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Global Trends in Bumble Bee Health

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Abstract

Bumble bees (*Bombus*) are unusually important pollinators, with approximately 260 wild species native to all biogeographic regions except sub-Saharan Africa, Australia, and New Zealand. As they are vitally important in natural ecosystems and to agricultural food production globally, the increase in reports of declining distribution and abundance over the past decade has led to an explosion of interest in bumble bee population decline. We summarize data on the threat status of wild bumble bee species across biogeographic regions, underscoring regions lacking assessment data. Focusing on data-rich studies, we also synthesize recent research on potential causes of population declines. There is evidence that habitat loss, changing climate, pathogen transmission, invasion of nonnative species, and pesticides, operating individually and in combination, negatively impact bumble bee health, and that effects may depend on species and locality. We distinguish between correlational and causal results, underscoring the importance of expanding experimental research beyond the study of two commercially available species to identify causal factors affecting the diversity of wild species.

INTRODUCTION

Changes in abundance and distribution of insects have been reported globally over the past several years (68, 154). In particular, pollinator decline has received wide attention (123, 138). Wild bees are receiving increased attention (89, 185) due to their dominance as pollinators. Of the 87.5% of all wild plants that benefit from insect pollination, 20% depend on bee pollination (123). Among wild bees, bumble bee (*Bombus*) decline has been most studied (**Figure 1**), with multiple surveys in Europe (13, 143), North America (21, 27, 78), and South America (2, 116) revealing reductions in distribution and relative abundance of many species over the course of the century. The number of reports on bumble bee decline has grown exponentially during the past decade (**Figure 1**). We are aware, however, of the taxonomic and geographic biases in the peer-reviewed literature, which limit our knowledge of global bumble bee health.

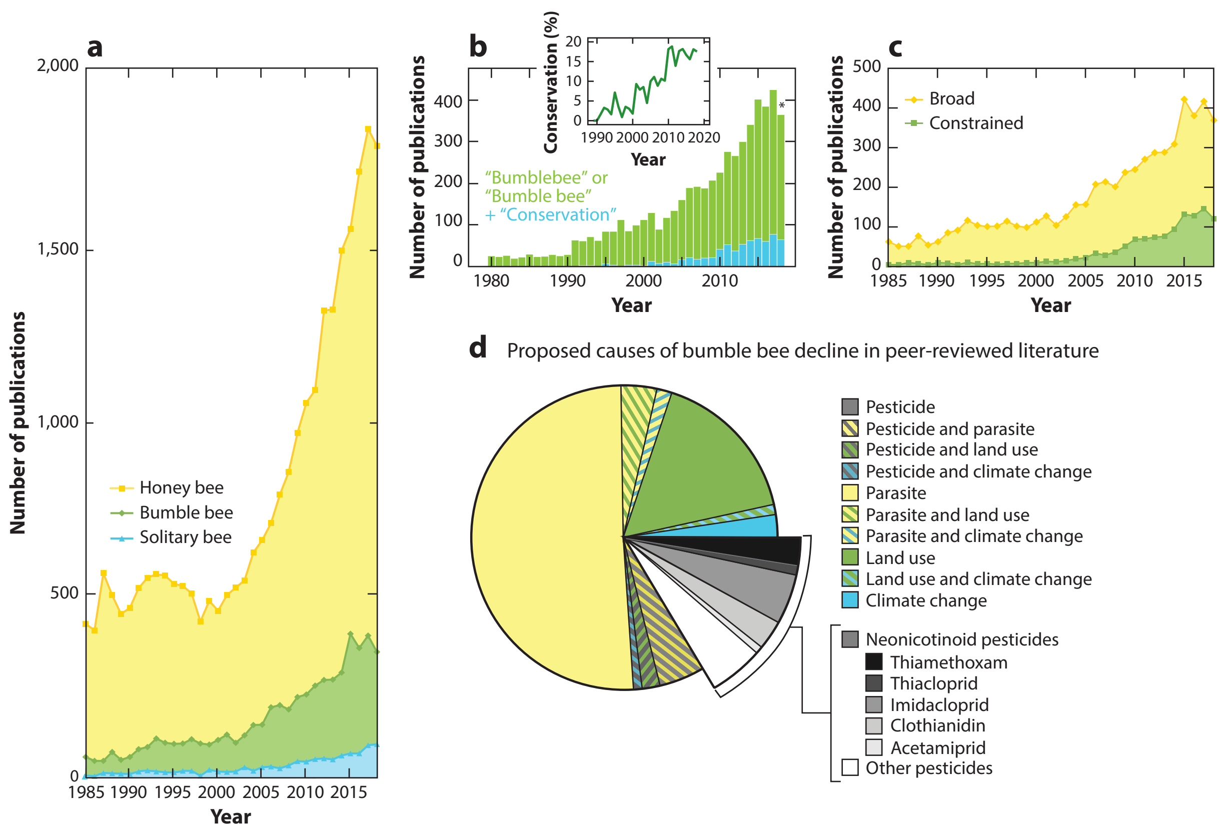

Figure 1

(*a*) The number of peer-reviewed papers published in the period 1985–2018 on the subject of decline or conservation (broad search; see **Supplemental Appendix**) for honey bees (*yellow*), bumble bees (*green*), and solitary bees (*blue*). (*b*) Histogram of all papers published in peer-reviewed journals in the period 1980–2018 on bumble bees (*green*). Blue shading indicates the number of those papers that focused on aspects of bumble bee conservation; the inset indicates the exponentially increasing percentage of papers on bumble bees mentioning conservation. (*c*) Two different search strategies, broad and constrained (see **Supplemental Appendix**). Regardless of the search strategy, the peer-reviewed literature on bumble bee decline or conservation shows an exponential increase from around 2005 to the present. (*d*) Pie chart indicating the proportion of papers published (broad search) on the different causal factors proposed for bumble bee decline; gray shading indicates published studies on pesticides (mostly neonicotinoids) connected to bumble bee decline (see **Supplemental Table 7**).

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Reports of multiple causes for the observed widespread declines of bumble bee populations have mushroomed since early studies in Britain pointed to large-scale losses of floral resources (178) to make way for arable cropland (177). Later studies incorporated climate change into the equation (9, 83, 180); most recently, research on pesticides (61, 148, 162, 163, 188) and, to a lesser degree, pathogens (16, 20, 56, 62) has dominated the literature (**Figure 1**). The recent availability of two well-annotated bumble bee reference genomes (*Bombus terrestris* and *Bombus impatiens*) (152) and a recently published third (*Bombus terricola*) (82), presents new opportunities for understanding direct responses to stressors, such as pesticides, pathogens, poor nutrition, and climate change. How bumble bees are affected by each of these environmental perturbations has implications for the maintenance of wild pollinator diversity and international protection.

