# Critical links between biodiversity and health in wild bee conservation

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# Critical links between biodiversity and health in wild bee conservation

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**Wild bee populations are declining due to human activities, such as land use change, which strongly affect the composition and diversity of available plants and food sources. The chemical composition of food (i.e., nutrition) in turn determines the health, resilience, and fitness of bees. For pollinators, however, the term 'health' is recent and is subject to debate, as is the interaction between nutrition and wild bee health. We define bee health as a multidimensional concept in a novel integrative framework linking bee biological traits (physiology, stoichiometry, and disease) and environmental factors (floral diversity and nutritional landscapes). Linking information on tolerated nutritional niches and health in different bee species will allow us to better predict their distribution and responses to environmental change, and thus support wild pollinator conservation.**

## Highlights

The diversity, abundance, and health of wild bees is jeopardized primarily by land-use modifications, among other global change drivers.

Defining and measuring health in wild bees requires an integrative approach across disciplines.

We use elements from chemistry, stoichiometry, ecology, physiology, pathology, and genetics to (i) contribute to a more comprehensive definition of wild bee 'health', and (ii) define a framework linking bee health with floral resource/nutritional landscapes through assessing species-specific nutritional niches.

We suggest a novel and holistic approach for capturing bee health through combining field and laboratory tools.

Knowledge gained by applying this framework will serve as a blueprint for stakeholders engaged in pollinator conservation.

## Bees decline because their food sources disappear

Animals pollinate >85% of flowering plants and 75% of the leading crops worldwide [1] which provide food and medicines for other animals and humankind. They also support natural habitats and play a key role in plant productivity, food webs, and ultimately in human well-being [1–3]. Bees (Apidae) are the most important group of pollinators, and the vast majority are represented by wild species (~20 000 species) [4].

Alarmingly, many wild bee populations are declining due to the impact of different biotic and abiotic stressors caused by human activities that act alone or in combination, such as pesticides, invasive species, pathogens, intensive land-use, and climate change [5–11]. In particular, agricultural intensification appears to negatively impact on wild bee communities [12,13]. In fact, overall biodiversity typically decreases with increasing land-use intensity [14,15], which directly or indirectly leads to loss of floral diversity and nesting sites [10,16], and may alter pathogen prevalence [17–19]. Declining floral diversity in turn decreases the spectrum of flowering plants that are available as food sources, and therefore restricts the nutritional landscape accessible to bees [20–23].

## Nutritional landscapes of bees

As nutritional intake and thus the nutrient composition (henceforth referred to as nutritional quality) of food strongly determine the health, resilience to pathogens, and fitness of animals [24], access to food resources that enable diverse and balanced nutrition is one key driver of population stability [21]. In this context, we consider a nutrient to be any chemical compound (i.e., from chemical elements, phospholipids, and amino acids to 'group components' such as proteins) that are part of the food/nutrition of bees. Bees obtain most nutrients and several potential

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medically active plant secondary metabolites from flowering plants by consuming mostly nectar and pollen [20,25,26]. Nectar primarily provides carbohydrates for maintaining energy and metabolic processes, whereas pollen is the main source of all other macronutrients (i.e., protein and fat) and micronutrients (e.g., vitamins, sterols) that are required for tissue homeostasis, development (e.g., ovary development), and larval growth [27–29]. Ideally, floral communities provide food resources of both sufficient quality and quantity. The quantity of food resources is determined by the abundance of flowers present in the landscape – namely the number of plants/flowers present per species and the overall amount of flowering species [30]. The quality of food resources depends on the composition of different flowering plant species because each plant species provides pollen and/or nectar with a specific nutrient profile [31]. In fact, the nutritional profiles of pollen and nectar vary greatly among different plant species [32–35] and even between plant individuals of the same species growing in different plant communities [36]. Floral communities, which are characterized by a specific composition and diversity of flowering plant species, consequently determine resource availability and diversity, and thus determine the nutritional landscape in which bees are foraging [21]. More details of variation in nutritional quality in pollen and nectar, the effect of different diets on bee performance and fitness, and differences in foraging preferences among bees are given in Vaudo *et al.* [21].

Although much less well understood, the nutritional needs of bee species are also expected to differ substantially between bee species [21]. The sustainability of bee populations thus depends on flowering plant communities that provide sufficient amounts of the different nutrients required because the quality of food, and in particular of pollen, directly determines offspring survival and development, and can therefore influence the entire population [21,37,38].

Surprisingly, the interaction between flowering plant communities, the available nutritional landscape, and the health status of different wild bee species has hitherto received little attention (*cf* [21,34]). This knowledge is, however, crucial for determining how floral communities and respective conservation measures can support wild bee populations. We therefore propose a conceptual framework for how anthropogenic changes in flowering plant communities can affect bee communities by altering the nutritional landscape and thus niches available to support healthy wild bee populations.

## Measuring wild bee health

Although human health is understood as the physical, mental, and social well-being of an individual or population, the health of wildlife has generally been understood as the absence of disease [39]. For pollinator communities, the term 'health' only recently appeared in the literature and its precise definition is still subject to debate [40]. López-Uribe *et al.* suggested a multilevel approach and the use of various parameters to measure bee health at the individual, colony, and population level [40]. The health status of a population should then be a direct consequence of the average health status of individuals, where population size is likely to correlate positively with average individual health.

We propose to apply a multidimensional concept of bee health to wild bees – defined as the status of well-being of each individual as a result of their interaction with the local environment (Figure 1). We suggest that all or several of the following physiological parameters should be recorded and integrated to comprehensively capture individual bee health – the composition and amount of stored nutrients in bee bodies (such as proteins, lipids, glycogen, chemical elements), body size [41], pathogen load, beneficial microbiota [42], immunocompetence [43], and fertility [44].

