

— Opinion —

# DELVING DEEPER: QUESTIONING THE DECLINE OF LONG-TONGUED BUMBLE BEES, LONG-TUBED FLOWERS AND THEIR MUTUALISMS WITH CLIMATE CHANGE

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**Abstract**—Miller-Struttmann et al. (2015) suggest that, in a North American alpine ecosystem, reduced flower abundance due to climate change has driven the evolution of shorter tongues in two bumble bee species. We accept the evidence that tongue length has decreased, but are unconvinced by the adaptive explanation offered. It posits foraging responses and competitive relationships not seen in other studies and interprets phenotypic change as evidence of evolutionary adaptation. By oversimplifying a complex phenomenon, it may exaggerate the potential for bees to quickly adapt to environmental changes.

**Keywords:** *adaptive evolution; Bombus; bumble bee; climate change; phenotypic plasticity; tongue length*

## INTRODUCTION

Climate change is widely expected to provoke range shifts or phenotypic responses, particularly in high-elevation regions where the rate of warming is magnified (Pepin et al. 2015). From historical data on various bumble bee species from the Colorado Rocky Mountains, Pyke et al. (2011, 2012, 2016) have reported elevational range shifts; Miller-Struttmann et al. (2015) have reported rapid evolutionary reductions in tongue length. Attributing phenotypic changes to climate change is onerous, as is demonstrating that those changes represent evolutionary adaptation. Indeed, few reports of climate-associated phenotypic change provide adequate evidence of evolution (rather than plasticity (Anderson et al. 2012)) being the mechanism (Gienapp et al. 2008). Merilä and Hendry (2014) outline the common challenges of attributing phenotypic changes observed over time as adaptive responses to climate change: 1) proving that the change is genetic rather than plastic; 2) demonstrating that the change is adaptive; and 3) establishing that climate change is the causal driver. Despite such calls for increased rigor (Gienapp et al. 2008; Merilä & Hendry 2014), tenuous inferences with inadequate data are still being published in high-impact journals. In particular, we are concerned that a recent report by Miller-Struttmann et al. (2015) of climate-driven adaptation in bumble bees overstates the ability of

organisms to adapt to rapid environmental change. Such findings can be further misconstrued when condensed into editor's summaries and media headlines about evolutionary rescue.

## THE PHENOMENON AND THE EXPLANATION

Miller-Struttmann et al. 2015 (henceforth M-S15) propose that tongue (proboscis) length reductions in two bumble bee species over 40 years represent adaptive microevolutionary responses to climate change, that “evolution is helping wild bees keep pace with climate change” (p. 1544). In some populations, body size also decreased significantly over time. That suggests that tongue-length reductions might be byproducts of selection for overall body size; however, the change in body size accounted for less than 20% of the variation in tongue length, leading M-S15 to treat tongue length as the primary target of selection. The two bumble bee species are *Bombus sylvicola* Kirby and *B. balteatus* Dahlbom (previously treated as *B. kirbyellus* Curtis (Inouye 1980; Pyke et al. 2012) and recently revised to *B. kirbiellus* Curtis (Williams et al. 2015)). M-S15 posit that having a shorter tongue allows greater resource generalization and that this is adaptive to current climate change. At their alpine study sites on the Eastern Slope of the Colorado Rocky Mountains, they have shown an overall decrease in floral resource abundance and changes in bumble bee community composition over time. They found that minimum summer temperatures above 3.25°C negatively affected peak floral density. M-S15

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assume that with decreasing nectar resources in a warming climate, a generalist foraging strategy has become more beneficial and selects for the evolution of shorter tongues in bees. M-SI5 state that although bees are able to adjust to a resource-poor environment, this leads to a functional mismatch between long-tubed flowers and formerly specialized, longer-tongued bees. Further, M-SI5 state that their findings may increase our understanding of widespread long-tongued *Bombus* declines.