Much of the published research linking potential drivers to observed declines has been correlational, indicating a temporal association between changing distribution or abundance with a potential driver. For instance, pathogens were implicated in bumble bee decline in North America (20, 26) when the prevalence of *Nosema bombi* was found to be significantly higher in populations of declining relative to stable species (21); moreover, the peak prevalence of *N. bombi* in declining populations coincided with the onset of published reports of species declines (20). Similarly, the decline of the native *Bombus dahlbomii* in Argentina is temporally linked to the arrival of the invasive European *B. terrestris* (116) (see the sidebar titled Effects of Global Trade on Bumble Bee Decline).

EFFECTS OF GLOBAL TRADE ON BUMBLE BEE DECLINE

Infrastructure development and accompanying commerce have vastly expanded routes for global trade beyond natural oceanic and land barriers, thus creating new opportunities for the inadvertent spread of exotic diseases that can devastate vulnerable native populations (2). This story may have played out dramatically with interregional and continental trade in commercial bumble bees (166), which has afflicted native populations in Japan (75), North America (20), and South America (115, 116), with potential threats in China (119) and Mexico (168). The most alarming case to date is the catastrophic decline of the native Patagonian bumble bee (*B. dahlbomii*) following introductions of the European *B. terrestris* for pollination services (2). Managed *B. terrestris* colonies were released in central Chile in the late 1990s and rapidly spread south and east at the startling rate of 200 km per year (155), crossing over the Andes into Argentina (San Martin de los Andes) by 2006. Within a decade, *B. terrestris* had spread east to the Atlantic and south to the tip of Tierra del Fuego (115). Wherever *B. terrestris* expanded, *B. dahlbomii* populations have disappeared.

B. terrestris appears to have carried with it at least two pathogens, *A. bombi* and *C. bombi*, that spilled over to the native Patagonian bumble bee (99, 155). Although the mechanistic explanation for the disappearance of *B. dahlbomii* throughout most of its original range (pathogens, ecological displacement, or both) remains uncertain, there is no disputing that its decline is directly related to contact with the invasive *B. terrestris*. In lieu of greater scientific understanding of the specific mechanisms of this and other population declines of bumble bees in different parts of the world, trade regulation guidelines must be enforced despite economic considerations. The intercontinental trade and subsequent invasion of commercial *B. terrestris* ranks among the top 15 topics among 100 emerging issues for global conservation and biological diversity (166). The BBSG issued a policy statement (**https://bumblebeespecialistgroup.org/policy/**) concerning the transport of commercial bumble bees (*B. terrestris* and *B. impatiens*), arguing that only local "species and subspecies should be grown for commercial development and employed within their native ranges." Moreover, all commercial bumble bees should be expertly screened for parasites by both commercial producers and independent regulators. The precautionary principle should be the governing factor.

At this juncture, a review of the large, exponentially growing body of work published over the past decade on the deteriorating state of bumble bee health worldwide, and the evidence for potential causes, will provide an informed framework for future research and governmental policy (139). We summarize what we know to be certain about species status around the globe and indicate those regions needing more work and support to complete assessments. We also examine evidence published over the past decade on proposed factors leading to population decline, focusing on habitat alteration, pesticide use, climate change, pathogen transmission, and global spread of invasive species, distinguishing between correlational and causal evidence. We show that bumble bee responses to anthropogenic factors, such as pesticides, are highly variable, likely due to the wide range of experimental conditions imposed on the commercially reared colonies used in most investigations to date. We argue for international guidelines and standards for pesticide use and trade in commercial colonies based on shared collaborative research across geopolitical boundaries. We do not advocate one policy over another but trust that the data that we present will speak for themselves.

GLOBAL HEALTH STATUS

Global Patterns of Bumble Bee Population Decline

There are reports of bumble bee species declines from Europe (173, 183), Asia (75, 190), South America (2), and North America (20, 21, 78). However, declines are not homogeneous nor ubiquitous. For example, in North America, some species appear to have undergone range reduction and decline in abundance gradually over many decades [*Bombus fervidus*, *Bombus pensylvanicus*, and *Bombus vagans* in Ontario (27); *Bombus fraternus*, *B. pensylvanicus*, and *B. vagans* in Illinois (67, 97)]; other species, notably the *Bombus sensu stricto*, appear to have undergone rapid population collapses within the past 20 years (21); and others, such as the *Pyrobombus*, have healthy, stable populations (21, 78). Some species are undergoing natural expansions [United Kingdom, *Bombus hypnorum*, *B. terrestris*, *Bombus lapidarius*, and *Bombus soroeensis* (179); northeastern North America, *B. impatiens*, *Bombus bimaculatus*, and *Bombus ternarius* (78); northwestern North America, *Bombus moderatus* (129)]. Additionally, commercially induced regional and intercontinental expansions have occurred as *B. terrestris* (see the sidebar titled Effects of Global Trade on Bumble Bee Decline) and *B. impatiens* (96, 131) have been used for crop pollination outside of their native ranges. The best source of information on the global status of bumble bee health at this time is the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (**https://www.iucnredlist.org/**), which provides the only objective international standard for assessing and tracking trends in species status at a global level. We summarize the available information and risk status based on these data.

International Union for Conservation of Nature Red Listing Efforts

Since the last major review of global trends in bumble bee health was published a decade ago (183), much progress has been made in evaluating the extinction risk of bumble bee species using the IUCN Red List of Threatened Species criteria and categories (76). The springboard for this effort was an IUCN international workshop held at the St. Louis Zoo in 2010, which led to the formulation of plans to organize the IUCN Species Survival Commission Bumblebee Specialist Group (BBSG) (**https://www.iucn.org/ssc-groups/invertebrates/bumblebee**). The BBSG was officially formed the following year (**https://bumblebeespecialistgroup.org/**), and its first activity report was released in 2012. Yearly reports through 2018 document the progress of the BBSG's Red Listing effort.