Physiological parameters were shown to be important for understanding the sensitivity of species to environmental modifications [45] because the physiology of individuals responds before changes in populations become visible [46]. For instance, diet quality correlates with increased

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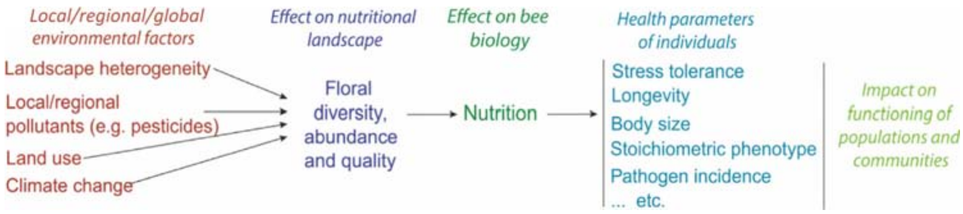


Figure 1. The multifaceted nature of bee health. The main landscape-scale environmental factors, their effects on the floral community and thus on the nutritional landscape and bee diets, and the consequences for bee nutrition and health. These can be observed by recording and integrating different parameters (right column). Bee health based on the physiology of individual bees can then be related to additional parameters, such as population density (i.e., the number of bees caught per plot for a given species and time-period) or variation in population dynamics over time, ideally obtained over multiple seasons to infer changes in population densities across years.

levels of the storage protein and antioxidant vitellogenin in individual honey bees, and this in turn correlates with higher overwintering survival of the entire colony [19,47]. Energy storage is crucial for bee survival. The main categories of macronutrients used for energy storage in insects (glycogen, lipids, and proteins) affect several life-history traits such as dispersal capacity, reproduction, diapause, and survival [48]. Moreover, both macro- and micronutrients are acquired through the consumption of pollen and nectar, and thus are at the interface between bees and floral resources. Variations in floral resource availability will therefore influence the energy budget and ultimately the health of bees.

Additional physiological health parameters *sensu lato* include morphometrics, stoichiometry, microbial communities, and pathogen loads. For example, wing morphometry and fluctuating asymmetry were found to correlate with different stressors [49–51]. In addition, floral composition and diversity are known to shape the bee microbiome composition, particularly in solitary bees, with consequences for nutrient uptake, detoxification, immunity, and health [44,52–54]. By defining stoichiometric phenotypes (i.e., the elemental composition of bee bodies) [55], deviations from optimal phenotypes, as expected in nutritionally impoverished landscapes and for declining populations, can be revealed, which can then also indicate reduced health.

All physiological health parameters mentioned previously are likely affected not only by multiple environmental parameters related to variation in floral resource diversity, abundance, and quality but also by environmental pollutants (e.g., pesticides, antibiotics, heavy metals) and pathogens (Figure 1). Measurement of multiple variables can therefore provide a more complete picture of pollinator health status than focusing on a single parameter.

## Floral diversity as an environmental driver of bee health

Floral diversity, abundance, and community composition correlate with the abundance and diversity of wild bee species [56,57] through food availability [58], nutritional quality or content [21,27,59,60], and resource phenology [23,58,61]. Bees thrive in environments where plant species diversity is high [12,62,63], as is the diversity and quantity of available food resources [23,64,65]. Moreover, resource diversity increases the opportunities for specialist (oligolectic) bee species with restricted pollen host plants to find suitable food resources. In generalist (polylectic) species, access to a diverse spectrum of resources supports immunity, health, performance, and survival (Table 1), presumably through ready access to adequate nutrition and beneficial plant secondary metabolites. By contrast, chronic intake of monotonous, nonsuitable, low quality, or toxic food reduces the immune-competence and vitellogenin levels of bees, thus affecting bee health through 'nutritional stress' [47,66]. Poor nutrition can also lead to higher

Table 1. Effect of floral diet on bee health: key studies on the effects of monofloral and polyfloral diets on the health and performance of different generalist (i.e., polylectic) bee species under both laboratory and field conditions

| Experiment | Bee species | Effects | Response variable | Refs |
|---|---|---|---|---|
| Landscapes, enriched or not with melliferous catch crops; effect on colony overwintering | Honeybee (*Apis mellifera*) | Access to more diverse floral resources was linked to a higher bee vitality (vitellogenin expression level) | Bee physiology (vitellogenin expression level) | [47] |
| Monofloral diet combined with pesticides; effects on colony performance | Buff tailed bumblebee (*Bombus terrestris*) | Additive negative effects of monofloral diet and pesticides on colony growth, drone size, and reproductive effort | Worker mortality, worker weight, colony weight gain, number of males, food uptake | [73] |
| Monofloral versus polyfloral pollen diets | Honeybee (*A. mellifera*) | When parasitized, bees fed with the polyfloral blend lived longer than bees fed with monofloral pollens | Longevity of adults | [74] |
| Diets with varying proportions of *Ranunculus* and *Sinapsis* | European orchard bee (*Osmia cornuta*) | Monofloral diets of *Ranunculus* are detrimental for larval performance | Larval performance | [75] |
| Royal jelly supplemented with mono- or polyfloral pollen diets | Honeybee (*A. mellifera*) | Larval resistance to disease was enhanced on a diet supplemented with either dandelion or polyfloral pollen | Larval resistance to disease | [76] |
| Landscapes differing in floral resource diversity; effect on colony performance and reproduction | Sugarbag bee (*Tetragonula carbonaria*) | Colony performance and reproduction correlated positively with floral diversity in the landscape | Colony performance and reproduction (brood) | [64] |
| Wild plant diversity gradient diet (including oilseed rape treated with a neonicotinoid) | Red mason bee (*Osmia bicornis*) | Resource diversity offset the effects of insecticides (interactive effects) and increased reproduction parameters | Brood cell production, bee reproduction, larval to adult development | [71] |
| Monofloral and mixed diets combined with pesticide in nectar; effect on nesting success | Common eastern bumblebee (*Bombus impatiens*) | Exposure to pesticides reduces survival and activity and brood size; the effect increased on a monofloral diet | Nesting success, queen mortality and activity levels, queen nectar consumption, colony development (brood) | [77] |
| Mixture of pollen in diet; effect on lifespan | Common eastern bumblebee (*B. impatiens*) | Survival of bees fed a pollen mixture with 50% unfavorable pollen (*Helianthus annuus*, Asteraceae) was as good as on a high-quality monofloral diet | Lifespan of bees in captivity | [78] |
| Mono-, di-, and trifloral diets; effect on colony development | Buff-tailed bumblebee (*B. terrestris*) | Colonies developed best on mixed pollen diets or high-quality monofloral pollen diets | Colony development (brood) | [38] |
| High pollen diversity and protein versus low pollen diversity and protein diets combined with pesticide; effect on the development of hypopharyngeal glands | Honeybee (*A. mellifera*) | Size and shape of hypopharyngeal acini was affected by pesticide and diet, whereas protein content in bee head was affected only by pesticide | Physiological development | [79] |
| Landscape gradient of floral resource abundance and diversity | Honeybee (*A. mellifera*) | Decline in pollen availability in summer led to decrease in pollen harvest, colony performance, and overwintering failure | Colony performance (brood, adult population size, honey reserve) and overwintering | [80] |
| Landscape gradient of semi-natural habitats | Buff-tailed bumblebee (*B. terrestris*) | Higher abundance of semi-natural habitats improved reproductive performance | Colony growth and reproductive performance (number of new queens produced) | [35] |
| Food resource limitation and pesticide exposure | Orchard mason bee or blue orchard bee (*Osmia lignaria*) | Pesticides and food limitation had additive effects and reduced reproduction | Survival, nesting, and reproduction | [72] |
| Diets differing in floral composition; effect on resilience to heat stress | Buff-tailed bumblebee (*B. terrestris*) | Colonies were less susceptible to heat stress when fed suitable/high-quality diets | Colony resistance to stress | [81] |