These intriguing results, published in *Science*, attracted media attention from various international news outlets. The quality of scientific reporting on the article was highly variable. We believe that an inaccurate Editor's Summary in *Science* contributed to poor reporting (Vignieri 2015). Interestingly, Vignieri (2015) does not adopt the evolutionary explanation for changes in tongue length proposed by M-SI5 and instead attributes the change to species turnover. The Summary states that M-SI5 observed a decrease in the number of long-tongued bumble bees and their replacement by 'generalist' short-tongued species as a result of warming summers and reduced floral resources. This statement does not describe a hypothesis tested by M-SI5, and it incautiously extends the proposed mechanism for tongue length shortening to account for other changes in community composition. In addition, the Summary states that M-SI5 have shown a disruption in the mutualism between long-tongued bees and long-tubed flowers, but we find little support for this claim. Instead of clarifying the results from M-SI5, the Summary misinterprets the key findings and makes erroneous claims. The bees in the M-SI5 study have not abandoned long-tubed flowers; whether changes in bee dietary breadth have caused decreased reproductive success in long-tubed plants has not been studied. Therefore, the message of eroding mutualisms in the Editor's Summary and numerous news reports is based on scant evidence. Although M-SI5 cannot be held responsible for editorial misinterpretations or uncritical media reports, we find shortcomings in the explanations offered in the paper itself. Some clarity may have been sacrificed to achieve the extreme brevity demanded by a high-impact journal. We hope to restore clarity by opening a further dialogue.

The evidence presented by M-SI5 for tongue length decreases in *B. balteatus* and *B. sylvicola* over recent decades is convincing. However, we are unconvinced by their adaptive explanation, and we take issue with the emphasis on long-tongued *Bombus* declines. Here, we present evidence from the published literature showing that the assumptions made by M-SI5 are inconsistent with general patterns in bumble bee ecology, and current knowledge of bumble bee declines in North America. In addition, we believe that the data are inadequate for detecting microevolutionary responses to climate change. M-SI5 overstate the speedy adaptability of bumble bees to environmental stressors and as a result, we suggest that the conclusions of this study be interpreted with caution.

#### ARE LONG-TONGUED *BOMBUS* MORE SUSCEPTIBLE TO DECLINE?

M-SI5 conjecture that their results "may inform our understanding of widespread declines in long-tongued

*Bombus* specialists" (p.1541). For North American habitats, positing a link between long tongues and population declines is premature. The IUCN Red List assessments (IUCN 2015) indicate that in North America, more short-tongued bumble bee species are vulnerable. Admittedly, the status of many long-tongued species is still unknown (Fig. 1). The evidence for long-tongued bumble bee declines cited by M-SI5 comes primarily from Europe. There, community-level changes at high elevation do show decreases in the relative abundance of long-tongued bees, but whether these changes are due to declines in long-tongued species or increases in short-tongued species is unclear (Bommarco et al. 2012). This is due to the inherent difficulty of assessing changes in absolute species abundance when the data are relative abundances, and potentially biased by sampling effort. M-SI5 present data on changes in relative bumble bee abundance at their study site and find evidence of increased species richness and a decrease in the relative abundance of long-tongued bees. By themselves, those responses could be caused by the addition to the community of new, short-tongued species, perhaps as immigrants from lower elevations. M-SI5 considered the hypothesis that competition from subalpine bumble bee species migrating upward could cause shifts in tongue length of their focal alpine species, but they dismissed it because their prediction of an associated decrease in floral resource breadth went unsupported. As we discuss below, that prediction depends on assumptions about competition that lack direct support.

M-SI5 state that declining, long-tongued bee species are specialists and that "shifts [in] foraging strategies may allow alpine bumble bees to cope with environmental change" (p. 1544). We do not agree with the assumption that resource specialization is a driver of decline. Williams et al. (2009) found no support for the hypothesis that *Bombus* species declines are associated with restricted dietary breadth. This casts doubt on M-SI5's proposition that tongue shortening will enable resource generalization and thereby aid population persistence. We can illustrate this with two examples from North America: *B. pensylvanicus*, a long-tongued species, and *B. occidentalis*, a short-tongued species, have widely disappeared from their once extensive ranges (Cameron et al. 2011). Neither of these bees is a food plant specialist; *B. pensylvanicus* was one of the most generalized bee species in Robertson's detailed plant-pollinator network from the late 1800s (Burkle et al. 2013). *B. occidentalis* has a wider dietary breadth than co-occurring short-tongued species that have not declined, because it is able to nectar rob from long-tubed flowers (Inouye 1983). Such examples reinforce the correlational conclusion by Williams et al. (2009) that factors other than limited dietary breadth are at play. Instead, suggested drivers of decline among vulnerable species are thought to be more complex. Among North American species, declines of bumble bees have been attributed, at least in part, to habitat loss (Hines & Hendrix 2005; Grixti et al. 2009), climate change (Kerr et al. 2015), and pathogen spillover (Cameron et al. 2011; Szabo et al. 2012).

