

Bumble bee competition revisited under global climate change

Douglas B. Sponsler Fabrice Requier Katharina Kallnik Alice Claßen
A. Fabienne Maihoff Ingolf Steffan-Dewenter

Introduction

The nascent reality of climate change has already revealed the fragile contingency of ecological paradigms that rely on the assumption of climate stability (Hannah et al. 2002; Walther et al. 2002). Thus, one of the central questions facing ecologists today is how climate change will affect the future fitness and distribution of species and, thereby, the composition and function of ecological communities. While it is intuitive that climate change should affect species and communities through environmental filtering, it is now recognized that climate change can also restructure biotic interactions (Tylianakis et al. 2008), such as competition and facilitation (Ettinger and HilleRisLambers 2017), altering the fitness landscape that governs community assembly and species coexistence (Chesson 2000).

Bumble bees (Hymenoptera: *Bombus* spp.) have become a model system for the study of biotic interactions in ecological communities. In particular, the broad and overlapping distributions of bumble bee species, together with their gross similarity in morphology, behavior, and dietary niche, have attracted the attention of researchers interested in questions of interspecific competition and, more broadly, the rules of community assembly and species coexistence (Plowright and Lavery 1984; Goulson, Lye, and Darvill 2008). In this regard, however, bumble bees have proven somewhat enigmatic. On the one hand, there is evidence that resource limitation can be a significant constraint on local bumble populations (Heinrich 1976; Bowers 1985), and certain bumble bee communities have been shown to be over-dispersed in terms of tongue length (a matching trait corresponding to floral corolla depth) or phylogeny (understood to encompass unmeasured trait variation), providing evidence for competition as a community assembly process (e.g. Inouye 1977; Pellissier et al. 2013). Nevertheless, bumble bee communities with an apparent excess of species richness and deficit of trait (or phylogenetic) dispersion are commonly observed (Ranta and Vepsäläinen 1981). To account for this inconsistency, Ranta and Vepsäläinen (1981) proposed that bumble bees communities are governed by a spatiotemporally heterogeneous mosaic of competitive conditions, such that competitive inequalities between species are sufficiently variable to allow more species to coexist than predicted by trait-based competition models. A complementary explanation, based on the core/satellite species hypothesis (Hanski 1982b), is that competitive forces are significant only among regionally abundant and widespread “core species”, and the effects of competition are more pronounced in the structure of regional species pools than in that of local assemblages (Hanski 1982a).

As pointed out by Williams (1989), however, the question of competition as a biogeographic/evolutionary-scale driver of community assembly differs from that of competition as a local/behavioral-scale driver of species’ interactions. While the role of competition in bumble bee community assembly remains somewhat obscure, there is broad empirical evidence that bumble bees facultatively partition resources to minimize competition (e.g Inouye 1978; Morse 1982; Ishii 2013; Brosi and Briggs 2013; Brosi, Niezgoda, and Briggs 2017). This distinction between spatiotemporal scales of competition, echoing the logic of Ranta and Vepsäläinen (1981), becomes especially important when the scope of inquiry switches from retrospective to prospective, and all the more so when there is reason to think that the ecological context of competition is undergoing rapid and unprecedented change. Since the height of bumble bee competition research in the 1980s, such a shift has indeed occurred, with retrospective questions of community assembly all but eclipsed by the urgency of conservation in the face of global changes in climate and land use (Goulson 2010). Given the uncertain spatiotemporal lags and exogenous drivers of community assembly, inferring the past role of competition through the study of bumble bee community structure may be of limited use in predicting the future fitness and distribution of bumble bee species. In this regard, the study of competition via behavioral

patterns of floral resource partitioning that respond in real-time to variation in ecological context (Spiesman and Gratton 2016) provides a vital complement to the classical study of community assembly.

The study of competition as a behavioral phenomenon, however, is empirically and analytically demanding, since species interactions, not merely community composition, must be measured and interpreted. The difficulty is compounded when the goal is to infer the effects of climate variation, since observations must be replicated across gradients of interest while minimizing the influence of confounding spatial or temporal effects. An elegant solution to both these challenges is the use of species interaction network analysis along steep elevation gradients (e.g. Hoiss, Krauss, and Steffan-Dewenter 2015; Albrecht et al. 2018). Interaction network analysis provides a tractable framework for the study of resource partitioning (Blüthgen, Menzel, and Blüthgen 2006), and steep elevation gradients can serve as space-for-time proxies in the study of climate effects, capturing a broad range of climate variation while minimizing the confounding effects of geographic distance (Blois et al. 2013).