susceptibility to disease [67] and pesticides [68]. In fact, nutritional stress as a consequence of restricted access to adequate floral resources is considered to be one of the main drivers of bee pollinator decline [21,69,70]. Although floral diversity may not provide added value *per se* or automatically yield beneficial synergistic effects compared with higher-quality monofloral diets [34,71,72], it can clearly mitigate the negative effects of poor diets and provide overall more choices to various bee species (Table 1).

However, how floral resource diversity and nutritional quality interact and affect bee health remains largely unclear. This is particularly true for wild bees that are considered to be less resilient to environmental changes and are more difficult to study than managed honeybees [72,82]. For example, how different nutrients or nutrient groups contribute to bee health is poorly understood, as is whether bee species differ in their tolerance to deviations from optimal nutritional profiles and thus to the available nutritional landscapes. Understanding these links will shed light on the mechanisms underlying the observed positive effects of, for example, polyfloral diets on bee performance (Table 1). This knowledge will also enable better strategies for conservation or restoration of biodiversity for pollinators, and thus contribute to combating ongoing bee declines (discussed later). We therefore propose to link floral communities, nutritional landscapes, and bee health and diversity through assessing bee species-specific nutritional niches.

## Nutritional niches of bees

The ecological niche of a species describes the range of environmental conditions and resources that are required for its persistence; it positions each species in relation to others in ecosystem space [83], taking into account physical conditions, such as climate, and food resources [84]. The nutritional niche is nested within the ecological niche and describes a specific proportion and ratio of nutrients which enable maximum growth, development, performance, and fitness (Figure 2A) [85–87]. Notably, precise values of the optimal niche can change with the internal state of an animal (e.g., larva versus adult) and with changing environmental conditions [87]. The nutritional niche can consequently be described by a multidimensional geometric space defined by food chemistry where each axis represents a nutrient (e.g., specific amino acids, chemical elements, or group of components) that are functionally relevant to a species (i.e., they are required for their development, survival, and reproduction [37,87,88]) (Figure 2). Within this space, some combinations of nutrients are more important for performance and fitness than others. If they are limited in the environment this can result in a discrepancy between the optimal nutritional niche of a consumer and the niche provided by the environment as suggested by ecological stoichiometry (stoichiometric mismatch) [89]. Such important nutrients are often regulated by animals, as revealed by the Geometric Framework of Nutrition (GFN) [85,90]. For instance, honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), and mason bees (*Osmia*

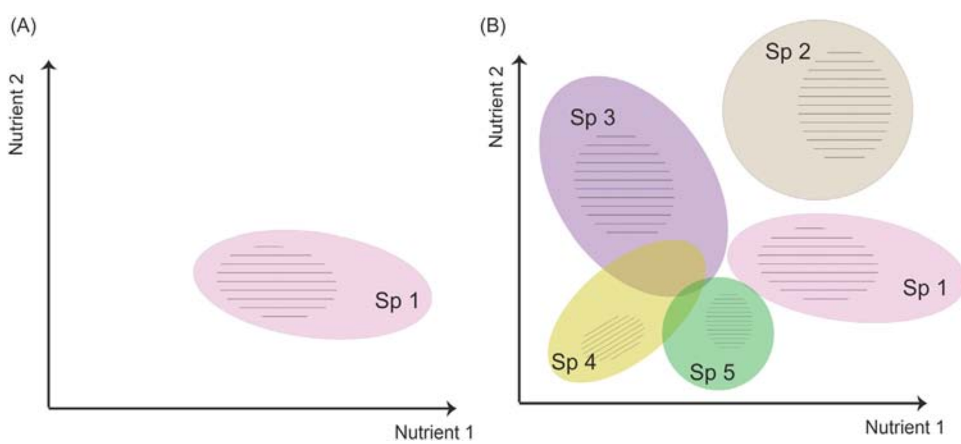


Figure 2. Nutritional niches of bee species in a multidimensional nutritional space. (A,B) The optimal niche space (shaded) and the tolerated niche space (lighter color) of a species (Sp), and species-specific nutritional niches. Each shaded space represents the combinations and concentration ranges of nutrients that are tolerated, and thus support the growth, development, performance, and fitness of a species. Strong deviations from the nutritional niche over extended time-periods will likely lead to negative impacts on health.