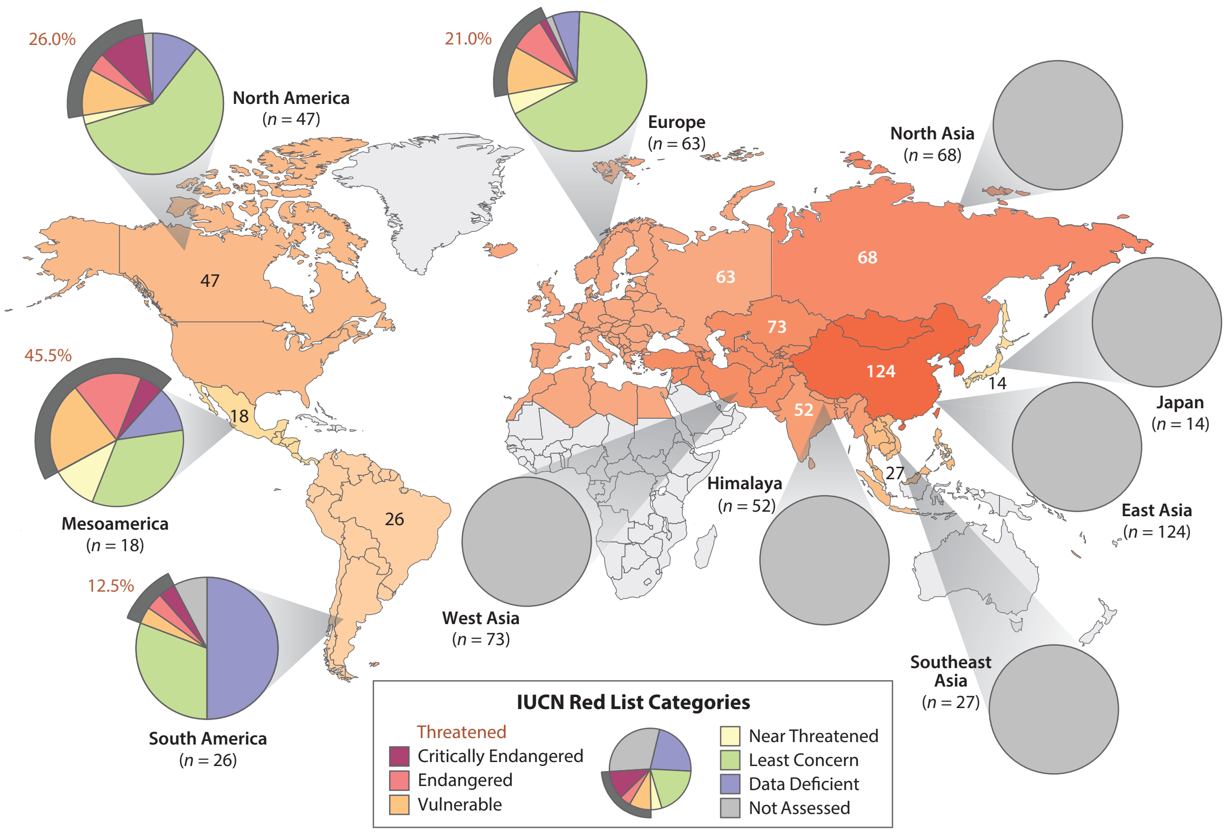

Figure 2

Global map of International Union for Conservation of Nature (IUCN) Bumblebee Specialist Group regions (color-coded in shades of red), each displaying a pie chart indicating proportions of the different Red List threat categories assessed for the bumble bee species of a given region (**Supplemental Table 8**); exclusively grey pie charts represent regions that have not yet submitted IUCN Red List assessments. "Threatened" comprises three categories in the IUCN Red List, Critically Endangered, Endangered, and Vulnerable, which are framed by thick dark gray borders in the pie charts. Percentages refer to the fraction of IUCN-assessed species designated as Threatened (**Supplemental Table 9**); numbers on the map and in parentheses beside region labels indicate the total number of described species (species richness) for that region. To date, 154 species total have been described for Europe, North America, Mesoamerica, and South America, and 150 species have been IUCN assessed, of which 36 (24%) are currently listed as threatened. (See **Supplemental Table 10** for species within each subgenus.) Note that regional species totals are not mutually exclusive, since some species occupy multiple regions.

In brief, the number of Red List–evaluated species increased from one in 2008 (84), prior to the formation of the BBSG, to 150 (approximately 58% of known species) in 2018 (**Figure 2**). To date, 62 of 63 (98.4%) European species recognized before 2017 have been assessed for the region, and there are now over 1 million individual records for European taxa, approximately 918,000 of which are integrated into the *Atlas of the European Bees: Genus Bombus* (144). Global assessments have been made for 46 of the 47 (98%) described North American species (70), and species distributions are relatively well databased (**https://www.leifrichardson.org/bbna.html**) or published (87); there are additional quantitative analyses at regional (27, 67, 78) and national levels (21, 87). All 18 described Mesoamerican species (**https://www.iucnredlist.org/search?permalink=84b3bfba-7f6a-4dc2-8e7c-eed6c835e6b6**) and 24 of 26 (92%) described South American species (**https://www.iucnredlist.org/search?permalink=7255f0a0-72e5-4258-8f06-f250b3226dc3**) have been globally assessed (**Figure 2**), with distributions databased and efforts underway to coordinate future research.

There are no IUCN assessments as yet for the remaining geographic regions (**Figure 2**), but the BBSG's goal is to provide status assessments for all of the approximately 260 species globally. Setting the stage for this effort in North, East, and West Asia, distribution data are available for 90 species in Russia based on museum material and field observations (92); extensive geographic surveys of the large Chinese bumble bee fauna (provisionally 130 species) are ongoing, with distribution records for approximately 50,000 specimens going into a central database (4, 181); and the new Iranian Bees Research Institute contains 4,000 bumble bees from across Iran (182).

Current Risk Status

Nearly one-quarter of bumble bee species on the IUCN Red List are declining. **Figure 2** summarizes current regional and global information for bumble bees based on the relevant IUCN Red List categories (76). According to this information, 26% (12 of 46 evaluated species) of all North American bumble bees are threatened, incurring varying degrees of extinction risk, from vulnerable to critically endangered; approximately 45% (8 of 18 species) are threatened in Mesoamerica; 12.5% (3 of 24 species) are threatened in South America; and approximately 21% (13 of 63 species) are threatened in Europe. Global assessments are available for North America, Mesoamerica, and South America, although half of the South American species are data deficient (**Figure 2**). European species have been assessed only for the European region, and given that there are only nine endemic species, approximately 54 require more extensive global assessments. Given the threatened status of many evaluated species, the absence of risk data from numerous world regions (**Figure 2**) indicates an urgent need for extended international monitoring. As highlighted above, major steps have been made in China to assess its large bumble bee fauna, which is critical given that species richness data (181) suggest that China is a species hotspot, containing approximately half of the world's bumble bee species. The potential threat from non-native *B. terrestris* in China (119) enhances the sense of urgency to complete ongoing assessments. As BBSG experts continue to work together in efforts to database new distributional surveys across regions, sharing expertise where possible, the global data gap will close.

