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April 8, 2016

Release from interspecific competition results in species niche expansion in bumble bees

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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
of Emory University in partial fulfillment
of the requirements of the degree of
Bachelor of Sciences with Honors

Department of Environmental Sciences

2016

Abstract

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Recently, there has been increasing attention in ecology to the importance of intraspecific variation resulting in individual specialization. Such specialization, which can be addressed in terms of dietary niche width, is especially important in pollinators, given that pollination has intense effects on ecological and evolutionary functioning. While previous work has demonstrated decoupled changes in niche width at the individual and species levels following release from interspecific competition, few field experiments have addressed the effects of ecological release on pollinators at multiple organismal levels. Here, we present a field experiment to test the effects of release from interspecific competition on niche breadth and specialization in bumble bees (Hymenoptera: *Bombus*), a critical clade of pollinators for both unmanaged and agricultural ecosystems. We conducted species removal experiments and observed the foraging behavior of individual bumble bees in order to assess the hypothesis that reduced interspecific competition leads to decoupled changes in bumble bee specialization and niche width at the individual, species, and guild levels. We found evidence of species niche expansion following release from interspecific competition, with important implications for pollination given ongoing bumble bee population declines.

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Acknowledgements

I am grateful to the National Science Foundation and the Rocky Mountain Biological Laboratory, for supporting this research; the 2010-2015 Brosi lab field teams, for collecting the data; Emily Dobbs, for managing logistics; Carolyn Ayers, for getting me started in R; Dr. Berry Brosi, for his continued guidance and generosity; Dr. Chris Beck and Dr. Gonzalo Vazquez-Prokopec, for serving on my committee; and my family and friends, for their patience and support.

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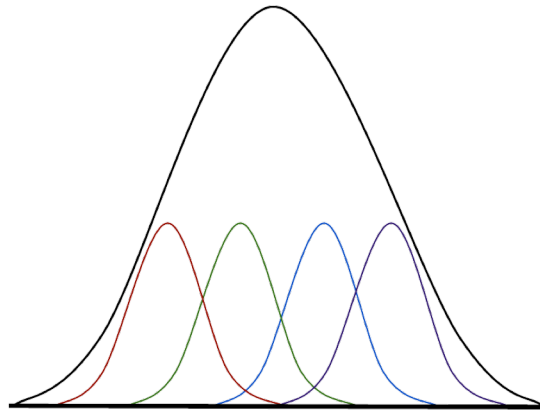
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Recently, there has been increasing attention to the importance of intraspecific variation in ecology (Bolnick *et al.*, 2011). Within a species or population, trait variation among individuals of the same sex or age may lead to specialization in resource use (Araújo, Bolnick, & Layman, 2011; Bolnick *et al.*, 2003, 2011). Such individual specialization has been observed in nearly 200 species (Araújo *et al.*, 2011). Thus, aggregating behavior to the population level can obscure individual-level patterns (Bolnick *et al.*, 2010), which may be relevant for understanding ecological processes as well as for conservation.