M-SI5's conclusion that "evolution is helping wild bees keep pace with climate change" (p. 1544) seems to depend

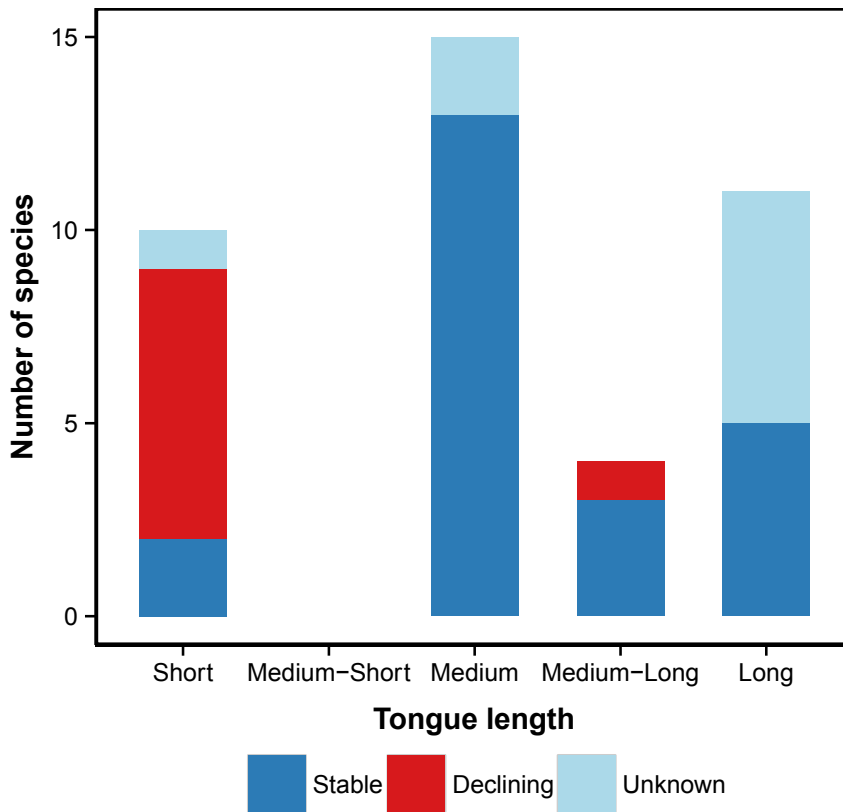


FIGURE 1. Number of North American *Bombus* species assessed as declining (i.e. at-risk of extinction and considered Critically Endangered, Endangered, Vulnerable or Near Threatened) or stable (i.e. Least Concern) by the IUCN Red List (IUCN 2015). Species shown as 'unknown' have not yet been assessed. The total number of North American *Bombus* species is 40, excluding the subgenus *Psithyrus*. We exclude *Psithyrus* because they do not produce a caste of worker bees, which was the caste studied by M-SI5. Tongue lengths were categorized based on Paul Williams' *Bombus of the World* (<http://www.nhm.ac.uk/research-curation/research/projects/bombus/>) [Accessed Oct 20, 2015].

on the assumption that shorter tongue-lengths are adaptive. To determine whether change in tongue length has allowed populations to thrive or escape decline through evolutionary rescue, we need a direct test of the adaptive hypothesis that bee tongue length shortening affects fitness. Since this was not investigated by M-SI5, it is difficult to know whether the above conclusion is reasonable. It might be expected that bee species that are 'keeping pace' will not have undergone population declines. This could be approximated by a negative correlation between changes in relative bee abundance and changes in tongue length across sites. Based on the few sites and two species studied, the correlation does not appear to be negative. We think that the relationships between tongue length shortening, adaptation, population declines, and conservation are likely much more complex than presented in M-SI5 and require further study. We therefore advise caution when interpreting the results from M-SI5 for conservation purposes, as the data are not strong enough to infer evolutionary rescue has occurred.