Tangible effects of BBSG efforts are coming to fruition in first-time policy mandates to protect *Bombus* species in North and South America. *Bombus affinis* was placed on the US Fish and Wildlife Service endangered species list in 2017, a first for any bee in the continental United States. *B. dahlbomii* in Patagonia is currently officially listed as Endangered, per its status in the IUCN Red List, and its rapid decline has aroused extensive media and outreach attention (**https://inibioma.conicet.gov.ar/presentacion-del-libro-mangu-un-abejorro-patagonico/**).

Why are some species declining, while others are expanding naturally? There is a phylogenetic association with regional (21) and global (5) declines (although see 173 for analysis of European ranges only). Species in the subgenera *Thoracobombus*, *Cullumanobombus*, and to a lesser extent *Alpinobombus* are especially at risk (5), but in North America the *Bombus sensu stricto* are notably in decline (21). Below, we address potential environmental factors affecting bumble bee health, highlighting some of the ecological hypotheses and what is known about differential susceptibilities of species. We consider the likelihood that multiple decline factors may be acting in concert or in a mosaic fashion across different regions and habitats. The ability to draw firm conclusions about which taxa are declining and to link those declines to causes will be improved when global assessments of all known species are complete.

PROPOSED THREATS TO BUMBLE BEE HEALTH

Land Use Intensification: Habitat Loss, Fragmentation, and Degradation

Landscape features and complexity that are important to bumble bees, including floral cover and composition, will be affected by urbanization (79), agricultural intensification (91), and climate change (discussed below). Spatial and temporal availability of diverse floral cover is considered to be critical to sustain bumble bee communities (184). In three studied species, survival of family lineages from colonies to spring queens the following year has been shown to increase with the proportion of high-quality foraging habitats (22). The floral resources in areas surrounding prairie patches (74) and meadows (71) have been shown to have a positive effect on bumble bee diversity and abundance, and a negative relationship has been demonstrated between species richness and current livestock grazing (71). As expected from these relationships, declines of bumble bee diversity and abundance have been associated with urban development (57), historical agricultural intensification (67, 124), and recent conversion of natural habitat to row crops (89).

The importance of floral resource availability is highlighted by positive outcomes of habitat supplementation or landscape ecology studies within disturbed areas. Late-season mass-flowering crops have been documented to positively affect colony densities (142). Within-season nest survival of *Bombus pascuorum* and *B. lapidarius* is positively associated with the presence of gardens, and the floral resource supplementation that they provide, in otherwise impoverished agricultural landscape (59). Supplementary agricultural stewardship practices that increase floral resources have also been associated with higher nest densities in two of four European *Bombus* species studied (189) and have a greater effect as overall landscape quality declines (23). Similar positive contributions of habitat supplementation have been reported for urban areas (12).

Effects of habitat loss and fragmentation on nutrition. In landscapes with a scarcity of high-quality floral resources, individuals and colonies will suffer from increased energetic costs of foraging and nutritional deprivation. Beyond simply presence or absence of appropriate forage plants, the quantity, quality, and temporal availability of nutritional resources may be affected. Energy for colony maintenance tasks comes principally from nectar, whereas pollen provides micronutrients, lipids, and protein essential for development and reproduction (172). Although it is not considered critical for adult workers to consume pollen, it can enhance adult immune responses (18). Protein, lipid, essential amino acid, and sterol contents differ between pollen sources (112, 171), and single-source diets differentially affect aspects of larval development. Diversity of pollen per se may, however, be less important than individual identity, with a key role for sterols being identified (112). Nonetheless, diverse floral resources allow for diet optimization (171). Maize-dominated habitats, for instance, are depauperate in floral diversity, and maize cover in agricultural landscapes is negatively associated with the diversity of pollen collected by *B. terrestris* foragers, with collected pollen diversity positively related to colony weight, a surrogate for colony growth (69).

Effects of habitat loss and fragmentation on nest-site availability. Habitat degradation can affect nest-site availability, in addition to foraging resources. Quantification of nest density (121) and potential nest-site availability (107) can be laborious, and estimates are difficult to validate. As a result, there is less consensus on the effects of nest-site limitation on bumble bee abundances. However, preferred nesting habitat and favored landscape elements positively influence *B. pascuorum* nest numbers (59) and the presence of the rare *B. muscorum* (38). Within urban parks in San Francisco, estimated nest-site availability positively explained bumble bee abundance across two years, while floral resource availability was associated in only one of the two years (107). Moreover, the effect on species richness of a purported dominant nest-site competitor, *Bombus vosnesenskii*, was greater on *Bombus sitkensis* than on *Bombus melanopygus* as a result of greater niche overlap in nest sites with *B. sitkensis* (107). Nest-site limitation has also been suggested to be an important factor in determining effects of the invasive *B. terrestris* in Japan, with a greater negative effect seen on *Bombus hypocrita sapporoensis* than on *Bombus pseudobaicalensis* (75).

Habitat alteration and species-specific effects. Vulnerability to habitat alteration may be dependent on inherent factors relating to colony and species traits. The declines or local extirpation of bumble bees in the US state of Illinois coincide with large-scale agricultural intensification, but declines are not uniform or even evident across all species (67). One intriguing hypothesis for species-specific declines is the food preference hypothesis, positing that declining species have a narrow dietary niche, using fewer plant species for pollen than do stable species. Species with broader diets are buffered against habitat degradation or are more likely to switch pollen sources. In line with the predictions of this hypothesis, studies using museum specimens to determine historical dietary breadth in both Europe (85) and North America (187) have found a relationship between less diverse pollen usage and decline (but see 28). Other studies on habitat alteration–related declines implicate different traits. In Sweden, for instance, detrimental effects of urbanization were driven largely by changes in small, long-tongued species (1). Moreover, bumble bee foragers show a preference for landscape patches with high floral cover, and when overall resources are low, they may exhibit increased foraging effort and travel significantly farther to these patches (137, 146). Thus, in addition to colony and morphological traits, longer foraging flight distances, such as those of *B. terrestris*, may buffer against depauperate habitat in the near vicinity (125).