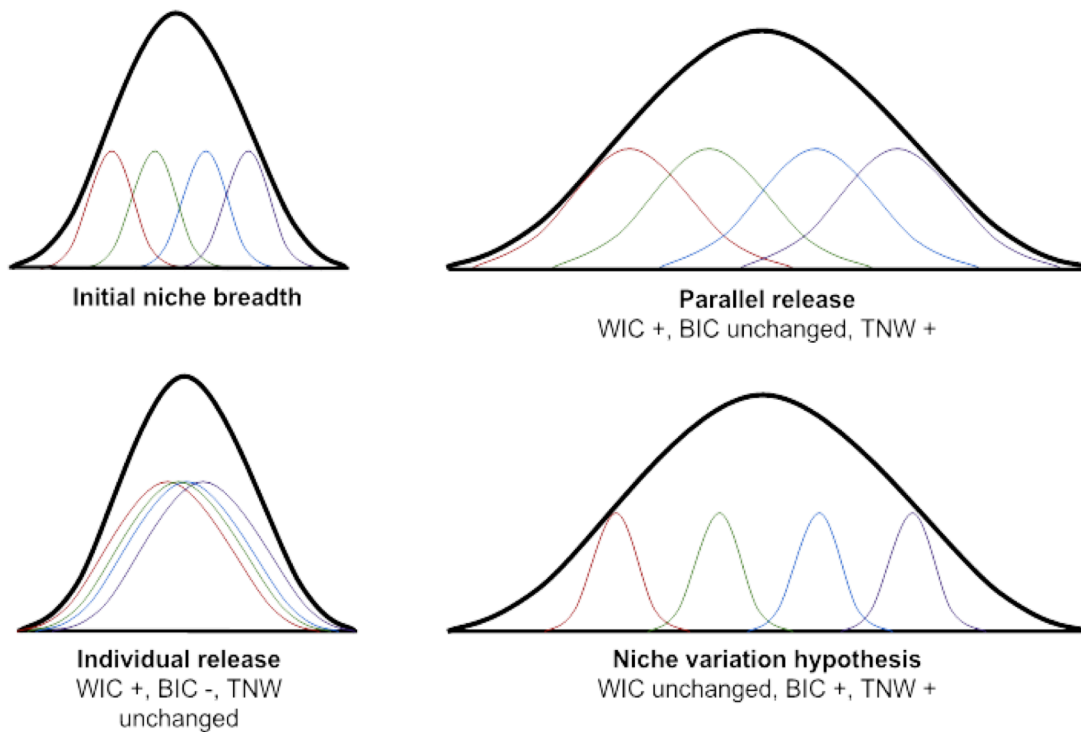
One concrete way to measure specialization in resource use is niche width, which represents the interaction between the constraining effects of interspecific competition and the diversifying effects of intraspecific competition (Bolnick *et al.*, 2010; Roughgarden, 1972; Svänback & Bolnick, 2007). Specialization can occur at multiple levels in organismal hierarchies. Just as individuals can specialize in resource use based on intraspecific trait variation, so can species or populations. In the case of niche width as a measure of specialization, the aggregate of individual niches composes the population niche (Bolnick *et al.*, 2010). Similarly, multiple species niches add up to form the guild niche. Specifically, species total niche width (TNW) is comprised of a within-individual component (WIC), the variation in resources used by individuals of the population, and a between-individual component (BIC), the variation between the resources used by members of the population (Figure 1; Bolnick *et al.*, 2010; Roughgarden, 1972). This definition can be scaled to the multi-species guild level, in which guild TNW is the sum of the within-species component (WSC) and between species-component (BSC). Given that specialization results from the balance between intraspecific and interspecific competition, a shift in competition may lead to decoupled changes in species- and individual-level specialization (Bolnick *et al.*, 2010), but to our knowledge such changes have not been examined between the species and guild levels.

Figure 1.



$TNW = WIC + BIC$. In this case, the outer curve represents the species or guild niche width, while the inner curves indicate individual or species niche breadths. BIC is determined by the degree of overlap between individual or species niches. Adapted from Bolnick et al. (2010).

Figure 2.



Models of release from interspecific competition. Each model can be adapted to the species-guild level, in which the outer curves indicate guild niche width and the inner curves represent species niche breadths. Adapted from Bolnick et al. (2010).

Three models explain how niche width may change in response to ecological release from interspecific competition: parallel release, niche variation hypothesis, and individual release (Figure 2; Bolnick *et al.*, 2010; Roughgarden, 1972; Van Valen, 1965). Parallel release occurs when individuals begin to use novel, high-value resources following release from interspecific competition, thereby increasing their individual niche widths (WIC) and species niche width simultaneously (Bolnick *et al.*, 2010). This type of adaptive niche expansion is consistent with the idea that each individual can potentially use all of the resources utilized by the population (Bolnick *et al.*, 2010; Roughgarden, 1972). By contrast, the niche variation hypothesis describes increases in TNW driven by less overlap between individual niches (that is, greater BIC) (Van Valen, 1965). Such expansion may occur when new resources become available, but functional trade-offs limit how many resources an individual can use; examples include memory constraints or time costs of learning to utilize a new resource (Bolnick *et al.*, 2010; Bolnick, Svänback, Araújo, & Persson, 2007). Finally, TNW may not change as a result of decreased interspecific competition. In the case of individual release, individuals add new resources to their niches, causing WIC to increase, but the population converges on the same set of resources such that BIC decreases and TNW remains constant (Bolnick *et al.*, 2010).