*bicornis*) regulate their protein, lipid, and/or carbohydrate intake depending on their age and the presence of brood [91,92]. For these important nutrients, species likely show little tolerance to deviations from the concentrations that best support their performance/fitness, whereas they are likely more tolerant to deviations from concentrations that are less crucial for performance/fitness (as shown for *Bombus terrestris* [93]).

Such differences in tolerance to deviations are captured by the tolerated nutritional niche – which deviates from the optimal niche – and thus captures the range that is still physiologically manageable by organisms and results in positive growth, development, and fitness [87]. If the actual nutritional niche offered by the available nutritional landscape deviates too far from the tolerated nutritional niche, individuals will fail to achieve successful growth, development, or reproduction [87]. In turn, the degree of variation in the tolerated niche space denotes the tolerance of a specific animal to a suboptimal diet. Different species likely vary not only in the position of their optimal niche (i.e., the specific proportions and ratios required) but also in their tolerance to deviations from the optimum, resulting in species-specific nutritional niche shapes and sizes (Figure 2B). Determining the tolerated nutritional niche of a species can thus provide valuable information to predict the spatial and temporal distribution of that species and its responses to environmental change [87,94].

As a consequence of the complex and diverse chemistry encountered in different plant species, animals must perform nutrient-selective foraging so as to ensure healthy offspring development [95]. In the case of bees, this means that they should choose pollen with a nutritional composition that matches their nutritional needs, as shown for several bumble bee species that thrive on pollen with high protein to lipid (P:L) ratios and low lipid content [21,96], or *O. bicornis* bee larvae that prefer diets with a high carbohydrate content [91]. The chemical profile of pollen jointly collected by individual (female) bees of a population can therefore represent a proxy for their species-specific nutritional niche.

Recent advances in analytical methods facilitate accurate quantitative chemical analysis of pollen, including fatty acids and protein-bound and free amino acids [97], sterols [98–100], plant secondary metabolites [101], and chemical elements [89]. The chemical/nutritional profile of the overall pollen diet of a bee individual can thus be calculated by integrating information on the proportional contributions of the nutritional profiles of pollen of all plant species visited for pollen collection (e.g., obtained through metabarcoding or palynological studies). Notably, this approach does not allow the optimal nutritional niches of species to be determined, which would require cage (semi-field) experiments with manipulated artificial diets. However, through linking measured (actual) nutritional niches and animal health, the nutritional niches measured at sites where populations show generally good health status and high population density can be a good proxy for the tolerated nutritional niches of a species.

## Dietary versus nutritional generalists and specialists in bees

The degree of dietary specialization of a species is determined by its physiological (e.g., ability to break down/tolerate specific plant compounds), sensory (e.g., intrinsic bias towards specific flowers/plants), and morphological (e.g., proboscis length and wing morphology) characteristics. It is typically described by the range of plant taxa used for pollen collection (i.e., pollen hosts) [102,103]. In bees, the full spectrum of flower specialization – sometimes referred to as dietary breadth [53,104] – ranges from species that collect floral pollen from a single plant species or genus only (monolecty, oligolecty) to generalists that do not appear to have distinct flower preferences (polylecty) [20]. However, even generalists, including many social bees, forage pollen from a limited range of flowering species [105–107]. A classification of floral specificity of pollen collection in bees covering all levels of specialization was suggested by Cane and Sipes [108] and Müller and Kuhlmann [105]. This classification, however, does not consider pollen nutrients, thus is not based on the nutritional niches of a species [105,108].

We propose that bee species differ not only in the specific nutrient amounts and ratios that are required for optimal survival and reproduction (see earlier) but also in the degree of variation in nutrient space that is tolerated, that is, the tolerated nutritional niche, and thus differ in the nutritional landscapes in which they can thrive. Nutritional specialists are thus species with comparatively narrow nutritional niches, whereas generalists are species with a comparatively wide nutritional niche (Figure 3). Nutritional niche breadth and dietary breadth can correlate with each other, but do not necessarily need to be correlated. Although it is likely that dietary specialists also show a narrow nutritional niche, some dietary specialists may have a broader nutritional niche than some generalists. For example, some bees may visit a broad spectrum of plant species with chemically similar pollen profiles, for example, bee species that collect pollen