Climate Change

Bumble bees are generally considered to be cold adapted, and contemporary climate change, particularly patterns of warming, may be affecting the population viability and distributions of certain species. Current predictions of warming trends and heatwaves imperiling bumble bees stem from both direct effects on bees and indirect effects through changing floral resources (122).

Shifts in bumble bee distributions consistent with those expected from ongoing climate change are well documented. Uphill elevational shifts have been demonstrated for several species, with a frequent conclusion that upward shifts at lower elevations are not mirrored by comparable upward shifts at higher elevations, resulting in overall range contractions (11, 83, 136). For example, the low elevational limit of *Bombus alpinus* has shifted upward by 479 m since 1984, while its upper limit has not changed (11). Poleward shifts in latitude have also been demonstrated (83). This includes not only cases of range contractions, as upper latitude limit changes lag behind poleward shifts in lower latitude limits (105), but also cases of range expansion of species historically restricted to lower latitudes (83, 104). In the northeastern United States, species with lower northern latitude range boundaries have seen increases in abundance, despite a general trend of decline across the genus over the past century (8). Models based on future climate change scenarios predict further dramatic shifts in species ranges (140), with major range reductions in high elevation specialists. For example, in Switzerland, several alpine bumble bee species are predicted to undergo range contractions of over 50% by 2085 under conservative climate stabilization scenarios and contractions of over 80% by 2085 under more extreme climate warming scenarios (140).

As suggested above, vulnerability to warming is likely species dependent. Some species do not exhibit expected range shifts, even when others around them do (136). Species also differ in their thermal limits (103), with interspecies differences reflective of native range thermal extremes (130). In the United Kingdom, declining species have narrower climate niches and persist in areas that climatically match more closely their predecline niches (180); climate niche breadth appears to be informative for predicting species responses to climate change more broadly (73).

Direct and indirect effects of climate change. Direct effects of warming, in particular, extreme climatic events, such as heatwaves, could negatively influence bumble bees (145). In a 10-year survey in the Eastern Pyrenees, the lowest abundances of many species were associated with hot and dry conditions in the preceding August (145). Although thermal limits have been characterized (103, 130), rarely will upper limits be surpassed, even under extremes. Instead, detrimental sublethal direct effects below these limits merit further investigation.

The diversity, flowering time, and distributions of native plants, along with the spread of invasive plant species, are affected by climate change (48, 80, 159), leading to a cascading influence on organisms utilizing these plants, including foraging bumble bees. An analysis of phenology of bee pollinators and plants demonstrated parallel phenological advances in both groups (9), but the bumble bee species used in this analysis (*B. bimaculatus* and *B. impatiens*) have not experienced recent range contractions or reductions in relative abundances (21, 25). In other cases, however, spatial and temporal mismatches between floral resources and bumble bees could provide an important indirect link between climate change and declines. In the Rocky Mountains, climate change is driving a mid-season paucity of critical floral resources (3) and a decrease in synchrony of plants and bumble bees (141). Furthermore, the abundances of three subalpine *Bombus* species tracked over eight years were driven by indirect effects of climate on the temporal distribution of their floral resources, more than by any direct effects studied (122). In particular, it is theorized that reductions in floral abundance in plant communities will be more detrimental to specialist foragers compared to generalists, which potentially explains why shorter-tongued replaced longer-tongued bumble bee species over 40 years of warming summers that reduce available flowers (111).

Population isolation: a consequence of habitat fragmentation and climate change. Climate change and habitat fragmentation can lead to contraction of species ranges, reductions in abundances, and restricted gene flow. For example, gene flow in *B. vosnesenskii* was limited across impervious urban habitat and agricultural land (79). Smaller and isolated populations will be subject to inbreeding, reduced genetic diversity, and a greater risk of extinction. With climate change, we are seeing predicted uphill movement of some bumble bee species (11, 83, 136), further isolating populations within disconnected higher elevation patches, especially in lower latitudes where alpine habitats are higher. For example, contrasting *B. vosnesenskii*, highly connected throughout its low-elevation range, and *Bombus bifarius*, restricted to high-elevation habitats in its southern distribution, demonstrated that reduced genetic diversity and gene flow can be an outcome of increased isolation (77). Significant genetic structuring and reduced diversity have also been shown for declining *B. muscorum* (35) and *Bombus sylvarum* (43) relative to related stable species. Dispersal abilities may further influence relative susceptibility to population isolation (36). Low genetic diversity and inbreeding detected in declining species such as *Bombus veteranus* (98) and *B. terricola* (82), and small effective population sizes for others, such as *Bombus distinguendus* (24), while likely the result of declines and population isolation, may also limit the ability of species to react further to drivers of decline.

Pathogens

Shared flower use facilitates pathogen transmission among bumble bee colonies (63); among bumble bee species (147); and to bumble bees from other pollinators, including managed honey bees (86). This may aid the processes of spillover and spillback, which could enhance the threat of pathogens to native bumble bees (e.g., see 62). Spillover, in which a pathogen prevalent in one host type is transmitted to another, has been proposed to have occurred from commercial and invasive bumble bees and honey bees to wild species (20, 26, 155). The presence of these other species could also result in spillback, a relatively less appreciated process (81) in which a pathogen is transmitted from its native host to another, whereupon its prevalence or abundance is dramatically amplified before transmission back to the original host. The list of pathogens found in bumble bees has grown dramatically in recent decades (52, 132, 135, 158). Although by their very nature pathogens undeniably curtail bumble bee health, causal roles in declines remain unresolved. We focus on a subset of described pathogens that have been particularly well-studied or implicated in bumble bee declines.

***Crithidia*.** A gut trypanosome of bumble bees, *Crithidia bombi*, is widespread but its prevalence varies considerably by location (30, 52). It has been used as a model system in host–pathogen evolutionary ecology (151). Effects of infection include impaired foraging ability (53, 126), worker longevity (17), queen hibernation (45), and colony foundation (15). Several studies indicate that infection and virulence are context dependent, for instance, varying with diet (15, 17, 95). When investigated, *C. bombi* has not been associated with declining species (30). However, its widespread study and ease of detection provide evidence for processes that could also be occurring with other pathogens. Infections have been documented in commercial bumble bee colonies (66), and evidence for spillover (26, 118) and, potentially, spillback (175) exists at sites of commercial colony use. *C. bombi* has been found at high prevalence in Chile and Argentina, with genetic evidence suggesting a historical spread of the pathogen with invasive *B. terrestris* (155; see the sidebar titled Effects of Global Trade on Bumble Bee Decline).