Despite the ecological importance of specialization, there is a dearth of experiments addressing functionally relevant changes in niche width. Manipulative field experiments in natural settings with unaltered resources and multiple focal taxa are especially lacking. However, such tests are necessary to understand the effects of species loss on how dynamic changes in specialization may impact ecological functioning. A second gap, mentioned previously, is that no studies to our knowledge have addressed how changes in niche breadth at the species level scale to the multi-species guild level.

One ecological function for which specialization is especially important is pollination (Waser & Ollerton, 2006). Plants require conspecific pollen for fertilization, and the movement of individual pollinators determines the distribution of pollen, leading to strong potential ecological and evolutionary

impacts of pollinator specialization (Arceo-Gómez *et al.*, 2015; Brosi & Briggs, 2013; Flanagan, Mitchell, Knutowski, & Karron, 2009; Morales & Traveset, 2008). Therefore, understanding how pollinator specialization changes with species loss is especially important for conservation purposes.

Here, we present a field experiment to test the effects of release from interspecific competition on pollinator specialization. We focused on bumble bees (Hymenoptera: *Bombus*), a critical guild of pollinators in both agricultural and unmanaged ecosystems. Individual bumble bee behavior can be highly flexible in the short term (Waser & Ollerton, 2006), with important implications for conservation. In addition to being one of the few experimental tests of ecological release in a field setting with unmanipulated resources and multiple focal taxa, our experiment examines the effects of reduced interspecific competition at the guild level, as well as at the individual and population levels. We assessed the hypothesis that reduced interspecific competition for floral resources leads to decoupled changes in bumble bee specialization and niche breadth at the individual, species, and guild levels. Additionally, we sought to determine whether bumble bee species respond differently to decreased interspecific competition, and which model of ecological release fits best in each case.

Materials and Methods

Field Sites

During the summers of 2010-2015, we conducted experiments in the landscape surrounding the Rocky Mountain Biological Laboratory in Gothic, Colorado (38° 57.5'N, 106°59.3'W, 2,900 m above sea level) in the Gunnison National Forest, western Colorado, United States. The study landscape hosts eleven species of native bumble bees. We established 20 sites, each comprised of a 20 x 20 m plot, separated by at least 1 km, in subalpine meadows that were roughly comparable in terms of plant and pollinator communities and other biophysical plot characteristics.

Species Removal Experiments

To simulate bumble bee species loss, we conducted experimental removals of interspecific competitors. At each plot, we first conducted surveys of flowering plants and bumble bees to measure richness and abundance of floral resources and bumble bee species. The most abundant bumble bee species at a site was determined by a 20-minute non-destructive aerial net sample focused on bumble bees, involving two field team members. The bees were identified to species and released once sampling was finished. The most abundant species was later experimentally removed to simulate reduced interspecific competition. We also collected data on weather conditions during experiments.

At each site, we conducted observations in a control and a manipulated state. In the control state, all bees were allowed to forage undisturbed while we recorded observations. Approximately two days later, we assessed the same site in the manipulation state in order to minimize changes in floral resources between the two stages. In the manipulation state, we non-destructively removed the most abundant bumble bee species at the site. Individuals of the target species were removed via aerial netting capture and placed in a cool, dark space in separate vials for the duration of the experiment. We then conducted observations while the remaining bees foraged. For the entirety of the experiment, one field team member patrolled the perimeter of the plot to catch any individuals of the target species that might try to enter. Following the observations, the removed bees were warmed and released.

Measuring Niche Breadth

In order to measure niche breadth, we observed the foraging behavior of individual bumble bees. In both the control and manipulated states, we identified bees to species and followed them from plant to plant, recording each flower visit and identifying the plants to species (where possible). Each bee was observed for a maximum of 10 minutes or 100 visits, or until they flew more than 5 meters

outside the plot. Observations of fewer than 5 plant visits were discarded, as we assumed that we could not accurately estimate niche breadth with fewer observed visits.

Quantifying Niche Breadth and Specialization

We assessed bumble bee specialization across organismal levels by quantifying niche breadth and testing the impact of reduced interspecific competition on specialization at the species and individual levels. We excluded from analysis observations of species which were not present in both the control and manipulation states at a particular site or for which fewer than three individuals were observed in either state. In addition, at the guild level we included only sites which had at least 2 species present in both the control and manipulation states.

