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the deglacial ventilation and circulation events from a more broadened view.

SUPPLEMENTARY MATERIALS

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EVOLUTIONARY ECOLOGY

Functional mismatch in a bumble bee pollination mutualism under climate change

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Ecological partnerships, or mutualisms, are globally widespread, sustaining agriculture and biodiversity. Mutualisms evolve through the matching of functional traits between partners, such as tongue length of pollinators and flower tube depth of plants. Long-tongued pollinators specialize on flowers with deep corolla tubes, whereas shorter-tongued pollinators generalize across tube lengths. Losses of functional guilds because of shifts in global climate may disrupt mutualisms and threaten partner species. We found that in two alpine bumble bee species, decreases in tongue length have evolved over 40 years. Co-occurring flowers have not become shallower, nor are small-flowered plants more prolific. We argue that declining floral resources because of warmer summers have favored generalist foraging, leading to a mismatch between shorter-tongued bees and the longer-tubed plants they once pollinated.

Long-tongued bumble bees have coevolved to pollinate plants that possess elongated corolla tubes in a mutualistic relationship. Recent declines in such long-tongued bee populations suggest that historical selection regimes in these systems are changing (1–3), yet the mechanisms driving these declines are unclear. Spatial and temporal discrepancies with food plants, habitat destruction, and pressure from invasive competitors have been implicated (3–6), but the details of these declines and their causes remain unresolved.

Matching of functional morphology between partners increases benefits and reduces costs in mutualisms (7, 8). The match between flower tube depth and pollinator tongue length influ-

ences resource acquisition and pollination effectiveness (9, 10). For bees, hummingbirds, bats, moths, and flies, morphological matching increases handling efficiency on flowers (9–14). Thus, changes that disrupt such matching can alter plant species recruitment and the trajectory of coevolution. Although the climate change impacts on phenological and spatial overlap of mutualists are well known, the role of climate change in generating functional discrepancies between them is less understood. Using historical data, we show that reduced flower abundance in bumble bee host-plants at the landscape scale has accompanied recent warming, leading to evolutionary shifts in foraging traits of two alpine bumble bee species (*Bombus balteatus* and *B. sylvicola*). Rapid evolution of shorter tongues in these species may inform our understanding of widespread declines in long-tongued *Bombus* specialists.

We measured the change in tongue length of *B. balteatus* and *B. sylvicola* using specimens collected from 1966–1980 and 2012–2014 in the central Rocky Mountains (15). These two species historically comprised 95 to 99% of bumble bees at our high-altitude field sites (16–18). *B. balteatus* workers were collected from three geographically isolated locations: Mount Evans (39°35.033'N, 105°38.307'W), Niwot Ridge (40°3.567'N, 105°

37.000'W), and Pennsylvania Mountain (39°15.803'N, 106°8.564'W).

B. sylvicola workers were collected from Niwot Ridge and Pennsylvania Mountain. Mean tongue length has decreased 0.61% annually and 24.4% cumulatively in these taxa ($F_{1,23} = 17.02$, $P = 0.0004$ and $F_{1,67} = 46.14$, $P < 0.0001$) (Fig. 1 and table S1). Using archived specimens and field surveys of bumble bees and host plants, we explored four potential mechanisms for this change in tongue length: (i) decreasing body size, (ii) coevolution with floral traits, (iii) competition from subalpine invaders, and (iv) diminishing floral resources.

Temporal changes in bumble bee tongue length are not explained by plasticity in body size. When phenotypic variance in tongue length is partitioned among underlying sources, size accounts for less than 20% of variation (table S1) (15). Size has declined in some populations (*B. balteatus*: $F_{2,96} = 8.61$, $P = 0.0004$; *B. sylvicola*: $F_{1,76} = 29.01$, $P < 0.0001$) (fig. S1 and table S1) and is phenotypically correlated with tongue length [correlation coefficient (r) = 0.50 to 0.60, $P < 0.005$] (fig. S1) but contributes little to its reduction over time. After removing variance explained by body size, analysis of covariance shows significant temporal changes in tongue length (*B. balteatus*: $F_{1,23} = 17.02$, $P = 0.0004$; *B. sylvicola*: $F_{1,67} = 46.14$, $P < 0.0001$) (Fig. 1 and table S1).