***Nosema*.** Several microsporidian pathogens have been purported or demonstrated to infect *Bombus* species (for a thorough review, see 16). Of those definitively shown to infect bumble bees, *N. bombi* and *Nosema ceranae* have received the most recent attention, in particular, because they appear to fit the designation of emerging or reemerging infectious diseases (117). *N. ceranae*, first described in the Asian honey bee *Apis cerana* and considered to be an emerging pathogen of the European honey bee *Apis mellifera* (50), has also been detected in many bumble bee communities worldwide (51, 52, 65, 94) and in commercial *Bombus* colonies (66). Importantly, it has been experimentally shown to infect bumble bees (51) and may display higher virulence in bumble bees relative to honey bees (65). A link between *N. ceranae* prevalence in *A. mellifera* and its prevalence in some *Bombus* species in the United Kingdom indicates potential spillover driving its development as an emerging bee disease (51).

N. bombi, also widespread in its occurrence in bumble bee communities (20, 21, 88, 94), has documented fitness effects and species-specific patterns of infection that have led to suggestions that it is a potential driver of recent bumble bee declines in North America. In the European *B. terrestris*, infections reduce queen colony founding success (170), male and worker longevity in the lab (127), and colony size in the field (128). Moreover, infections early in the colony cycle lead to males and new queens with effective functional fitnesses of zero in the laboratory (127) and an absence of sexual production in the field (128).

As with *Crithidia*, there is evidence of spillover from commercial bumble bees (26, 118). Notably, commercial rearing of a now declining North American species, *Bombus occidentalis*, was abandoned in the mid-1990s due to catastrophically high levels of *N. bombi* infection at a rearing facility (49). Moreover, additional declining North American species have a relatively higher *N. bombi* prevalence (21, 30), with a retrospective study using museum specimens showing increasing prevalences in these species during the mid-1990s (20), coinciding with the infection problems at commercial facilities. No support was found for the hypothesis that a novel *N. bombi* strain from Europe was introduced during the establishment of commercial rearing in North America; the strain that was present in North America prior to the establishment of the commercial trade appears genetically identical to the European strain (20). Yet the timing of the increase in *N. bombi* prevalence and its nonrandom infection pattern with respect to stable and declining species make this pathogen a prime suspect in declines. In light of a contradictory pattern in Alaskan *B. occidentalis*, which exhibits high *N. bombi* prevalence but no evidence of decline (88), further research on species-specific susceptibility and associated fitness consequences is required to conclusively link *N. bombi* to declines in the continental United States.

Apicystis. Similar to *N. bombi*, due to its temporal patterns of infection and high virulence, the neogregarine *Apicystis bombi* has been touted as a causative agent of *Bombus* decline, particularly in South America (2). High *A. bombi* prevalences have been detected in commercial colonies of *B. impatiens* in Mexico (150) and *B. terrestris* in the United Kingdom (66), and infections can be transmitted to other bumble bees and honey bees (66). There is suggestive evidence of *A. bombi* spillover to natural bumble bee communities in close proximity to greenhouses employing commercial colonies (64). There are limited experimental evaluations of virulence, but dramatically reduced survival of *Apicystis*-infected *Bombus pratorum* queens collected posthibernation, relative to uninfected individuals (149), suggests that virulence can be high. *A. bombi* appears to have hitchhiked on the invasion of *B. terrestris* into South America (2). The native *B. dahlbomii* and an earlier invasive species, *Bombus ruderatus*, were found to be free of *A. bombi* infection prior to the invasion of *B. terrestris*, but postinvasion, all three species showed infections, suggesting sequential invasion and spillover (116). Evidence that Argentinian and European *Apicystis* isolates may be closest relatives (99) offers further support for invasion and spillover, although this evidence alone does not reveal directionality of movement. Yet the presence of the European haplotype of *A. bombi* in *Bombus atratus* in Colombia (52), far from the range front of invasive *B. terrestris*, either suggests another original source or highlights an alarming epidemiological spread of this pathogen.

Viruses. Several previously considered obligate honey bee viruses have been identified in bumble bees. The presence and infectivity to bumble bees has been known for some species for at least half a century (6), but recent molecular analyses have demonstrated the widespread occurrence of these prevalent honey bee pathogens in commercial (66, 150) and wild bumble bees (51, 52, 108). In several cases, active replication has been confirmed, and experimental exposures have led to established infections (51, 64, 133), with negative effects reported for worker survival (51, 64) and experimental microcolony productivity (109). Context-dependent virulence has been shown for *Slow Bee Paralysis Virus*, typically considered avirulent (120), with decreased survival under nutritional stress (102). It is assumed that the majority of the detected shared bee viruses have spilled over from honey bees, but directionality often cannot be determined conclusively (51, 108). A phylogeographic analysis of *Deformed Wing Virus* partially supports this hypothesis, suggesting that a global pandemic has spread from the European honey bee *A. mellifera*, including to bumble bees (176). Although the severity of the threat of multihost viruses is evident, their role in declines requires further study. Prevalence data for *Acute Bee Paralysis Virus* is indicative of species variation in susceptibility (108), but this has not been tested directly with respect to decline status. Additionally, novel bumble bee viruses represent a largely unexplored field (132).

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Pesticides

The forfeiture of natural habitat to intensive agricultural production not only results in the loss of native floral and nesting resources for wild bumble bees (22, 184), but also generates a recurrent need for the application of pesticides to control pests. Bumble bees can be exposed to a cocktail of insecticides and fungicides (153), some of which have been shown to affect bumble bees and other wild bees directly (148) (reviewed in 58, 139, 169). In this section, we concentrate on neonicotinoid insecticides, such as imidacloprid and thiamethoxam and its metabolite, clothianidin, which have received considerable attention and study. This does not preclude the possibility that other agrochemicals could influence bumble bee health, nor should it be presumed that regulation of neonicotinoids alone is sufficient. In fact, sulfoximine-based insecticides, likely successors of neonicotinoids, have been shown recently to have substantial sublethal effects on worker and reproductive production of *B. terrestris* colonies under chronic exposure (162).