The numbers of individual bees observed varied across site, state, and year combinations, and this variation in sampling intensity could have strong effects on niche breadth results, since the probability of observing an unseen resource increases with sampling. Thus, a population with more foraging observations may appear to have greater niche breadth. To correct for this, we first used a bootstrapping approach to standardize sample size between control/manipulation pairs. We performed this resampling at the individual level, in order to ensure that the numbers of bees observed in each experiment pair was comparable. Using the smallest number of individuals observed in each experiment pair, we determined all possible combinations of individual bee observations in each control/manipulation site pair (using the “combn” function in the R Statistical Programming Language) (R Core Team, 2015). For each control/manipulation site pair, we conducted the niche breadth calculations and averaged the results.

We used the *RInSp* package (Zaccarelli, Mancinelli, & Bolnick, 2013) in R to calculate TNW, WIC, and BIC following Roughgarden (1972). While Roughgarden's original niche width formulas were meant for continuous data, our data are discrete, so we used an adaptation of the formulas that replaces

variance with the Shannon-Weaver diversity index to measure variation in resources used by individuals and species (Bolnick, Yang, Fordyce, Davis, & Svänback, 2002). The Shannon-Weaver diversity index takes into account the richness of plant species used by a bee or species and the evenness with which those floral resources are utilized to calculate the proportional abundance of plant resources on which an individual bee or species forages. We calculated WIC/TNW as a measure of diet specialization for individuals; that is, the proportion of all floral resources used by a species that the average individual of that species utilizes (e.g., Bolnick *et al.*, 2010). At the species-guild level, we calculated WSC/TNW as a measure of diet specialization by species.

We performed these calculations at two levels in order to quantify guild, species, and individual niche breadths. To examine guild niche breadth, we aggregated all interactions by individuals of a species to represent population resource use, and aggregated the values for all populations at a site to represent the guild TNW. In this case, WSC/TNW represented specialization by species. We then performed the same calculations, without aggregating observations by species, to address individual specialization. Within each site, we calculated TNW, BIC, and WIC for each species, so that TNW represented species niche width and WIC/TNW represented specialization by individual bumble bees.

Statistical Analyses

To test the significance of observed specialization by individuals and species, we used Monte Carlo simulations with the null hypothesis that individuals and populations sample equally and stochastically from the same set of resources (Bolnick *et al.*, 2010). To assess the impact of reduced interspecific competition on bumble bee niche breadth and specialization, we used paired sample Wilcoxon Signed-Rank Tests (Wilcoxon, 1945). We tested for changes in WIC, BIC, TNW, and WIC/TNW between control/manipulation pairs. Once again, we performed these calculations at both the

individual-species and species-guild scales. We compared the magnitude and direction of changes at each level, and compared responses across different species.

There were several sources of variation across control/manipulation site pairs that could have substantially affected niche breadth. One of these variables was the community of competing bumble bee species at each site. We assessed this by including species richness, diversity (Shannon-Weaver) and evenness (Pielou's J) as additional explanatory variables (calculated using the R package *vegan*) in linear mixed-effects models with site and bumble bee species as crossed random-intercepts terms, using the *lmerTest* and *lme4* packages in R (Bates, Maechler, Bolker, & Walker, 2015; Kusnetsova, Brockhoff, & Christensen, 2016; Oksanen *et al.*, 2016). Since tongue length may affect which floral resources bees access, we also included in these models the tongue length of the species removed in each site, assessed categorically as either “long” or “short” tongued, following data that show two basic tongue length categories of bumble bees in this region, with substantial overlap among individuals in each class (Inouye, 1976). Additionally, we examined the same variables using random effects models on the differences in niche breadth measures between control/manipulation pairs. Since we did not find strong relationships between cloud cover or temperature and niche width or total observed plant visits at any level, we did not include weather in the models. We confirmed the normality of model residuals using Q-Q plots. The mixed-effects and random effects models were applied only at the species-guild scale, since niche width data at the individual-species scale were not normally distributed. Due to the high numbers of zero and one values in the individual-species observations, the data did not follow a normal distribution despite a variety of transformations.

Results

We observed >20,500 plant visits by >490 individual bumble bees over the course of 38 control/manipulation experiments. The bees observed represented seven bumble bee species. We

compared 18 site experiment pairs at the species-guild level. At the individual-species level, many control/manipulation pairs yielded observations of more than one species, so we compared 62 species/site experiment pairs.

Table 1. Results of Wilcoxon Signed-Rank Test at individual-species scale.