Selection to track the floral traits of host plants should favor short-tongued pollinators when flowers become shallower or deep flowers less common (9, 10). We tested this hypothesis by comparing flower depth of herbarium specimens collected from 1960–1982 and 2012–2013 near Mount Evans and Niwot Ridge (15). In six species that historically provided 88% of floral resources for *B. balteatus* and *B. sylvicola* (18), the change in flower depth over time varied among species ($F_{6,13} = 9.42$, $P = 0.0004$). Species that now have shallower flowers received few (<10%) bumble bee visits historically (fig. S2A). On Pennsylvania Mountain and Niwot Ridge, short-tubed flowers show no systematic increase in abundance [coefficient of determination (R^2) = 0.227, $t_{1,4} = 1.21$, $P = 0.294$; $R^2 = 0.0004$, $t_{1,9} = -0.62$, $P = 0.952$, respectively] (fig. S2, B and C), suggesting that recent changes in floral trait distributions are insufficient to drive tongue length adaptation in bumble bees.

Alternatively, shifts in bumble bee tongue length may reflect competition from subalpine congeners moving upward with climate change.

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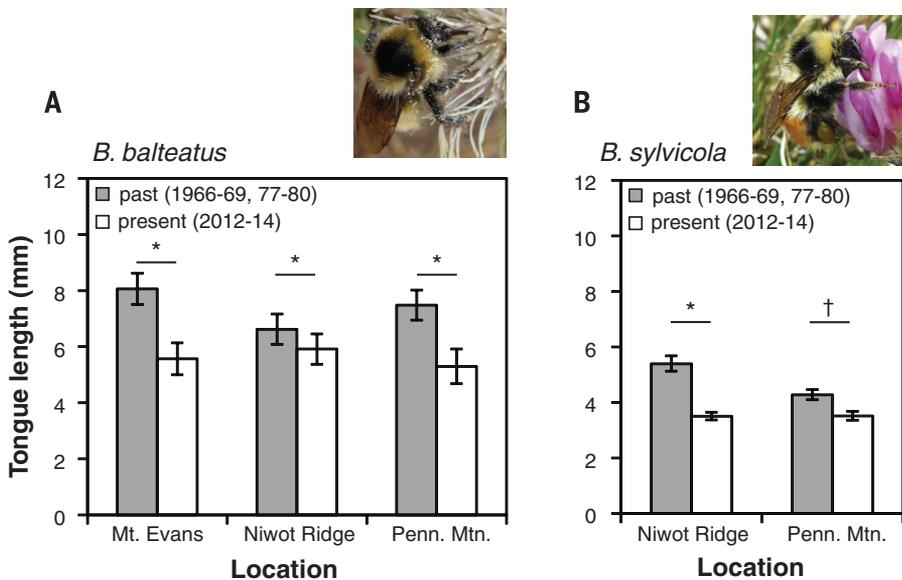


Fig. 1. Change in tongue length for *B. balteatus* and *B. sylvicola* on Mount Evans, Niwot Ridge, and Pennsylvania Mountain. (A) *B. balteatus*. (B) *B. sylvicola*. Bars represent least squares means \pm SE. (15). Asterisks denote significant differences ($P < 0.05$) between means. Dagger denotes a trend ($P < 0.06$).

Comparisons of past (1960s and 1970s) (16, 17) and present (2008 and 2011–2014) bumble bee communities on Pennsylvania Mountain and in the Front Range [Mount Evans and Niwot Ridge combined (16)] indicate increased species diversity (respectively, $\chi^2 = 293.4$, $df = 7$, and $\chi^2 = 579.4$, $df = 12$, $P < 0.001$) (Fig. 2, A and B), immigration of short-tongued species from lower altitudes, and a 24.1% decrease in the frequency of long-tongued bees (Front Range: $F_{1,1998} = 94,618$, $P < 0.0001$; Pennsylvania Mountain: $F_{1,1988} = 85.6$, $P < 0.0001$) (Fig. 2, C and D, and table S2) (15). With increasing competition from immigrant species, foraging breadth of resident bees should contract (19, 20). Yet alpine bumble bee host choice shows the opposite trend. In 2012–2014, we re-surveyed bumble bee visitation on Mount Evans and Niwot Ridge in accordance with historical observations (18). Despite a 10-fold difference between past ($n = 4099$ visits observed) and present ($n = 519$ visits observed) collection effort, surveys indicate that resident bumble bees have broadened their diet. Resampling historical visitation data to match present collection effort reveals that foraging breadth (Levin's niche breadth) (15) increased from 2.61 to 7.01 for *B. balteatus* [z score (Z) = 28.48, $P < 0.0001$] and 2.09 to 5.07

