectation</li></ol>
H2: Interspecific competition	<ol style="list-style-type: none"><li>1. BB density <math>\sim</math> FL density</li><li>2. BB trait dispersion &gt; null expectation</li><li>3. BB-FL trait-matching &gt; null expectation</li></ol>
H3: Intraspecific competition	<ol style="list-style-type: none"><li>1. BB density <math>\sim</math> FL density</li><li>2. BB diet breadth <math>\sim</math> BB conspecific-packing</li><li>3. BB-FL trait-matching <math>\sim</math> 1/BB conspecific-packing</li></ol>

**Table 1:** Hypothesized competitive processes with empirical predictions. BB = bumble bee; FL = floral.

*H1: No competition.* The hypothesis that floral resource competition is not a significant process governing a bumble bee community functions as a “null hypothesis” when competition *per se* is the phenomenon in question, but it is not “null” in the sense of mere negation of mechanistic explanation. To the contrary, at least two plausible and ecologically meaningful mechanisms can be proposed that would account for a lack of competition in bumble bee communities (Ranta and Vepsäläinen 1981). First, it is possible that a super-abundance of floral resources could saturate the foraging capacity of a local bumble bee population. Indeed, this may be a common (though transient) phenomenon associated with the bloom of mass flowering crops (Ranta and Vepsäläinen 1981). Alternatively, competition could be attenuated if abiotic stress, such as low temperature, suppresses bumble bee populations below competition-inducing densities. This pattern would be a prediction of the “stress-gradient hypothesis” (Bertness and Callaway 1994), and while it has not, to our knowledge, been documented for bumble bees specifically, a recent study of whole bee communities (of which bumble bees were a part) found evidence of dampened competition at high elevation sites along a montane-to-alpine gradient (Hoiss et al. 2012).

Under either mechanism, the most straightforward prediction is that bumble bee population density would be decoupled from resource density, since the latter would be non-limiting. For the same reason, the absence of competition would also predict that the trait dispersion of sympatric bumble bee species would not exceed that predicted by a random null model. Third, under a no-competition scenario, bumble bee species would suffer no displacement from their optimal floral resource species. Thus, holding other aspects of floral resource value constant (e.g. abundance, nectar volume/concentration), a lack of competition would predict that morphological trait-matching between bumble bee species and their chosen host flowers would exceed that predicted by a random null model.

*H2: Interspecific competition.* Resource partitioning by bumble bees is mediated by variation in matching traits, the most well-studied of these being tongue length. Bumble bee tongue lengths vary between species, and the efficiency with which a bumble bee can collect nectar from a given flower depends largely on the closeness of match between the tongue length of the bee and the corolla depth of the flower (Inouye 1980; Ranta and Lundberg 1980). Thus, under conditions of interspecific competition, a species’ “defensible” niche space (i.e. the space in which it is a superior competitor) should center on the floral trait space that corresponds to its tongue length, and the number of species that can be “packed” into a given locality should be limited by some minimal differentiation of tongue length (Inouye 1977; Pyke 1982) within the range of variation supported by the trait space of available flora.

Since resource limitation is a necessary condition for resource competition, a key prediction distinguishing interspecific competition from a lack of competition is that bumble bee density should vary in proportion to floral resource density. A bumble bee community under interspecific competition should also exhibit higher tongue length dispersion and stronger trait matching relative to the predictions of a random null model (Inouye 1977).

*H3: Intraspecific competition.* As noted by Ranta and Vepsäläinen (1981), theory predicts that intraspecific competition can promote species coexistence through the relief of interspecific competition (MacArthur 1984), and could thus, as an alternative to the “no competition” hypothesis, account for cases in which the observed diversity of sympatric bumble bee species exceeds that predicted by trait-based niche models. Under the pressure of intraspecific competition, individuals face the depletion of preferred resources and may respond by foraging more opportunistically within the constraints of their fundamental niche space []. Alternatively, a population may relieve intraspecific competition by subdividing, on the basis of intraspecific trait heterogeneity, into differently specialized “guilds” (Araújo et al. 2008). In either case, the population-level effect would be an increase in the species’ realized niche breadth (though see Parent, Agashe, and Bolnick 2014).