Niche width measure	Mean difference (control – manipulation)	Standard error	P value
WIC	0.02797	0.06069	0.703
BIC	-0.02622	0.03310	0.432
TNW	0.001754	0.05213	0.886
WIC/TNW	-0.007128	0.04715	0.899

Table 2. Results of Wilcoxon Signed-Rank Test at species-guild scale.

Niche width measure	Mean difference (control – manipulation)	Standard error	P value
WSC	-0.1315	0.05274	0.0342*
BSC	0.01105	0.05605	0.734
TNW	-0.1205	0.08120	0.182
WSC/TNW	-0.05222	0.04973	0.142

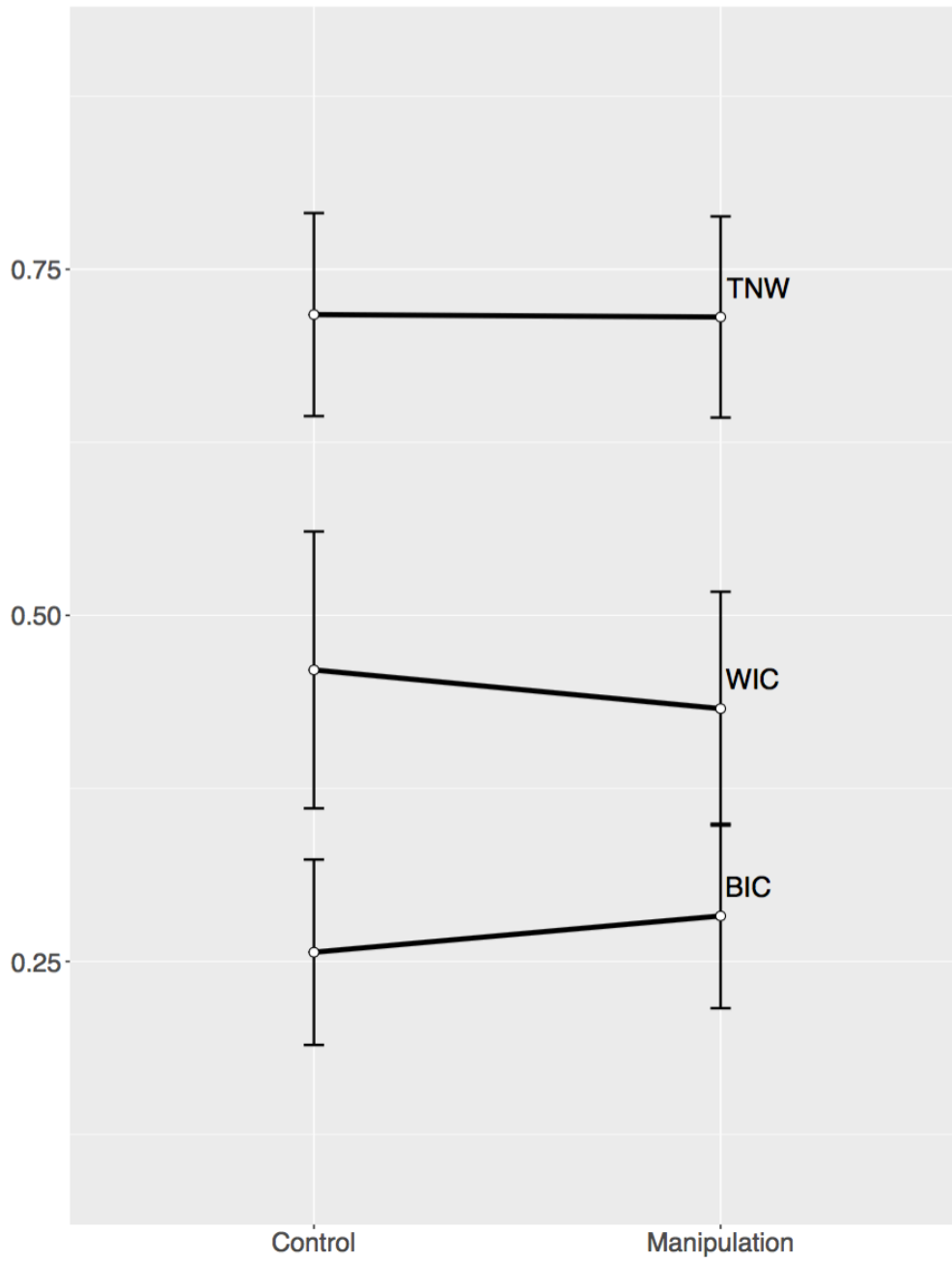
* $P < 0.05$

Table 3. Results of linear mixed-effects models at species-guild scale.