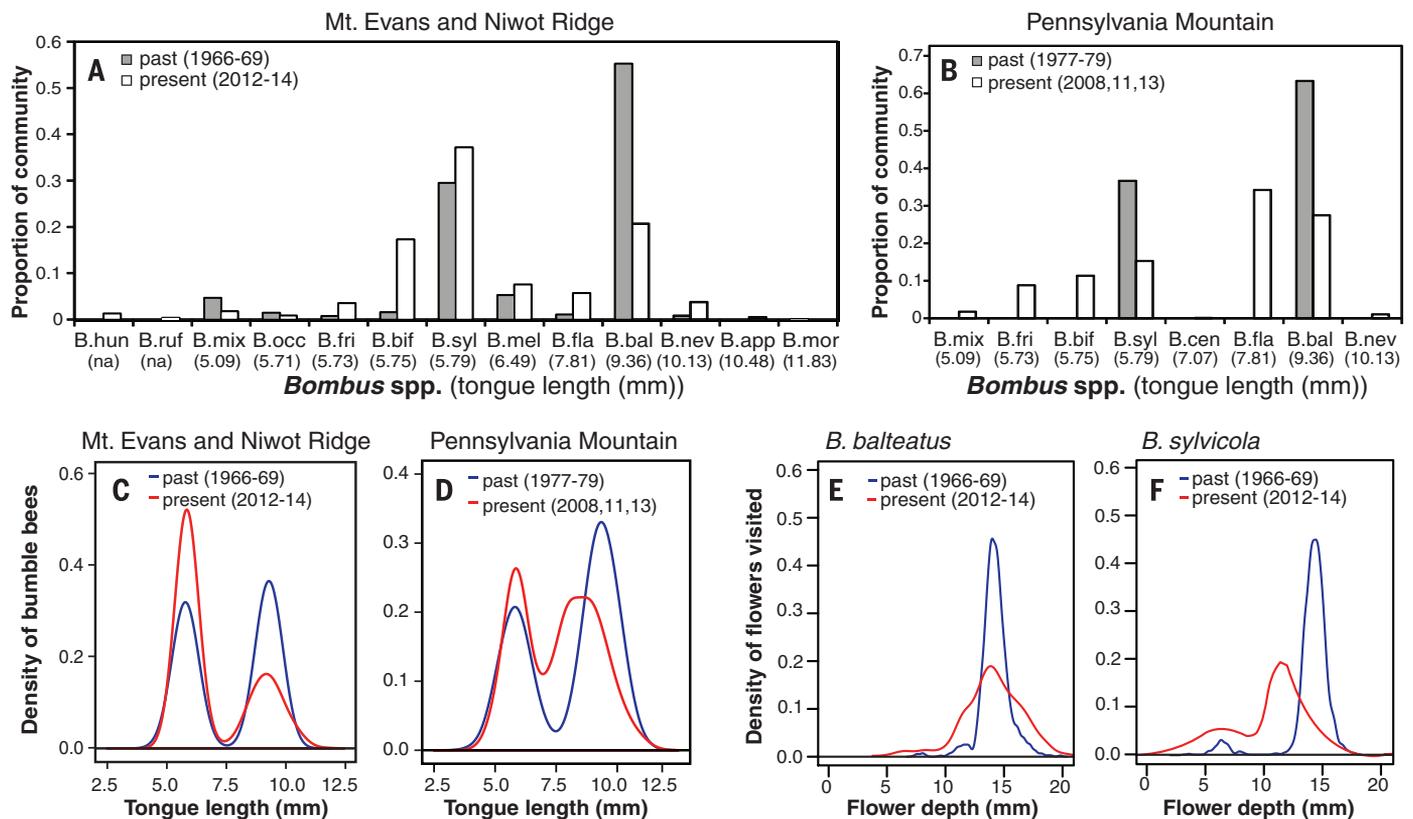


Fig. 2. Changing bumble bee community composition, bumble bee tongue length distributions, and tube depth distributions of visited flowers over time. (A and B) Bumble bee community composition. **(C and D)** Bumble bee tongue length. **(E and F)** Flower tube depth distribution. *Bombus* species abundance in alpine communities is indicated by the proportion of total foragers (15). Species are ordered by increasing tongue length [in (A), species' names follow (18)]. Bimodality of the den-