Neonicotinoid exposure. In the early 1990s, neonicotinoid insecticides based on the natural toxin nicotine were introduced as an alternative to the more human-toxic carbamate and organophosphate compounds and quickly dominated and expanded the global crop protection market (161, 167). They are applied as foliar treatments to fruit crops such as apples and pears (31, 163) but are most commonly used as a seed coating on crops (41), including oil seed rape (canola), sunflower, maize, and soybean. They are absorbed by the roots or leaves and transported systemically, including to floral nectar and pollen (14). They are toxic to feeding herbivorous insects, but overwhelming evidence indicates that they are also toxic to insects that collect nectar and pollen, mostly bees (139, 169). Today, neonicotinoids are pervasive in all terrestrial and aquatic environments (161), leading to concern over their effects on nontarget pollinators. Ironically, mounting evidence reveals that neonicotinoid seed treatments are often ineffectual in pest management of the target crops and that the economic and environmental costs are not only unsustainable in agricultural and nonagricultural systems, but are also unnecessary relative to the risk from most target pests (167).

Neonicotinoid mode of action. Neonicotinoids bind to nicotinic acetylcholine receptors in the synaptic membrane of insect neurons, resulting in overactivation (depolarization) of nerve cells and ultimate death of the neuron. This class of insecticides acts primarily on the Kenyon cells, dominant within the mushroom body of the bee brain (113). Typical field-level concentrations of approximately 1–10 μg/L (ppb) (58) are not acutely lethal to bees (113, 114), but with longer (chronic) exposure, imidacloprid concentrations of only 2.1 ppb (w/w) fed to *B. terrestris audax* were found to be neuroactive in the brain within 3 days (114). Given the mushroom body's role in olfactory processing, learning, and memory, it is not surprising that recent research has shown significant impairment of cognitive functions (164), foraging efficiency (54, 55), and colony fitness (174) in bumble bees fed field-realistic doses of imidacloprid, clothianidin, or thiamethoxam in pollen or nectar over 1–2 weeks, the typical life span of a forager. Just 24 h of exposure to imidacloprid at 10 ppb in sugar syrup, followed by free foraging in pesticide-free fields for 48 days, led to impaired colony growth and nest condition (114). Notably, bumble bees are not equally sensitive to all neonicotinoids; thiacloprid, for instance, appears to be less toxic to neurons than imidacloprid (101; but see 42 for colony-level effects), and clothianidin is many times more toxic (114). Differential sensitivity is determined by variation in metabolic efficiency by the CYP9Q family of enzymes belonging to the cytochrome P450 defense system linked to insecticide detoxification (101).

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Sublethal effects of neonicotinoids. There is mounting evidence that widespread use of neonicotinoid insecticides is problematic for wild and managed pollinators, including bumble bees, through sublethal effects of exposure to field-realistic doses. Bumble bee foraging activity is negatively influenced by neonicotinoid exposure (54, 55, 157, 163–165), which can in turn negatively influence the pollination services that they provide (163, 165). Additionally, realistic neonicotinoid exposures have shown negative effects on a variety of important colony-level traits and fitness measures, including queen and male production, both in the laboratory and under semifield (45, 46, 55, 90, 157, 174) and field conditions (148, 186). Although these studies demonstrate a general risk to bumble bees of neonicotinoid exposure, they cannot directly link exposure to bumble bee declines. In fact, all cited studies examine European and, to a lesser extent, North American species that are stable or even expanding in range, most commonly commercially reared *B. terrestris* and *B. impatiens*. We currently have no data to determine if declining species show similar responses to neonicotinoid exposure, and as with pathogens, a direct causation is unclear. Differential effects on feeding and ovary development among four assessed European species (7), however, demonstrate the potential for species-specific differences in neonicotinoid exposure outcomes.

Until recently, data from large-scale field experiments on neonicotinoid exposure for bees were unavailable due to the complexity and expense of such experiments. However, several field tests have been completed across diverse European countries, all of which show effects on bumble bees at some level. Rundlöf et al. (148) reported differential responses by diverse bee taxa to foraging on oilseed rape crops planted with clothianidin-coated seed versus uncoated (control) seed in matched landscapes. They found significantly reduced density of wild bees, including bumble bees, in and around the margins of clothianidin-treated fields. Bumble bee (commercial *B. terrestris*) colonies in treated fields showed reduced colony growth and queen and male production (compared to control fields). No measurable differences in honey bee colony strength were observed, suggesting that honey bees are more resilient to the effects of neonicotinoid exposure relative to bumble bees. This conclusion is supported by laboratory studies (32) in which honey bees exposed to the same concentrations of imidacloprid (98–125 ppb) as bumble bees maintained 12 times less of the compound in the body than did bumble bees as a result of continuous metabolic degradation; the comparative daily clearance was approximately 100% in honey bees versus approximately 80% in bumble bees. Imidacloprid at this concentration also significantly reduced the locomotory activity and feeding rates of bumble bees but not honey bees.

Few studies have directly connected the effects of neonicotinoid exposure on bumble bee foraging and the consequences for the ecosystem services they provide. Stanley et al. (163) show that neonicotinoid exposure at field-realistic levels can affect bumble bee foraging on apple crops, which feeds back on the pollination services that the bees provide for crop production. By altering the relative attractiveness of flower species to bumble bees, realistic neonicotinoid exposures may also affect natural ecosystem services and wild plant pollination (164).

Government regulation of neonicotinoids. In 2018, after an extensive review and risk assessment of outdoor use by the European Food Safety Authority (19, 44), the European Commission updated previous (2013) risk assessments of the neonicotinoids imidacloprid, thiamethoxam, and clothianidin, restricting their use to permanent greenhouses and banning all outdoor use (Commission Implementing Regulation No. 7832018). For the first time, wild bees (*Bombus* and *Osmia*) were included in the evidence leading to the ban; the earlier European Union neonicotinoid controls were based entirely on honey bee toxicity. There is continued concern, however, that pesticide risk assessments in general are based mostly on honey bee toxicity and related impacts on behavior and do not cover exposure risks to bumble bees and solitary bees. Neonicotinoid residues contaminate the soil where treated crops are planted (40), so the effects on ground nesting bees and overwintering bumble bee queens are of particular concern because of the risk of pesticide exposure through soil contact (61). Canada has also recently imposed major restrictions on the use of imidacloprid, thiamethoxam, and clothianidin to reduce pollinator exposure, incorporating evidence from research on solitary bees and bumble bees (72). The United States recently banned the use of some products containing clothianidin and thiamethoxam (47) due to concern over honey bee exposures. Regulatory decisions integrating multispecies evidence need to become commonplace, but even among bumble bees, it is important to understand species-specific effects and expand this understanding beyond traditionally studied and commercially available species.