Response	Fixed effects	Coefficient	Standard error	P value
<i>WSC</i>	(Intercept)	0.3548	0.05324	$5.74 \times 10^{-7} **$
	State	0.1315	0.05154	0.0202*
<i>BSC</i>	(Intercept)	0.3392	0.05497	$1.61 \times 10^{-6} **$
	State	-0.01105	0.05470	0.842
<i>TNW</i>	(Intercept)	0.6931	0.07372	$4.01 \times 10^{-10} **$
	State	0.1205	0.08017	0.150
<i>WSC/TNW</i>	(Intercept)	0.5542	0.05609	$7.65 \times 10^{-10} **$
	State	0.05222	0.04954	0.306

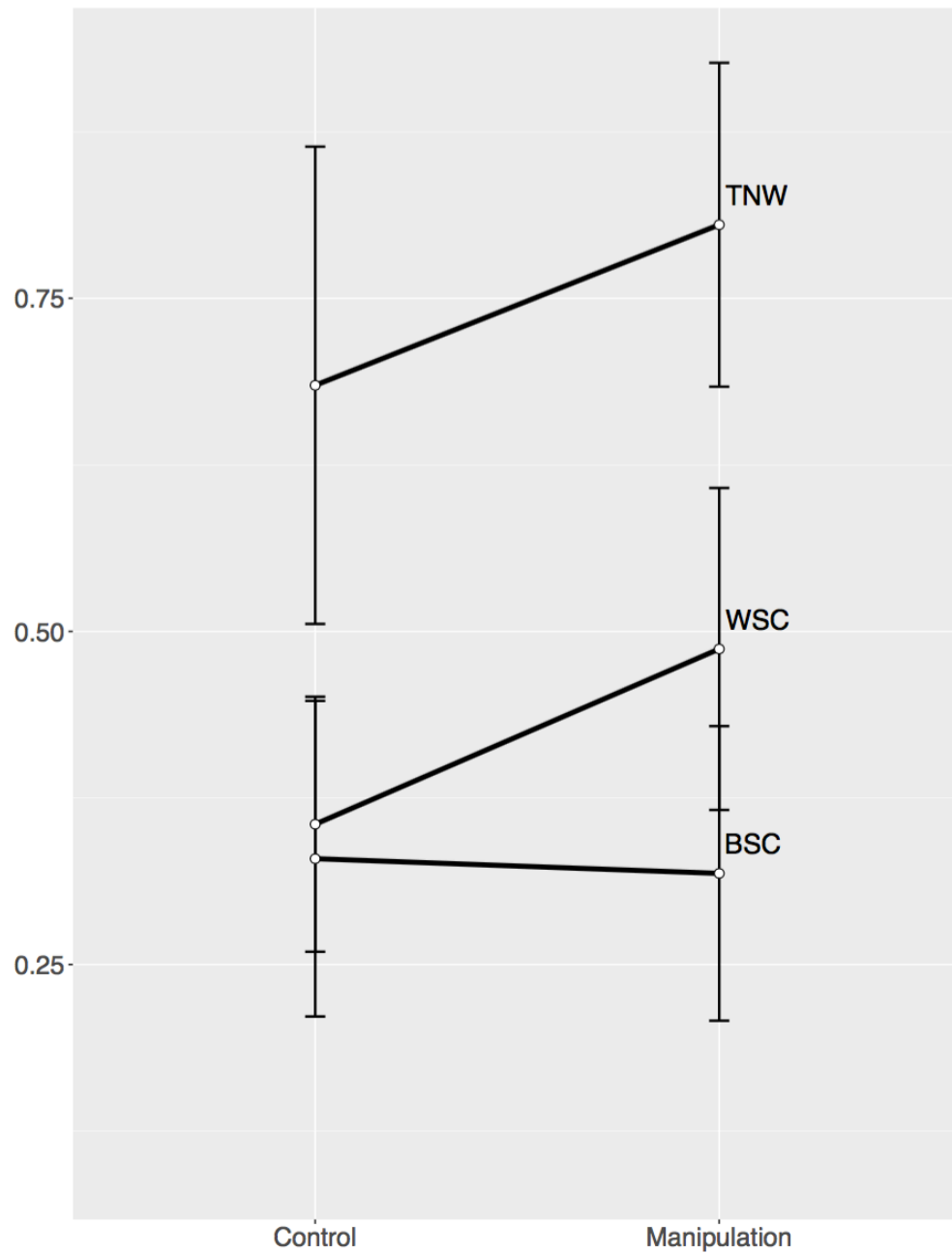
* $P < 0.05$; ** $P < 0.001$

Figure 3.