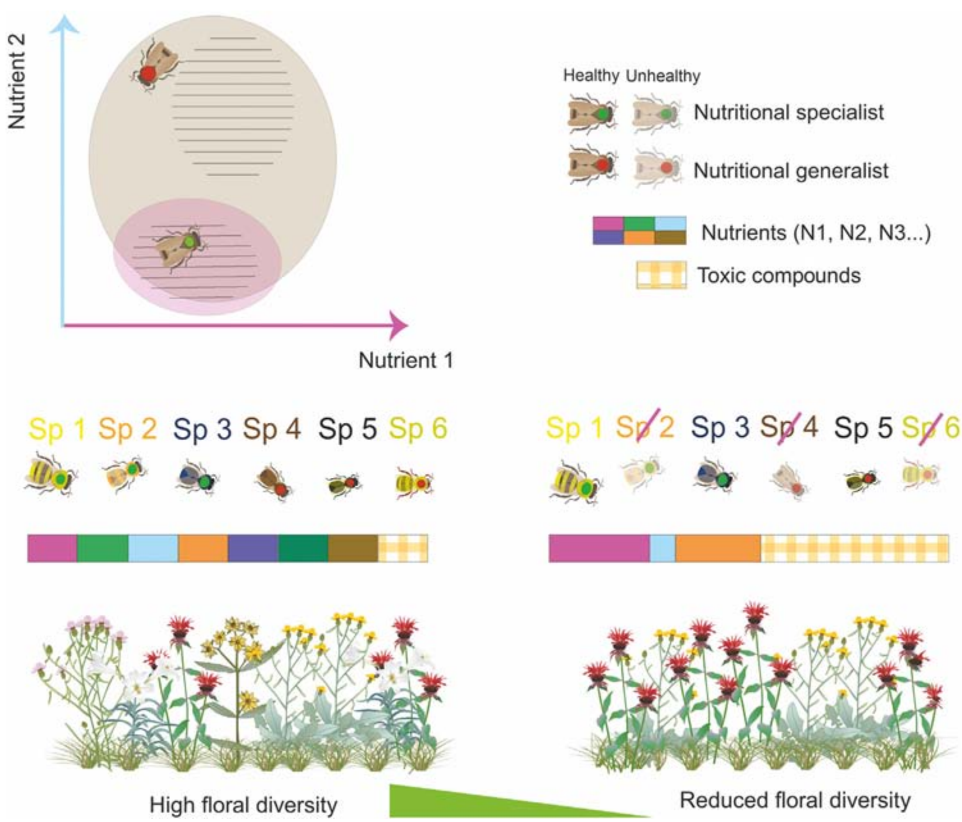


Figure 3. Link between floral diversity, nutritional landscapes, and nutritional niches.
For a Figure360 author presentation of Figure 3, see the figure legend at https://doi.org/10.1016/j.tree.2021.11.013
Bee species (Sp) with narrow nutritional niches (nutritional specialists, marked with green dots), and thus with little tolerance to changes in the nutritional space (purple area in the nutritional space), are likely to be more susceptible to changes in floral diversity than are bee species with broad nutritional niches (nutritional generalists, marked with red dots) and higher tolerance (brown area in the nutritional space). The nutritional landscape of each environment is reflected by different colors of nutrients (bars in the center). This landscape is more diverse and balanced, and thus provides more nutritional niches, in florally diverse environments (left) compared with environments with reduced floral diversity (right). Florally diverse environments also enable bees to dilute toxic compounds (e.g., harmful plant secondary metabolites or pesticides), thereby exposing them to overall lower levels of harmful compounds compared with environments with reduced floral diversity.

from Asteraceae. These are mostly specialized bees that forage on multiple different Asteraceae species, whereas generalist bee species avoid Asteraceae pollen despite the ubiquitous distribution of this plant family and the substantial amount of pollen provision (known as the Asteraceae paradox [105]). Although the reasons for this paradox remain unresolved, the abundance of specific chemical compounds (e.g., Δ7-sterols) in the pollen of Asteraceae species may offer an explanation [100].

## Linking bee health, floral diversity, and nutritional niches

Some generalist bees have been shown to mix pollen from different plant sources, either during one or several foraging trips, likely to achieve a nutritional balance and/or to dilute toxic compounds [72,75], indicating that nutritional generalists may even specifically target and clearly benefit from diverse pollen sources in florally diverse environments (Table 1). Nutritional specialists, conversely, depend on the presence of specific plant species which provide pollen with nutrient profiles that are close to their nutritional niches. Access to a nutritionally diverse landscape as typically provided in florally diverse environments would ensure that different species-specific macro- and micronutrient requirements can be met [24,109]. We therefore predict that nutritional specialists with a comparatively small nutritional niche are more common in florally diverse (and thus nutritionally diverse) habitats – where they have access to a broader spectrum of resources and thus of potential nutritional niches, including their own [110] (Figure 3).

Both nutritional generalists and nutritional specialists should therefore thrive in nutritionally diverse landscapes, which are expected to provide more nutritional niches than nutritionally poor landscapes (Figure 3). Bees in nutritionally diverse landscapes will more likely encounter their (potentially even optimal) nutritional niche. As a consequence, they should be better nourished and therefore be healthier than bees in nutritionally poor landscapes.

Notably, bees in more biodiverse environments may also harbor more diverse pathogens and parasites [44,67,111,112]. However, access to (nutritionally) diverse resources may render them more tolerant and resilient to pathogens and parasite virulence factors (through optimal physiology), and/or more resistant to associated infection risks (through optimal immunity) [10,74,81,113]. They may also more easily adjust their diet to combat infection, for example, by increasing the proportion of protein in their diet [114,115] or by collecting resources with antimicrobial plant secondary metabolites [25,33,116]. In fact, the resilience of bees, not only to diseases but also to other stressors (e.g., climatic or weather extremes), varies with floral/nutritional quality [81,117]. We therefore do not expect that more stressors are necessarily linked with decreased health, but instead predict a three-way interaction between nutrition, health, and stressors such as pathogen loads, which may result in different scenarios such as linear and nonlinear shifts in nutritional niches (Figure 4). For example, protein-rich diets improve the immune-competence of bumble bees (*B. terrestris*) exposed to a parasite [66], and lipid-rich diets increase survival in honey bees (*A. mellifera*) exposed to an organophosphate insecticide [117]. These studies indicate that bees can adjust their diets to compensate for different stressors, and this can result in altered nutritional niche spaces (Figure 4). Consequently, floral/nutritional diversity may convey health benefits to generalist and specialist bee species by providing a variety of nutritional niches which can increase the nutritional flexibility and resilience of bees when facing additional stressors.

## Concluding remarks

By integrating different physiological health measures and nutritional niches with floral diversity and composition, we can reveal meaningful interactions between nutritional landscapes and bee health (Figures 3 and 4). We can also investigate hitherto unknown interactive effects

### Outstanding questions

How can wild bee health be defined and measured? We propose specific guidelines and parameters to measure health in wild bees and to link it to floral resource/food landscapes by assessing nutritional niches. Applying our conceptual framework will enable better tailored management recommendations for the conservation of wild bees.