We conclude that long-tongued species may not be more susceptible to decline, based on IUCN assessments. We therefore dispute M-SI5's claim that their findings can provide insight into long-tongued *Bombus* declines. We also do not think their results are specific to specialist bee declines because evidence for resource specialization increasing *Bombus* species susceptibility to decline is lacking. More research is needed to determine whether long-tongued bees truly are more vulnerable and whether tongue length shortening is relevant to declines and/or could act as an evolutionary rescue from decline.

## TONGUE LENGTH AND RESOURCE SPECIALIZATION

M-SI5 hypothesize that "with lower floral resources, fitness advantages of long-tongued specialist phenotypes have diminished, potentially driving the rapid evolution of shorter-tongued bees" (p. 1544). If this hypothesis is correct, then we expect shortening only in long-tongued species. *B. balteatus* is clearly long-tongued, but *B. sylvicola*, which has tongue lengths on average 3.57 mm shorter, should be considered a short-tongued species, according to M-SI5 (p. 1542) and to records of host species use elsewhere (Pyke 1982). In subalpine to alpine habitats on the Western Slope of Colorado, *B. sylvicola* has been characterized as belonging to the guild of short-tongued bumble bees (Pyke 1982, Table 2). In those habitats, *B. sylvicola* clusters with other short-tongued species when ordinated by host-plant use (Fig. 2). It differs markedly from *B. balteatus*, which clusters with the other long-tongued species.

Despite their ecological differentiation, both species have evolved shorter tongues. Indeed, *B. balteatus* appears to be evolving toward the tongue length that *B. sylvicola* is evolving away from (M-SI5, Fig. 1). The interpretation presented by M-SI5 is couched in terms of long-tongued bees, but only one of their two species fits that category.

## ARE SHORT-TONGUED BEES GENERALISTS?

M-SI5 assert that "long-tongued pollinators specialize on flowers with deep corolla tubes, whereas shorter-tongued pollinators generalize across tube lengths" (p. 1541). This

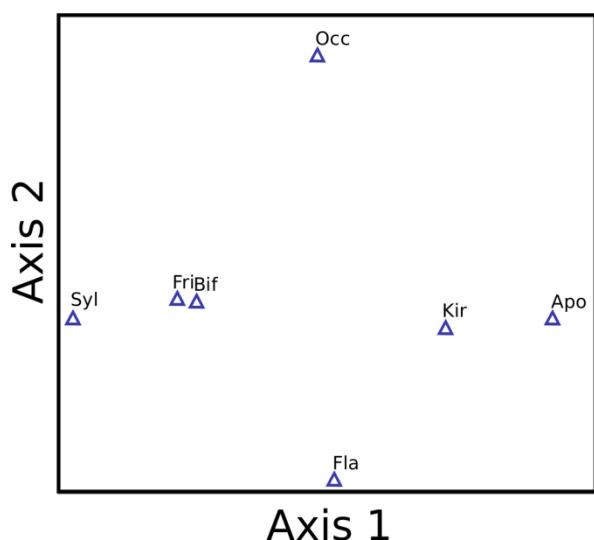


FIGURE 2. Bray-Curtis ordination of bumble bee species according to use of 34 host-plants near Gothic, Colorado (data from Pyke 1982, Table 2). Short-tongued species: *B. sylvicola* (Syl), *B. frigidus* (Fri), *B. bifarius* (Bif), *B. occidentalis* (Occ). Medium-tongued species: *B. flavifrons* (Fla). Long-tongued species: *B. balteatus* (Kir), *B. appositus* (Apo). *B. sylvicola* clusters with other short-tongued species; excluding *B. occidentalis*, which likely exploits different host-plants through its nectar robbing behaviour on long-corolla plants. *B. balteatus* clusters with the other long-tongued species *B. appositus*.