sity functions (15) indicates that bumble bee communities contain two predominant phenotypes, short-tongued and long-tongued [(C) and (D)]. (E) and (F) show the tube depth density functions for flowers visited by, respectively, *B. balteatus* and *B. sylvicola* in the Front Range [Mount Evans and Niwot Ridge (15)]. For tongue length [(C) and (D)] and tube depth [(E) and (F)], representative density functions for simulated communities (15) are shown.

Fig. 3. Change in flower abundance at landscape and local scales along a 400-m altitudinal gradient on Pennsylvania Mountain. (A) Map showing areas where PFD decreased (1.95 km²), is stable (1.29 km²), and increased (0.10 km²). Unshaded (excluded) areas contain cliff, talus, mining disturbance, and subalpine forest. (B) PFD (mean \pm SE) for plots in krummholz (KRUM); tundra slopes (SLOPE); wet meadow (SWALE); false summit (FSUMMIT); and summit (SUMMIT) habitats ($N = 6$ species; $F_{4,385} = 5.55$, $P = 0.0002$). Asterisks indicate significant differences at $P < 0.05$. (C) Total flower production (in millions) is the product of total surface area for (A) each habitat (table S5) (15) and (B) mean PFD.

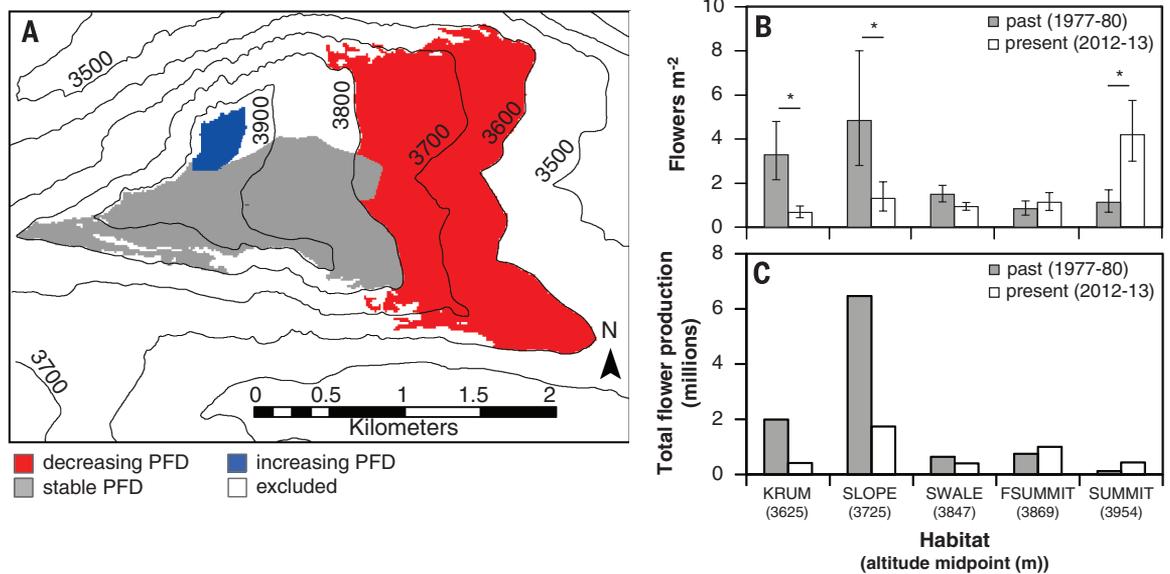
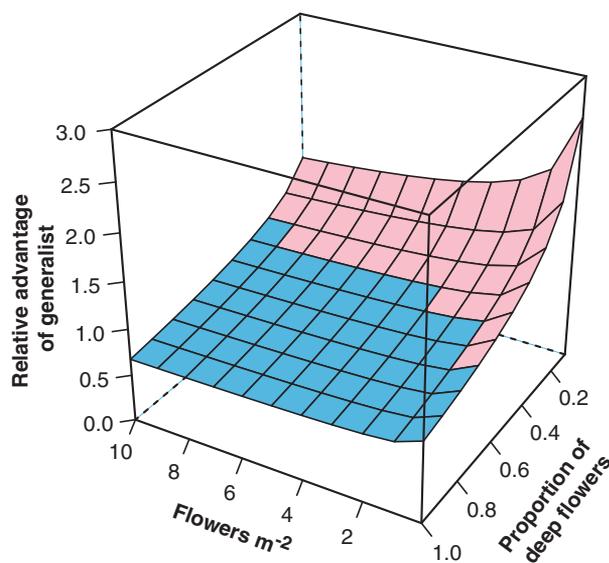