How do nutrition, health, and disease interact? Three-way interactions, such as between nutrition, health, and disease loads, are difficult to study for wild bees, in particular in the field. We propose to measure and integrate different elements, namely pathogen loads, physiological parameters, and nutritional niches, based on pollen metabarcoding and analytical chemistry, across environmental gradients that differ in plant diversity so as to disentangle such interactions.

Can knowledge about bee nutritional niches aid in conservation measures and thus support the maintenance of ecosystem services? We suggest that floral/nutritional diversity conveys health benefits to generalist and specialist bee species by providing nutritional landscapes that offer a variety of nutritional niches. Analyzing the nutritional requirements of different species, and of the plant species and communities that support them, will aid in better tailoring conservation measures to specific bee communities.

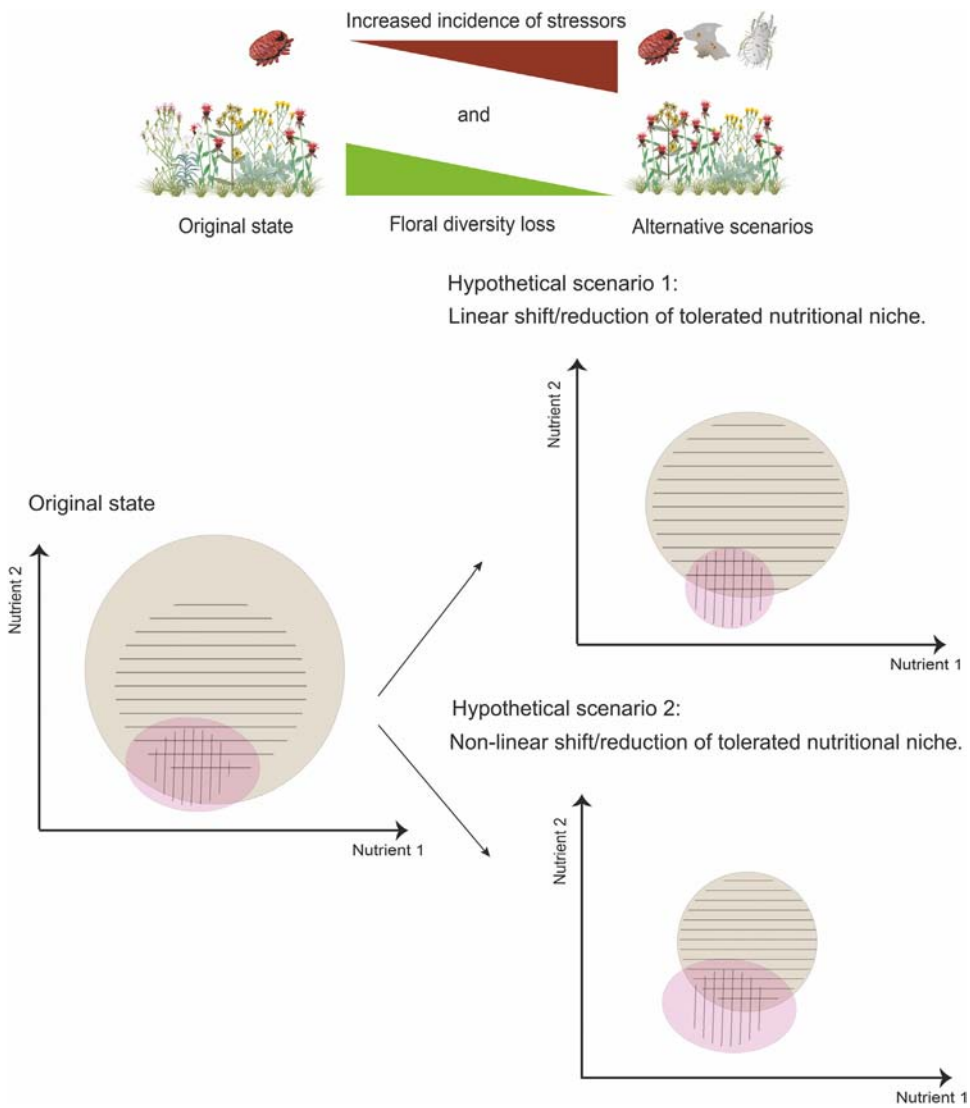


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Figure 4. Interactions between nutrition, health, and stressors are altered in florally impoverished landscapes. Hypothetical scenarios depict linear and nonlinear changes in the nutritional niches of nutritional specialists (purple areas) and generalists (brown areas) following loss of floral diversity plus additional stressors (e.g., increased pathogen prevalence). Stressors may shift the tolerated nutritional niche space of a bee species without affecting its optimal nutritional niche (scenario 1). Alternatively, it may result in a nonlinear change in overall nutritional niches (including both the optimal and tolerated niche space). Moreover, the magnitude and direction of ecological niche shifts under stressed scenarios is known to differ among taxonomic groups [118], demonstrating highly species-specific responses. Likewise, the nutritional niche of one species may be strongly decreased, whereas the optimal and tolerated nutritional niche of another species may remain unaffected in the presence of additional stressors (scenario 2). This in turn may result in a species-specific likelihood of becoming (locally) extinct under stressed conditions. To our knowledge no study to date has assessed nutritional niche shifts in different bee species exposed to different stressors.

between different physiological health parameters such as stoichiometry, physiology, and disease loads.

This integrative approach will enable better tailored management recommendations for bee conservation (see Outstanding questions). Until now most conservation measures have implicitly assumed that wild bee populations can be enhanced by increasing floral diversity [8]. However, this can lead to shortages in the types, amounts, and proportions of specific nutrients, and thus in a lack of the nutritional niches required by different bees, in particular by nutritional specialists. Such shortages can be elucidated, for example, by comparing bee and pollen stoichiometry to reveal stoichiometric mismatches [89]. Similarly, bee–nutrient networks and ordination analyses could reveal differences in link strength between specific nutrients or nutrient ratios and specific bee species, where strong links indicate important nutrients, nutrient groups, or nutrient ratios and the plant species providing them. This information can then be used to improve flower seed mixes or support the conservation of key plant species and their habitats.