statement is a necessary assumption for the M-S15 adaptive explanation, as it provides the basis for inferring that tongue length shortening is an adaptive response. As a general proposition, it lacks support in the literature. The relationship between generalization and tongue length depends on both morphology and competition for nectar. Long-tongued bees always have the potential to extract nectar from both deep and shallow flowers, and they frequently do generalize with respect to tube length (Heinrich 1976; Ranta & Lundberg 1980; Harder 1983, 1985). Long-tongued bees might be slower at visiting short-tubed flowers, but evidence is limited (Inouye 1980; Harder 1983; Plowright & Plowright 1997). There also appears to be no learning constraint on long-tongued bees that prevents them from successfully visiting open, short-tubed flowers (Lavery 1994). Of course, long-tongued bees have the option of specializing if particular plants offer enough resources. Short-tongued bees are more constrained. Foraging efficiency decreases sharply when bees visit flowers deeper than the length of their tongues; therefore, short-tongued bees will typically be restricted to shallow tubes (Harder 1983). In a study of eight *Bombus* species visiting 14 plant species, Harder (1985) reported, “[b]ee species with long glossae had access to nectar in a greater variety of flowers than those with short glossae, and they tended to feed from a larger number of plant species” (p. 198).

Turning from general patterns of specialization in bumble bees to the particular cases of *B. balteatus* and *B. sylvicola*, Pyke’s (1982) data are again instructive. The short-tongued group of species uses a diversity of plant species, but 85% of the observations for *B. sylvicola* in Pyke’s Table 2 come from 14 species of Asteraceae with floret depths

between 3.6 and 6.3 mm. Six of them are from the genus *Senecio*. The high species diversity of resources used by this bee reflects the high species richness of functionally identical composites in these habitats, not the species’ ability to generalize. In contrast, *B. balteatus* concentrates on deep-tubed flowers from various families with distinct handling requirements, in addition to occasionally visiting the short-tubed composites. It clearly has more potential to generalize across different flower depths if conditions demand it. The Eastern Slope of the Colorado Rocky Mountains where M-S15 worked presents a different flora, but even there, the foraging niches of the two study species differ to an ecologically meaningful extent (Miller-Struttman & Galen 2014, Fig. 4; M-S15, Fig. 2).

#### WHAT ARE THE ROLES OF FLORAL ABUNDANCE AND COMPETITION?

M-S15 state that with reduced flowering in alpine habitats, “foragers will expand their niche in response to such resource scarcity” (p. 1543). This prediction relies on implicit assumptions that may not be general, and we think that it ignores important differences between long- and short-tongued bees. For example, Rodríguez-Gironés & Santamaría (2006) modelled the dependence of generalization on resource abundance. In their model, both short- and long-tongued flower visitors visit every flower they encounter under low competition and become specialized only when competition is very high. This expectation runs counter to M-S15’s proposition that generalization should occur under resource scarcity. However, M-S15 Fig. 2 shows that the range of tube lengths that *B. balteatus* visits has changed little over time, whereas *B. sylvicola* has clearly abandoned the very longest tubed flowers. It has not expanded its foraging niche. Perhaps *B. sylvicola* was able to forage across a wider range of tube lengths because of low competition for resources during the summers of 1966-69 that Macior (1974) collected the data that form the historical portion of M-S15’s study. Indeed, 1966-69 were not years of extreme temperature or drought so floral resources were likely to be abundant (Greenland & Kittel 2002). In the contemporary sampling period, more intense competition might have depressed standing crops of nectar so that short-tongued bees could no longer reach the rewards in deep flowers. Shrinking tongues in short-tongued species could further exacerbate this. In this alternative scenario, the shifts in foraging breadth observed by M-S15 would not be attributable to tongue-length shortening of long-tongued bees. The drivers would instead be resource scarcity, increased competition, and potentially, tongue-length shortening of short-tongued bees.