Effects of reduced interspecific competition on niche width at the individual-species scale. Mean niche breadth values (with 95% confidence intervals) are represented for the control and manipulation states.

Figure 4.



Effects of reduced interspecific competition on niche width at the species – guild scale. Mean niche breadth values (with 95% confidence intervals) are represented for the control and manipulation states.

Individual-Level Effects of Release from Interspecific Competition

Comparison of niche breadth and specialization measures between the control and manipulation states indicated that removal of the most abundant bee species did not significantly affect individual niche width or specialization in resource use (Table 1; Figure 3). Individual niche breadth (WIC) and the extent to which individuals specialized in resource use (measured by WIC/TNW) decreased non-significantly between control/manipulation pairs ($N = 62$). Likewise, the overlap in plant species visited by individual bees did not change significantly with release from interspecific competition, as BIC tended toward increasing non-significantly. Both within and across experiment pairs, there was substantial variation in the direction and magnitude of changes in niche and specialization for each species.

Species-Level Effects of Release from Interspecific Competition

When assessed at the species-guild scale ($N = 18$), by aggregating individual interactions to define species and combining species observations to form the guild, release from interspecific competition was associated with a significant increase in species niche width (WSC) (Table 2; Figure 4). In control/manipulation observation pairs, WSC expanded by on average 0.1315 ($P = 0.03$), indicating additions to the set of plants visited by a particular species. Overlap in resources between species tended toward increasing non-significantly, while the degree of species specialization decreased non-significantly between control/manipulation pairs. The observed expansion in species niche width was robust across tests, as the linear mixed-effects model confirmed the significant increase in WSC between control/manipulation pairs, yielding an average increase of 0.1315 ($P = 0.02$) in species niche width following release from interspecific competition on WSC (Table 3). No significant changes in BSC or WSC/TNW were observed with either the mixed-effects or random effects models.

In contrast to the species-guild level result, when examined at the individual-species scale ($N = 62$), in which TNW represents species niche width, we did not find evidence of significant change in species niche breadth with release from interspecific competition (Figure 3). Rather, comparison of control/manipulation pairs at this scale indicated non-significant contraction in mean TNW (Table 1). This contrast likely arises from the different subsets of data analyzed at each scale.

Guild-Level Effects of Release from Interspecific Competition

At the species-guild scale of analysis ($N = 18$), in which TNW represents guild niche breadth, we did not observe significant effects of release from interspecific competition on guild niche width (Table 2; Table 3; Figure 4). Each of the models tested indicated that guild TNW tended toward non-significant expansion in the manipulation state.

Effects of Species, Tongue Length, and Guild Composition

In addition, we used linear mixed-effects models and random effects models to assess differences in responses to release from interspecific competition based on species identity, the tongue length of the species removed, and guild composition. We did not find evidence of a significant effect of species identity or of the tongue length of the removed species. Likewise, models did not yield evidence of a significant relationship between the Shannon-Weaver diversity index, Pielou's evenness, or species richness and changes in any of the niche breadth or specialization measures.

Discussion

To assess the impacts of release from interspecific competition on bumble bee niche width and specialization at the individual, species, and guild levels, we conducted field experiments simulating bee species loss and observed the foraging behavior of individual bees. At the species-guild scale, species niche width expanded significantly in the absence of the most abundant bumble bee competitor. By contrast, no other measures of niche width and specialization showed significant changes at either the species-guild or individual-species scale. Neither tongue length of the removed species nor guild composition were good predictors of how species responded to release from interspecific competition, and species responses did not differ significantly.