Notably, the quantity and quality of available floral resources can be modulated by environmental conditions, such as water availability [119], rendering nutritional landscapes and bee foraging highly sensitive to global change [120]. For example, global change will likely affect the functional complementarity of bee–plant interactions, for example, through advancing seasonal flowering events. It remains open which bee species are sufficiently plastic in their phenology and/or resource requirements to maintain their floral associations and pollination service [121,122]. It is also poorly understood how such shifts in phenology or resource use induced by global change interact with bee health. Can we use knowledge about links between species-specific nutritional niches (breadth) and health to predict which bees will be able to forage in specific landscapes? Can we adjust floral enhancement schemes to take into consideration factors other than bee nutrition, such as edaphic conditions, climate sensitivity, interactions with other plants within communities, and stakeholder interests? Understanding how global change affects the physiology and adaptability of both bees and plants – and thus (nutritional) niche shifts and health requirements across species – is one of the biggest challenges of ongoing and future research.

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### Declaration of interests

The authors declare no conflicts of interest.

### Author contributions

M.A.P. drafted the manuscript, developed figures and tables, and coordinated co-author contributions until finalization. All co-authors contributed to the original grant application upon which this conceptual paper is based. All co-authors provided comments, proof-checked citations, contributed to text and figures in particular to develop paragraphs specific to their expertise areas (pathogens, stoichiometry, niche theory). S.D.L. initialized the manuscript, invited co-authors, and supervised manuscript development until finalization.

### References

1. Klein, A.-M. *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci.* 274, 303–313
2. Klein, A-M. *et al.* (2018) Relevance of wild and managed bees for human well-being. *Curr. Opin. Insect Sci.* 26, 82–88
3. Ollerton, J. *et al.* (2011) How many flowering plants are pollinated by animals? *Oikos* 120, 321–326
4. Potts, S. *et al.*, eds (2016) *Assessment Report on Pollinators, Pollination and Food Production – Summary for Policymakers*, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)