Fig. 4. Relative advantage of generalizing as a function of flower density and the proportion of deep flowers in the community. Outcomes with flight speed of 0.5 m s⁻¹ are shown (15). The generalist is favored when its relative advantage is >1 (pink shading).



for *B. sylvicola* ($Z = 19.78$, $P < 0.0001$). Bumble bees have added flowers with shorter and more variable tube depth to their diet (*B. balteatus*: $F_{1,1997} = 7554$, $P < 0.0001$; *B. sylvicola*: $F_{1,1997} = 64,851$, $P < 0.0001$) (Fig. 2, E and F, and table S3).

In response to warmer temperatures and drying soils, flowering has declined in alpine and arctic habitats worldwide (21–24). Optimal foraging theory predicts that foragers will expand their niche in response to such resource scarcity (25, 26). When bumble bees (*B. balteatus*) encounter low densities of preferred host plants, they incorporate shallower flowers into their diet ($F_{1,194} = 29.39$, $P < 0.0001$) (table S4) (15). The expansion of foraging breadth over time in Front Range bumble bees is congruent with this behavior (Fig. 2, E and F, and table S3). Climate

records from Niwot Ridge show warming summer minimum temperatures over the past 56 years (27). We see similar changes on Mount Evans ($R^2 = 0.383$, $t_{1,52} = 5.68$, $P < 0.0001$) and Pennsylvania Mountain ($R^2 = 0.341$, $t_{1,52} = 5.20$, $P < 0.0001$) (fig. S3, A and B), where summer minimums have increased $\sim 2^\circ\text{C}$ since 1960. We used a nonlinear model to characterize the relationship between peak flower density (PFD; flowers per square meter) and summer minimum temperature. For four bumble bee host species monitored in 6 years between 1977 and 2014 (15), average PFD on Pennsylvania Mountain rose as minimum summer temperature increased from 1.8°C to 3.25°C but declined above this value (quadratic $R^2 = 0.19$, $t_{1,17} = -2.18$, $P = 0.040$) (fig. S3C) (15). Temperatures that are associated with reduced flowering (greater than

3.25°C) have become more frequent, occurring on Pennsylvania Mountain in only 12% of years from 1960 to 1985 but 48% of years since 1985 ($\chi^2 = 8.19$, $df = 1$, $P < 0.0041$) (fig. S3B).

On Pennsylvania Mountain, alpine bumble bees forage over hundreds of meters to provision their nests (28). To ask how warming has affected floral resources at this scale, we measured PFD of six bumble bee host plants from 1977–1980 and 2012–2014 in five habitats along a 400-m altitudinal span (table S5). Land surface area decreases with altitude above tree line in the Rocky Mountains (29), declining by more than an order of magnitude on Pennsylvania Mountain, where 58% of habitable terrain is found below 3800 m and only 4% above 3938 m on the summit (Fig. 3A and table S5). Because bumble bees forage across the 400-m altitudinal range (28), we evaluated the temporal change in flower production at this landscape scale. For each habitat, we multiplied PFD (flowers per square meter) within sampling plots by surface area (square meters) to estimate of total flower production (15). PFD fell by 73 to 80% within krummholz and slope habitats below 3800 m, which occupy 1.95 km². Conversely, PFD increased by 75% in 0.10 km² of summit habitat ($F_{4,385} = 5.55$, $P = 0.0002$) (fig. 3B and table S6). Because declines in flowering occurred at low altitude, they affected the majority of the mountain landscape; in these extensive habitats, millions of flowers were lost. Thus, even with gains of a few thousand flowers on the summit, total food resources for alpine bumble bees on Pennsylvania Mountain have fallen by 60% since the 1970s (Fig. 3C).