To test accurately whether changes in nectar resources can lead to “evolutionary shifts in foraging traits of two alpine bumble bee species” (p. 1541), we need direct evidence for improved resource acquisition through tongue length shortening and subsequent increases in fitness. M-S15 do not provide such evidence and instead present two competing hypotheses before settling on a mechanism of nectar foraging driving selection on tongue length: 1) diminished floral resources due to climate change result in

greater nectar resource *generalization* and 2) competition for resources due to changes in community composition results in greater nectar resource *specialization*. We cannot envision how these two hypotheses result in opposite outcomes (i.e., generalization vs. specialization), because competition (hypothesis 2) generally translates to reduced resource availability (hypothesis 1). Even if we accept that these two outcomes are possible, we think that the adaptive trajectory for tongue length would be the same. That is, for either specialization on long-tubed flowers or generalization to visit whatever tube-lengths are available, we think a long tongue is more energetically favourable and should be selected for if considering *only* nectar foraging (Harder 1983; Rodríguez-Gironés & Santamaría 2006). However, it is possible that tongue length changes result from selection imposed by pollen foraging constraints, physiological constraints, or some other aspect of life history, rather than changing nectar resources. It would be important to know how much nectar foraging efficiency contributes to colony recruitment and how this compares with the importance of pollen foraging. If nectar foraging efficiency is relatively unimportant, then it becomes hard to believe that tongue length matching to nectar resources could be driving such rapid selection on tongue length.

#### HAS CLIMATE CHANGE PRODUCED FUNCTIONAL MISMATCH THAT DISRUPTS A MUTUALISM?

M-SI5 propose that a switch from specialist to generalist foraging has led “to a mismatch between shorter-tongued bees and the longer-tubed plants they once pollinated” (p. 1541). The reanalysis of Macior’s *Bombus* visitation data from 1966-69 by Miller-Struttman & Galen (2014) found that long-tongued bees had wider foraging niches in the alpine altitudinal zone than in other zones, and that both *B. sylvicola* and *B. balteatus* were highly generalized in the alpine. Those characterizations are inconsistent with M-SI5, where these alpine species are portrayed as former specialists that have recently become more generalized. Perhaps this inconsistency is due to differences in focus of the two papers, from taxonomic niche breadth to functional variance in flower tube depths. Despite this discrepancy, there appears to be a correlation between these measures, as generalization across species still results in generalization across corolla tube depths (M-SI5, Fig. 2, Fig. S2). Although we accept that M-SI5 have found both increased niche breadth and corolla tube depth generalization, we do not agree that these species can be described as former specialists. Instead, *B. balteatus* and *B. sylvicola* are former generalists, and the changes for each species are nonequivalent. In addition, we think it is unlikely that the differences in niche breadth that M-SI5 observed will have lasting impacts on long-tubed alpine plants, as these plants likely evolved with the various selection pressures imposed by highly generalized bumble bee foraging (Miller-Struttman & Galen 2014). Long-tubed plants are still being visited by *B. balteatus*, despite a change in tongue length and therefore, the purported “mismatch between shorter-tongued bees and the longer-tubed plants they once pollinated” (p. 1541) does not apply. This statement is more relevant to *B. sylvicola*, which has more drastically decreased its visitation to long-tubed flowers over

time (M-SI5, Fig. 2, Table S3). However, *B. sylvicola* is a short-tongued bee; it was mismatched to long-tubed flowers to begin with. In certain special cases, such as hawkmoths and orchids, specialization may become associated with tongue length through extreme coevolution of long nectar spurs and long tongues, but we are reluctant to extrapolate from such cases to the typically generalized relationship of bumble bees to their nectar plants (Waser et al. 1996; Rodríguez-Gironés & Santamaría 2006). M-SI5’s characterization of a disrupted mutualism goes beyond the data they present.

M-SI5 have inferred that the observed changes in tongue length are adaptive. This may well be the case, but was not directly tested. Instead, M-SI5 have presented arguments on changes in resource breadth and specialization. Although several aspects of their explanations are plausible, alternatives have not been adequately explored. The focus on long-tongued bees seems misplaced. We do not think M-SI5 have presented the most parsimonious explanation for tongue length shortening or adequately explored alternative hypotheses (i.e., tongue length shortening may be unrelated to nectar resources or may even be maladaptive). Furthermore, claims of mutualism disruption and functional mismatch have little direct support.