Previous studies of pollinator and plant communities along elevation gradients have tended to find decreased specialization and/or increased niche overlap at high elevation, which is often interpreted as an indication of reduced interspecific competition, though other mechanisms cannot be excluded (Hoiss et al. 2012; Miller-Struttmann and Galen 2014; Hoiss, Krauss, and Steffan-Dewenter 2015; Classen et al. 2020). If, in fact, competition in pollinator communities is attenuated at high elevation, this would be broadly consistent with the “stress-gradient hypothesis”, which posits that prevailing biotic interactions shift from negative (e.g. competition) to positive (e.g. facilitation) along ascending gradients of environmental stress (Bertness and Callaway 1994). As applied to pollinator communities, the logic would be that environmental stresses at high elevation, such as low temperatures and short growing seasons, suppress pollinator densities more strongly than the densities of their shared resources, thus causing a per-capita increase in food availability and a corresponding relaxation of competition.

In this study, we analyze patterns of resource partitioning in a bumble- bee-wildflower network sampled along an elevation gradient in the Berchtesgadener Alps of southeastern Germany. We first analyze species- and group-level network metrics of specialization and niche overlap to determine whether the bumble bees in our study system exhibit the expected pattern of decreased specialization and increased niche overlap at high elevation. To evaluate the plausibility of interpreting specialization and niche overlap as indices of competition, we then use independent floral surveying data to determine whether observed patterns in specialization and niche overlap correspond to variation in per-capita resource availability. Finally, we use the within-year temporal resolution of our dataset to test for reciprocal population dynamics of species within sites as a direct indication of interspecific competition. From these results, we derive predictions concerning the effects of climate change on competition as a constraint on bumble bee species and communities.

Methods

Field sampling. Our study is set in the Berchtesgadener Alps of southwestern Germany, a system in which both plant and pollinator communities have been well-studied [Hoiss et al. (2012); Hoiss2012-kr; Hoiss2015-gv]. Our study sites are the same as those ranging in elevation from 641 to 2032 m above sea level.

Degree day modeling.

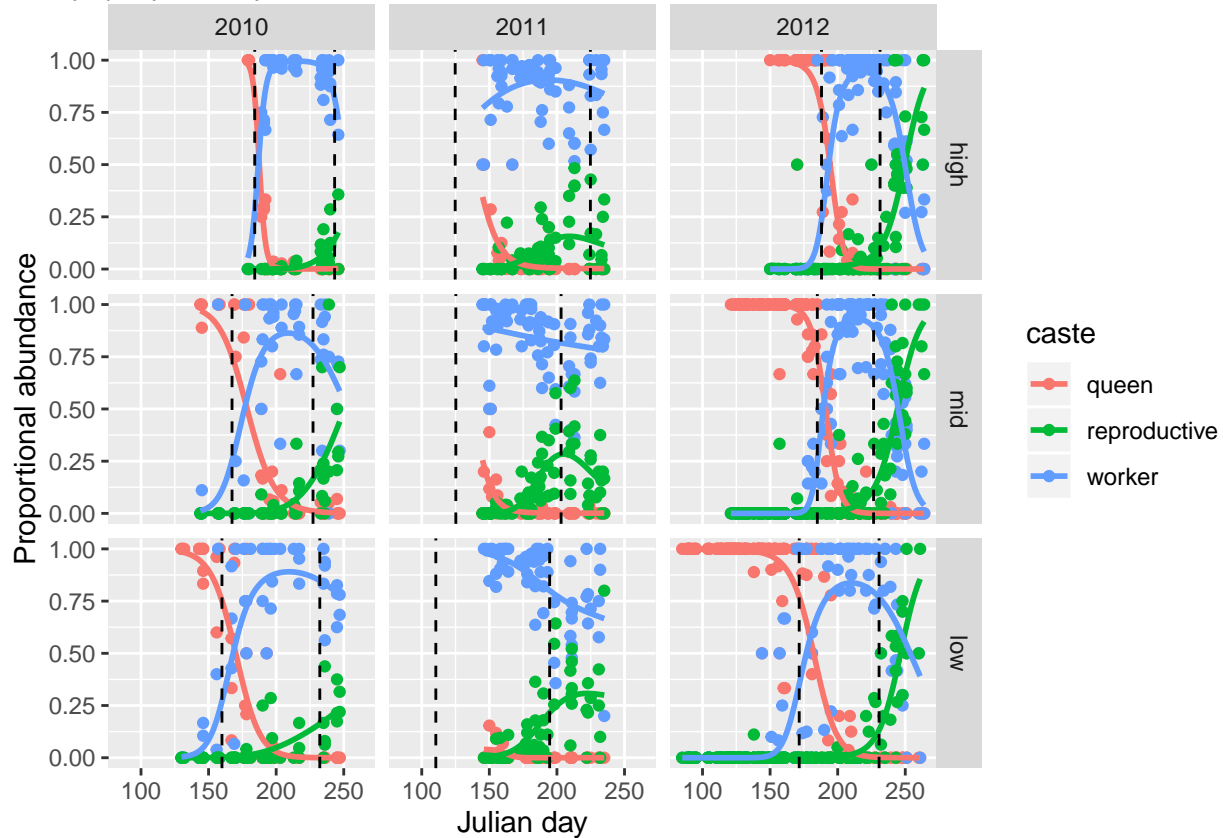
Colony life cycle analysis. Bumble bee colonies exhibit three distinct life history phases: a “founding” phase during which colonies are initiated by solitary queens, a “build-up” phase during which workers are produced, and a “reproductive” phase where colonies produce new queens and males (Goulson 2010). A formal delimitation of these phases serves both as a temporal framework for analyzing bumble bee and floral dynamics and as a check that different elevational subsets of our data capture the same life history interval and are thus comparable in terms of network structure.