We found that species-level niche breadths increased in response to release from interspecific competition, providing evidence for population niche expansion as a result of ecological release (Bolnick *et al.*, 2010; Roughgarden, 1972; Van Valen, 1965). Our results most closely resemble the individual release model of niche expansion. Concurrently with species-level niche breadth expansion, the overlap between species niches also increased, resulting in only a slight, non-significant broadening of guild niche width. This indicates that while species added new resources to their niches in the absence of the most abundant interspecific competitor, all species converged on the same set of resources. Therefore, guild niche breadth did not increase significantly. In other words, species foraging behavior became more generalist in response to release from interspecific competition, with all populations in an area approaching use of the same plants. The observed increase population niche breadth is consistent with the results of network analysis conducted in the same study system, which found that niche expansion occurred for the entire pollination network (not just bumble bees, as studied here) following removal of one bumble bee species (B. Brosi, unpublished data).

Release from interspecific competition has previously been found to result in decoupled changes in population and individual niche width, although the reasons for this decoupling remain

unclear (Bolnick *et al.*, 2010). We extended previous work (at the individual and species levels) by testing for changes in niche breadth and specialization at the guild level as well. Species niche width significantly increased with ecological release, while parallel changes were not observed at the individual and guild levels. However, we did not find significant evidence in support of decoupled changes at the individual, species, and guild levels.

The fact that we did not detect significant changes in niche breadth and specialization at the individual and guild levels may be a result of limitations in the data collection. One key limitation is that our measurements of individual niche breadth were based on non-destructive foraging observations, and as such were very small snapshots into resource use. By contrast, many other studies focused on niche breadth use metrics such as gut content analysis (e.g., Bolnick *et al.*, 2010) that integrate an individual's foraging activities over much longer time periods. To partially overcome this limitation, future work on pollinators could use identification of pollen loads in addition to direct observations of plant visitation. Additionally, although we observed tens of thousands of plant visits by hundreds of individual bumble bees and conducted more than 40 control/manipulation experiments, the need to balance the species and number of individuals observed in each pair limited the overall availability of usable data. We were forced to discard many observations, at both the individual-species and species-guild scales, in order to maintain comparable numbers of individuals and species between experiment pairs. As a result, the sample size at the species-guild scale was relatively small ($N = 18$) and covered a limited taxonomic range. Moreover, while we did not observe strong relationships between niche breadth or total observed visits and weather measurements, such as cloud cover and temperature, conditions in the field were highly variable and impacted data collection in multiple instances. Likewise, the number of bees that had to be removed in each manipulation state, and the degree to which the target species was successfully excluded from the plot, varied based on the characteristics of the different sites and local bee populations. To avoid the limitations on data availability outlined here,

future work must emphasize the collection of equal numbers of observations of both individual bees and species within experimental pairs whenever possible.

The expansion of species-level niche width and individual release at the species-guild scale may have important implications for pollination. Most pollinators are generalists, meaning that they transfer both heterospecific and conspecific pollen to the plants on which they forage (Briggs *et al.*, 2015; Brosi & Briggs, 2013; Waser *et al.*, 1996). Our results suggest that bumble bee species foraging behavior becomes more generalist with reduced interspecific competitors, as the guild converges on the same set of floral resources. Therefore, bees may transfer greater proportions of heterospecific pollen to plants during their foraging bouts (Briggs *et al.*, 2015; Brosi & Briggs, 2013). Since plants need conspecific pollen for fertilization, while heterospecific pollen may have deleterious effects on plant reproduction (Briggs *et al.*, 2015; Brosi & Briggs, 2013; Morales & Traveset, 2008), expansion of bumble bee species niche breadth and individual release at the guild level may significantly alter the distribution of pollen by bumble bees, with negative impacts on plant reproductive success. These results are relevant not only to the conservation of unmanaged ecosystems, but to agricultural systems as well.

As we have demonstrated, release of bumble bees from interspecific competition leads to expansion of species niche width. Given ongoing pollinator declines (Biesmeijer *et al.*, 2006; Potts *et al.*, 2010) and the importance of plant-pollinator interactions in determining pollen distribution and plant reproduction (Briggs *et al.*, 2015; Brosi & Briggs, 2013), our findings that the loss of one bumble bee species can result in individual release and increased generalization at the species-guild scale have serious implications for conservation. In order to better understand the effects of reduced interspecific competition on pollinators and the mechanisms driving the possible decoupling of individual, species, and guild niche breadth and specialization, further experiments conducted at multiple organismal levels are necessary.

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