Effects of Multiple Environmental Stressors on Bumble Bee Health

Despite the individual treatment of environmental stressors above, bumble bee population declines are more realistically multifactorial (60). Bumble bees, along with other pollinators, do not face threats in isolation, but we still lack sufficient information to identify the interactive effects of chronic stressors on their declines.

Studies that empirically investigate two-factor combinatorial effects on bee health have increased, but the vast majority of these focus on honey bees (e.g., see the studies cited in Reference 60). For bumble bees, such studies are still in their infancy and currently show extreme taxonomic bias toward the laboratory model and commercially available *B. impatiens* and *B. terrestris*. The limited studies performed offer mixed support for the multiple stressor hypothesis, which predicts that detrimental effects of individual factors will be compounded when experienced in combination.

Variation in nutrition, resulting from altered floral landscapes, is a plausible partner in several interactions, yet few studies have directly investigated links between nutrition and other stressors. Low-quality diet was found to act additively with neonicotinoid exposure in reducing fitness of *B. terrestris* microcolonies (34), but such an effect was not found in a study of *B. impatiens* (93). Nutrition may also influence parasite and pathogen infection. A model of the effects of parasitic conopid flies on bumble bee colony productivity demonstrated the negative effects exacerbated under low-resource conditions (100). While nutritional deprivation may directly limit immunity (18; but see 156), its influence on actual individual infection outcomes appears complex (29, 95). We currently do not know how these effects will scale up to colony and landscape levels, nor do we have a good understanding of how variation in infection as a result of other factors corresponds to colony fitness.

Habitat fragmentation and its effects on nutrition and landscape heterogeneity may have effects on both within- and between-host infection processes (110). For example, fragmentation of optimal floral landscapes leads to a heterogeneous density distribution of foragers of multiple species, similar to the effect of supplementing otherwise poor-quality habitat with wildflower patches to attract an abundant multispecies pollinator assemblage (134). If the foraging density of potential hosts with shared pathogens increases at specific locations, then these locations might become transmission hotspots, leading to elevated pathogen loads (134).

For pesticides, with multiple classes applied and encountered by bumble bees (153), there is great potential for enhanced pesticide interactions. Indeed, synergistic mortality occurs in *B. terrestris* when the neonicotinoid clothianidin combines with an ergosterol biosynthesis-inhibiting fungicide (160). Further assessment of realistic exposures is, however, required. Attention has also been given to potential interactions between neonicotinoids and bee pathogens (60). A large body of evidence in honey bees has linked neonicotinoid exposure to reduced immunity and resistance to infection (e.g., 37, 39). Similar studies in bumble bees are limited but indicate that immunity can be compromised following exposure to imidacloprid (33). Effects on live infections are less apparent; neonicotinoid exposure influenced a number of colony traits in *B. terrestris*, but a detrimental interaction with simultaneous exposure to *C. bombi* was found only for parental queen survival (46), and no interaction with *Crithidia* exposure affected egg laying in neonicotinoid-exposed queens (7). In hibernating *B. terrestris*, infection with *Crithidia* reduced survival, but there was a less than additive interaction with coexposure to neonicotinoids (45). It is important to note that *C. bombi* has relatively low, albeit context-dependent, virulence under several conditions (151), and it has never been associated with declining species (30). We lack studies of the multiple stressor hypothesis that examine pathogens linked to declines, such as *N. bombi* (21). A recent landscape-level analysis, however, found a relationship between the extent of use of the fungicide chlorothalonil and *N. bombi* prevalence in declining North American bumble bee species (106), a pattern that deserves further attention.

Ultimately, identifying causal links between proposed interacting factors and bumble bee population declines requires a holistic empirical approach of well-crafted laboratory, semifield, and field studies. Within these studies, it is important to consider that a statistical interaction is not a requirement for combined stressors to have a greater detrimental effect than single stressors at either the individual or population level (e.g., 45). Current studies are also limited by extrapolating broadly from *B. terrestris* and *B. impatiens*, both nondeclining species. More complex multifactorial designs that investigate interspecies differences are constrained by logistics, but they must be carried out to explore how diverse stressors interact in complex ways to reduce individual and colony-level fitness. Alternative approaches, including systems modeling (10) and landscape analysis (106), can offer additional insights and have the potential to provide focused hypotheses of stressor interactions that can be tested in the field.

CONCLUSIONS

The value of maintaining high levels of wild biodiversity (species richness) for healthy ecosystem functioning, including bumble bees for pollination services (185), is irrefutable. It is also irrefutable that human activity through the modification of habitat, overuse of pesticides, interregional and continental trade of species, and burning of fossil fuels is damaging ecosystems and reducing bumble bee biodiversity. There is, however, a desperate need for more published field data on the long-term and interactive effects of these destructive perturbations; short-term studies miss the dynamics of population fluctuations, and lab study results, while critical for examining the potential impacts of a given stressor, must be tested under realistic field conditions. These are difficult and complex studies to carry out, but they are urgently needed. Research funding agencies have a critical role in filling the knowledge gap by supporting and promoting the vital importance of long-term population data collection. Following the lead of the European Union for neonicotinoids, strong regulations based on the precautionary principle for existing and novel agrochemicals and interregional and intercontinental trade in non-native commercial bumble bee species for crop pollination are required. To achieve this goal, connections should be forged between the BBSG and other experts, governments, and commercial pollination and agricultural stakeholders.

Some bumble bee species are clearly declining in some parts of the world, including Europe and the Americas. Yet the species status across much of the remaining world is unknown or unpublished. This dearth of knowledge impedes regional and global conservation policy. We cannot rigorously answer important questions such as why some species are declining, while others have stable, healthy populations and may even be expanding their range. Enhanced international collaboration will accelerate the collection of the missing status data and create published online databases that will be available for detailed ecosystem analyses of changing geographic ranges,

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relative abundance, and phenological shifts. Without dependable support for our natural history collections to allow ongoing comparisons of current and historical distributions and relative abundances, the realization of species decline and ability to determine the risk status will be impossible. Filling in these major knowledge gaps will enable sound policies to protect global bumble bee health and the vital pollination services that they provide to natural and agricultural systems.

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