To delimit colony phases, we fit binomial regression models to the proportional abundance of foundress queens (Q) and new reproductives (R) (males + new queens), respectively. We set the breakpoint between the founding and build-up stages at $Q = 0.75$, and the breakpoint between buildup and reproductive stages at $R = 0.1$. These cutoffs are somewhat arbitrary points in a continuous process, but their primary purpose is to facilitate comparison across sites. This analysis was performed on both a GDD and Julian temporal scale. All operations were done in R.

Inferring resource limitation. During the founding phase, it would be hard to detect resource limitation even if it were occurring, since the population would not be able to respond to it except by actual starvation of queens. In other words, until workers emerge, the relationship between bumble bee density and floral density would be expected to be null. At least if competition is the proposed mechanism. If mere concentration of foragers is the mechanism, then you would expect to see BB density respond positively to floral density, and the fact that it does not in our data suggests that, at least during the founding phase, forager concentration is not an important mechanism. That's good news.

Results

Colony life cycle analysis.



The colony life cycle intervals captured by our sampling varied across years, but were consistent across elevational classes within years, validating the comparison of foraging patterns along our elevation gradient (**Figure 2**). In 2010, all three colony phases are represented in our samples, but the founding phase appears somewhat truncated, suggesting that sampling began after colony founding was already underway. In 2011, the founding phase was missed entirely, with sampling beginning mid-way through the build-up phase. In 2012, we achieved the longest and densest sampling, yielding good representation of all three colony phases. It is worth noting that as elevation increases, colony lifecycle is delayed in onset and contracts in duration, but the phase breakpoints remain approximately equal (on a Julian time scale) across elevation classes.

Specialization and niche overlap.

Resource limitation. Per-transect bumble bee abundance is positively correlated with per-transect floral cover (log-transformed). To the extent, therefore, that our metrics of bumble bee and floral density reflect true site-scale abundance and not just co-aggregation, this pattern suggests that bumble bee density is resource limited, particularly at sites with very low floral density. Importantly, this approach does not distinguish between inter- and intraspecies (or even intra-colony) competition (Ranta and Vepsäläinen 1981).

Note, moreover, that this relationship varies seasonally. For now, we will use Julian month as a stand-in for GDD, which we'll use once we have analyzed our weather station data. Early in the year, the relationship between BB density and floral density is weak; this makes sense because colonies are just getting established

during the first couple of months, and BB density is more limited by the autocorrelation component of colony size (bigger colonies can raise more brood) than by floral resource availability. In mid- to late-season, however, BB density becomes strongly dependent on floral resource density. Interestingly, in September, the relationship is strongest and floral density is also lowest.

Reciprocal population dynamics.

Colony life cycle analysis.

Discussion

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