Alpine regions are considered “canaries in the coal mine” for their sensitivity to global warming (29). Using a simple model adapted from (26), we tested whether reduced flowering in other ecosystems could drive the evolution of pollinator

foraging traits as indicated for alpine bumble bees (15). The model predicts changes in the energetic advantage of generalization with floral density. Long-tongued bumble bees exhibit greater specialization than that of short-tongued bees (16, 30). Across a range of flight speed and plant community composition (15), the advantage of generalizing increases as flower density declines (Fig. 4). Theoretical and empirical studies alike suggest that with lower floral resources, fitness advantages of long-tongued specialist phenotypes have diminished, potentially driving the rapid evolution of shorter-tongued bees. We have documented decreases in bumble bee tongue length within species and communities on three peaks in the Rocky Mountains. Our analyses suggest that reduced flower density at the landscape scale is driving this shift in tongue length. Although populations of long-tongued bees are undergoing widespread decline (1, 3), shifts foraging strategies may allow alpine bumble bees to cope with environmental change. We see broader bumble bee foraging niches, immigration by short-tongued bumble bees, and shorter tongue length within resident bee populations as floral resources have dwindled. In remote mountain habitats—largely isolated from habitat destruction, toxins, and pathogens (31)—evolution is helping wild bees keep pace with climate change.

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SUPPLEMENTARY MATERIALS

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MITOCHONDRIAL IMPORT

Molecular architecture of the active mitochondrial protein gate

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Mitochondria fulfill central functions in cellular energetics, metabolism, and signaling. The outer membrane translocator complex (the TOM complex) imports most mitochondrial proteins, but its architecture is unknown. Using a cross-linking approach, we mapped the active translocator down to single amino acid residues, revealing different transport paths for preproteins through the Tom40 channel. An N-terminal segment of Tom40 passes from the cytosol through the channel to recruit chaperones from the intermembrane space that guide the transfer of hydrophobic preproteins. The translocator contains three Tom40 β -barrel channels sandwiched between a central α -helical Tom22 receptor cluster and external regulatory Tom proteins. The preprotein-translocating trimeric complex exchanges with a dimeric isoform to assemble new TOM complexes. Dynamic coupling of α -helical receptors, β -barrel channels, and chaperones generates a versatile machinery that transports about 1000 different proteins.

Mitochondria are pivotal for cellular adenosine triphosphate (ATP) production, numerous metabolic pathways and regulatory processes, and programmed cell death. Most mitochondrial proteins are synthesized as preproteins in the cytosol and are imported into mitochondria. Preproteins either contain N-terminal targeting sequences (pre-sequences) or internal targeting information in the mature part (*I-3*). The protein translocator of the outer membrane (the TOM complex) functions as the main entry gate of mitochondria (*I-3*). Over 90% of all mitochondrial proteins are imported by the TOM complex, followed by transfer to distinct translocators for individual classes of preproteins. Whereas all structurally known membrane protein complexes consist of either α -helical or β -barrel proteins, the TOM complex is composed of both α -helical and β -barrel integral membrane proteins. The complex consists of the channel-forming β -barrel protein Tom40 and six other subunits, each containing single α -helical transmembrane (TM) segments: the receptor proteins Tom20, Tom22, and Tom70 and the regulatory small Tom proteins (*I-3*). The molecular

architecture of the complex has not been elucidated. How α -helical and β -barrel membrane proteins can be combined into a functional

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Functional mismatch in a bumble bee pollination mutualism under climate change

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Climate change decoupling mutualism

Many coevolved species have precisely matched traits. For example, long-tongued bumblebees are well adapted for obtaining nectar from flowers with long petal tubes. Working at high altitude in Colorado, Miller-Struttman *et al.* found that long-tongued bumblebees have decreased in number significantly over the past 40 years. Short-tongued species, which are able to feed on many types of flowers, are replacing them. This shift seems to be a direct result of warming summers reducing flower availability, making generalist bumblebees more successful than specialists and resulting in the disruption of long-held mutualisms.

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