#### ALTERNATIVES TO RAPID EVOLUTION

The observed changes in tongue length have not been demonstrated to be responses to natural selection, but even if they were, need the selective mechanism have been gradual, directional climate change? To answer this we need to consider whether M-SI5 have presented adequate evidence that warming summers have resulted in consistent reductions in floral resources over time. M-SI5 lack replication in studying this relationship; they present data on historical and contemporary floral abundance from only a single mountain that shows inconsistent responses across habitat types (M-SI5 Fig. 3). Similar to the variability across habitats, it is likely that there has been variability in floral abundance across years. In particular, for some years plants have likely benefitted from increased temperatures, as floral abundance tends to increase with average minimum summer temperature up to a certain point (M-SI5 Fig. S3C). An alternative possibility is that bees might have responded to highly unusual years where all floral resources are drastically diminished. That is, selection on tongue length may be highly variable from year to year with no relationship to directional climate change. Ideally, we would need a year-to-year study measuring direction and strength of selection to determine if changes in tongue length are really a function of climate and nectar resource availability. Because these data are not available, we are left to speculate.

As an alternative to selection, we can postulate that years with extreme resource scarcity could also result in severe population bottlenecks for bumble bee species. M-SI5’s study included 2012, a particularly dry year. On the Western Slope of the Colorado Rockies, that year was noteworthy for particularly low winter snowpack and early snowmelt, a lack of summer rains (Campbell & Powers 2015; Gezon et al. 2015), and, anecdotally, low numbers of flowers and of

bumble bees (Gezon et al. 2016). If similar extremes occurred in M-S15's sites, this unusual year might have undue influence on the patterns they observed. Plastic changes in worker morphology could have arisen from food shortages during critical stages of colony development. If bee populations fell so far as to undergo bottlenecks, genetic drift might have played a role in addition to selection. If such stresses were important, then the current shorter-tongue phenotype should not be assumed to be adaptive, and could even be maladaptive for nectar foraging. We think this an important consideration given the decreased efficiency of shorter tongues on long-tubed flowers and unlikely generalization of short tongues under low resource conditions (Harder 1983; Rodríguez-Gironés & Santamaría 2006).

When we consider what factors could potentially drive the evolution of a shorter tongue more generally, the model presented by M-S15 offers a robust mechanism: the importance of a decrease in the proportion of long-tubed flowers. For example, if it is costly to maintain a long tongue in the absence of long-tubed flowers, then decreases in long-tubed floral abundance could well play a pivotal selective role in tongue length adaptation. Although this may generally be true, it is still not an adequate explanation for M-S15's empirical data, because the declines in floral abundance they report for both Niwot Ridge and Pennsylvania Mountain were unrelated to floral tube depth. The importance of a disproportionate decline in deep-tubed flowers is emphasized in the model employed by M-S15. In order to predict when the evolution for shorter tongues could be favoured, the predictor variables in the model include not only floral abundance but also the proportion of deep flowers. Without evidence for reduction in the proportion of deep flowers, the model fails to align with empirical findings.

Changes in phenotype need not arise from changes in genotype. Since we do not have genetic data to assess whether changes in phenotype are associated with changes in allele frequency, we cannot rule out phenotypic plasticity. For example, the body size of flower-visiting insects can be reduced due to plastic responses of accelerated development under increased temperatures (Scaven & Rafferty 2013). It is possible that tongues require more time for development than overall bee body size, so changes in developmental timing could result in a disproportionate decrease in tongue length. This is an alternative hypothesis that warrants further study. It is also important to note that plastic responses to climate change are not always found to be adaptive (Merilä & Hendry 2014).

Based on the current evidence, we think that some sort of plastic response deserves consideration as an explanation for the tongue length shortening observed by M-S15. It could readily apply to both long- and short-tongued bees. That is not true of explanations based on nectar-plant use; the two species of bees differ so much in their feeding choices that it is hard to see how M-S15's single explanation for tongue length shortening could apply to both of them. In addition, because the same trend of tongue length shortening was observed in both species, it seems unlikely that random genetic processes are to blame. It is possible that an entirely

different mechanism that has to do with constraints on pollen foraging or any other aspect of bumble bee life history may have created selection for shorter tongues, but we have no evidence to support this one way or another.

Although we have tried to root our caveats in the scientific literature, we are still not confident that we have produced a winning alternative hypothesis for the patterns revealed by M-S15's painstaking work. Nevertheless, we hope that our questions will stimulate further dialogue and more research. For the present, we advise against accepting M-S15's inference that bumble bees can adapt rapidly and successfully to environmental stressors. The data are not strong enough to warrant such optimism.

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