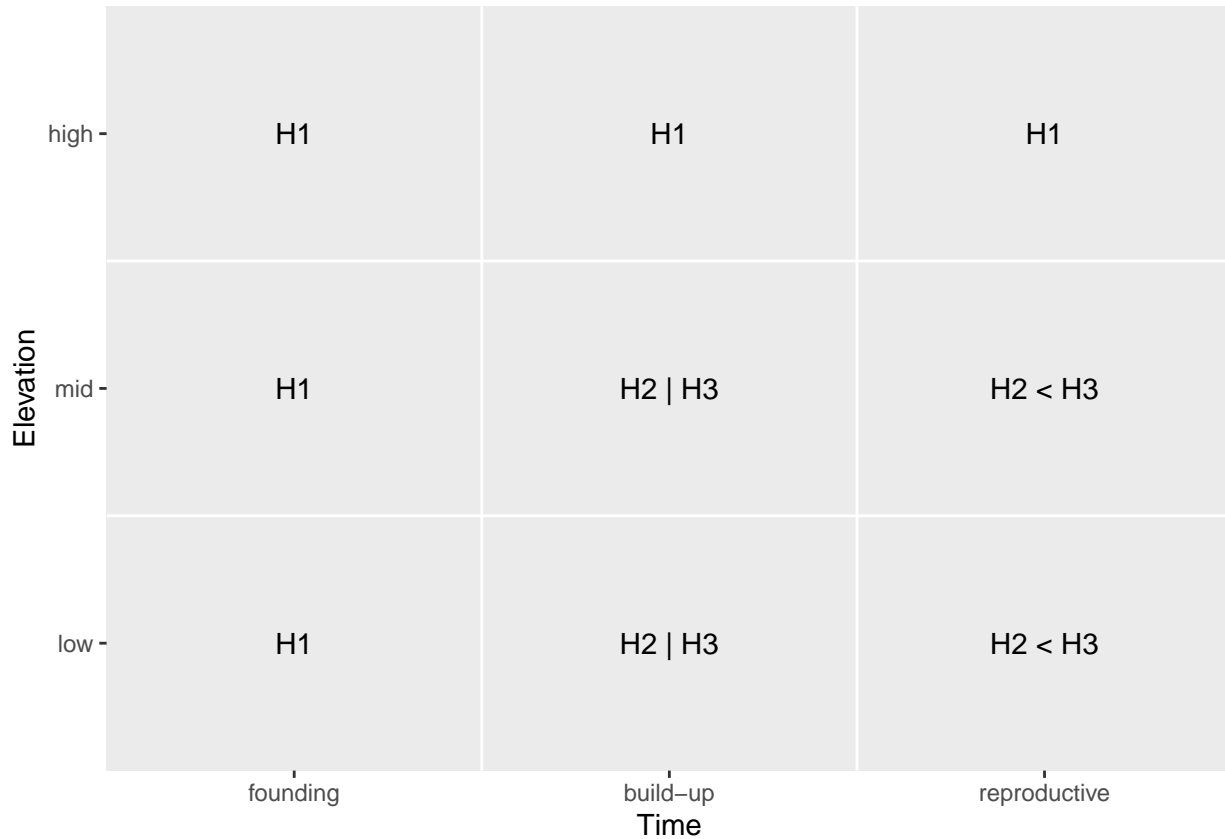
Thus, the predictions of intraspecific competition can be formulated as follows. First, as in interspecific competition, resources must be limiting, so bumble bee density should vary in proportion to floral density. In the case of intraspecific competition, though, we can refine this prediction to say that the density of a given bumble bee species should vary in proportion to the density of the portion of the floral resource community

belonging to its dietary niche, since the effects of intraspecific competition are realized on a per-species basis. Second, the dietary breadth of a given species should vary in proportion to the density of conspecifics per density of floral resources (we will refer to this as a “conspecific-packing” index). Conversely, a broadening of diet should entail a relaxation of trait-matching, so the strength of trait-matching should vary inversely with conspecific-packing.

*Seasonal-Elevational metahypothesis.* That any of the processes hypothesized above should obtain universally is both empirically and theoretically doubtful (Ranta and Vepsäläinen 1981). More plausibly, which of these processes prevails – and which species are favored by the prevailing process – vary in both space and time, and this heterogeneity of process could explain the structural idiosyncrasies of observed bumble bee communities (Ranta and Vepsäläinen 1981). Rather than viewing this heterogeneity as an obstacle to inferring some universal rule of bumble bee community assembly, our aim in the present study is to investigate the heterogeneity itself as an ecological phenomenon, characterizing the variation in competitive processes (or lack thereof) in bumble bee communities through time and space.

Our study is set in the Berchtesgaden Alps of southwestern Germany, where a steep elevation gradient permits the study of wide environmental variability while minimizing the confounding effects of geographical distance (e.g. Hoiss, Krauss, and Steffan-Dewenter 2015). In this context, we formulate a “metahypothesis” concerning the variation of hypothesized competition processes through elevation and time (**Figure 1**). Consistent with the stress-gradient hypothesis (Bertness and Callaway 1994) and with previous empirical work in our study system (Hoiss et al. 2012), we hypothesize an inverse relationship between competition and elevation. Along a temporal axis, we hypothesize that the strength of competition is structured by the seasonal life history pattern of bumble bee colonies (Goulson 2010). During the solitary phase, when the bumble bee community consists only of foundress queens, competition should be low. Both inter- and intraspecific competition should intensify as colonies increase in size during the social phase. After the switch point, when colonies begin producing gynes and males instead of workers, intraspecific competition should decrease due to the strong morphological differences between queens, males, and workers within each species, but interspecific competition might intensify due to the effective “over-packing” of trait space with the introduction of multiple morphological castes per species.

In addition to clarifying the basic ecology of bumble bee community assembly, parsing competitive processes in this way has an applied significance for the conservation of bumble bees in the changing environments of the Anthropocene. Under the forcing of environmental change, such as climate warming or land use conversion, bumble bee communities might not be affected only in terms of range shifts, but also by a restructuring of competitive interactions, the nature and consequences of which may be difficult to predict.



**Figure 1:** Hypothesized variation in prevailing competitive processes through time and elevation.

## Methods

## Results

## Discussion

## References

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