5. Dicks, L. *et al.* (2021) A global assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* 5, 1453–1461
6. Eggleton, P. (2020) The state of the world's insects. *Annu. Rev. Environ. Resour.* 45, 61–82
7. Rhodes, C.J. (2018) Pollinator decline – an ecological calamity in the making? *Sci. Prog.* 101, 121–160
8. Storkey, J. *et al.* (2020) Wild pollinators in arable habitats: trends, threats and opportunities. In *The Changing Status of Arable Habitats in Europe: A Nature Conservation Review* (Hurford, C. *et al.*, eds), pp. 187–201, Springer International
9. Zattara, E.E. and Aizen, M.A. (2021) Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123
10. Goulson, D. *et al.* (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347, 1255957
11. Potts, S.G. *et al.* (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353
12. Lichtenberg, E.M. *et al.* (2017) A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Change Biol.* 23, 4946–4957
13. Raven, P.H. and Wagner, D.L. (2021) Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proc. Natl. Acad. Sci.* 118, e2002548117
14. Kleijn, D. *et al.* (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* 9, 243–254
15. Newbold, T. *et al.* (2014) A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proc. Biol. Sci.* 281, 20141371
16. Thomson, D.M. (2016) Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecol. Lett.* 19, 1247–1255
17. Figueroa, L.L. *et al.* (2020) Landscape simplification shapes pathogen prevalence in plant–pollinator networks. *Ecol. Lett.* 23, 1212–1222
18. Piot, N. *et al.* (2021) More is less: mass-flowering fruit tree crops dilute parasite transmission between bees. *Int. J. Parasitol.* 51, 777–785
19. Smart, M. *et al.* (2016) Linking measures of colony and individual honey bee health to survival among apiaries exposed to varying agricultural land use. *PLoS ONE* 11, e0152685
20. Michener, C.D. (2007) *The Bees of the World*, Johns Hopkins University Press
21. Vaudo, A.D. *et al.* (2015) Bee nutrition and floral resource restoration. *Soc. Insects Vectors Med. Vet. Entomol.* 10, 133–141
22. Ziska, L.H. *et al.* (2016) Rising atmospheric $CO_2$ is reducing the protein concentration of a floral pollen source essential for North American bees. *Proc. R. Soc. B Biol. Sci.* 283, 20160414
23. Requier, F. *et al.* (2015) Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecol. Appl.* 25, 881–890
24. Simpson, S.J. and Raubenheimer, D. (2012) *The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity*, Princeton University Press
25. Koch, H. *et al.* (2019) Flagellum removal by a nectar metabolite inhibits infectivity of a bumblebee parasite. *Curr. Biol.* 29, 3494–3500
26. Stevenson, P.C. (2020) For antagonists and mutualists: the paradox of insect toxic secondary metabolites in nectar and pollen. *Phytochem. Rev.* 19, 603–614
27. Filipiak, M. (2018) A better understanding of bee nutritional ecology is needed to optimize conservation strategies for wild bees – the application of ecological stoichiometry. *Insects* 9, 3
28. Nicolson, S.W. (2011) Bee food: the chemistry and nutritional value of nectar, pollen and mixtures of the two. *Afr. Zool.* 46, 197–204
29. Wright, G.A. *et al.* (2018) Nutritional physiology and ecology of honey bees. *Annu. Rev. Entomol.* 63, 327–344
30. Timberlake, T.P. *et al.* (2019) Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585–1596
31. Jachuła, J. *et al.* (2021) Habitat heterogeneity helps to mitigate pollinator nectar sugar deficit and discontinuity in an agricultural landscape. *Sci. Total Environ.* 782, 146909
32. Belsky, J. and Joshi, N.K. (2019) Impact of biotic and abiotic stressors on managed and feral bees. *Insects* 10, 233
33. Palmer-Young, E.C. *et al.* (2019) Chemistry of floral rewards: intra- and interspecific variability of nectar and pollen secondary metabolites across taxa. *Ecol. Monogr.* 89, e01335
34. Vaudo, A.D. *et al.* (2020) Pollen protein: lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects* 11, 132
35. Requier, F. *et al.* (2020) Limitation of complementary resources affects colony growth, foraging behavior, and reproduction in bumble bees. *Ecology* 101, e02946
36. Venjakob, C. *et al.* (2020) Inter-individual nectar chemistry changes of field scabious, *Knautia arvensis*. *Insects* 11, 2
37. Filipiak, Z.M. and Filipiak, M. (2020) The scarcity of specific nutrients in wild bee larval food negatively influences certain life history traits. *Biology* 9, 12
38. Moerman, R. *et al.* (2017) Pollen nutrients better explain bumblebee colony development than pollen diversity. *Insect Conserv. Divers.* 10, 171–179
39. Stephen, C. (2014) Toward a modernized definition of wildlife health. *J. Wildl. Dis.* 50, 427–430
40. López-Uribe, M.M. *et al.* (2020) Defining pollinator health: a holistic approach based on ecological, genetic, and physiological factors. *Annu. Rev. Anim. Biosci.* 8, 269–294
41. Dellicour, S. *et al.* (2017) Distribution and predictors of wing shape and size variability in three sister species of solitary bees. *PLoS ONE* 12, e0173109
42. Engel, P. *et al.* (2016) The bee microbiome: impact on bee health and model for evolution and ecology of host–microbe interactions. *mBio* 7, e02164-15
43. Alaux, C. *et al.* (2010) Diet effects on honeybee immunocompetence. *Biol. Lett.* 6, 562–565
44. Keller, A. *et al.* (2020) (More than) Hitchhikers through the network: the shared microbiome of bees and flowers. *Curr. Opin. Insect Sci.* 44, 8–15
45. Tracy, C.R. *et al.* (2006) The importance of physiological ecology in conservation biology. *Integr. Comp. Biol.* 46, 1191–1205
46. Ellis, R.D. *et al.* (2012) Integrating landscape ecology and conservation physiology. *Landsc. Ecol.* 27, 1–12
47. Alaux, C. *et al.* (2017) A 'landscape physiology' approach for assessing bee health highlights the benefits of floral landscape enrichment and semi-natural habitats. *Sci. Rep.* 7, 40568
48. Arrese, E.L. and Soulages, J.L. (2010) Insect fat body: energy, metabolism, and regulation. *Annu. Rev. Entomol.* 55, 207–225
49. de Freitas Brito, T. *et al.* (2021) Orchid bees (Apidae, Euglossini) from oil palm plantations in Eastern Amazon have larger but not asymmetrical wings. *Neotrop. Entomol.* 50, 388–397
50. Gerard, M. *et al.* (2018) Stressful conditions reveal decrease in size, modification of shape but relatively stable asymmetry in bumblebee wings. *Sci. Rep.* 8, 15169
51. Lima, C.B.S. *et al.* (2016) Morphometric differences and fluctuating asymmetry in *Melipona subnitida* Ducke 1910 (Hymenoptera: Apidae) in different types of housing. *Braz. J. Biol.* 76, 845–850
52. Dharampal, P.S. *et al.* (2019) Pollen-borne microbes shape bee fitness. *Proc. Biol. Sci.* 286, 20182894
53. Rothman, J.A. *et al.* (2019) The bumble bee microbiome increases survival of bees exposed to selenate toxicity. *Environ. Microbiol.* 21, 3417–3429
54. Voulgari-Kokota, A. *et al.* (2019) Drivers, diversity, and functions of the solitary-bee microbiota. *Trends Microbiol.* 27, 1034–1044
55. Jeyasingh, P.D. *et al.* (2014) Testing the ecological consequences of evolutionary change using elements. *Ecol. Evol.* 4, 528–538
56. Albrecht, M. *et al.* (2020) The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498
57. Dainese, M. *et al.* (2019) A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* 5, eaax0121
58. Kaluza, B.F. *et al.* (2018) Social bees are fitter in more biodiverse environments. *Sci. Rep.* 8, 12353

59. Roulston, T.H. and Goodell, K. (2010) The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312
60. Scheper, J. *et al.* (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proc. Natl. Acad. Sci.* 111, 17552
61. Blüthgen, N. and Klein, A-M. (2011) Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.* 12, 282–291
62. Crone, E.E. and Williams, N.M. (2016) Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production. *Ecol. Lett.* 19, 460–468
63. Goulson, D. *et al.* (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* 130, 267–273
64. Kaluza, B.F. *et al.* (2017) Generalist social bees maximize diversity intake in plant species-rich and resource-abundant environments. *Ecosphere* 8, e01758
65. Trinkl, M. *et al.* (2020) Floral species richness correlates with changes in the nutritional quality of larval diets in a stingless bee. *Insects* 11, 2
66. Brunner, F.S. *et al.* (2014) Protein-poor diet reduces host-specific immune gene expression in *Bombus terrestris*. *Proc. Biol. Sci.* 281, 20140128
67. Dolezal, A.G. and Toth, A.L. (2018) Feedbacks between nutrition and disease in honey bee health. *Curr. Opin. Insect Sci.* 26, 114–119
68. Tosi, S. *et al.* (2017) Neonicotinoid pesticides and nutritional stress synergistically reduce survival in honey bees. *Proc. R. Soc. B Biol. Sci.* 284, 20171711
69. Bartomeus, I. *et al.* (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* 110, 4656–4660
70. Leach, M.E. and Drummond, F. (2018) A review of native wild bee nutritional health. *Int. J. Ecol.* 2018, 9607246
71. Klaus, F. *et al.* (2021) Floral resource diversification promotes solitary bee reproduction and may offset insecticide effects – evidence from a semi-field experiment. *Ecol. Lett.* 24, 668–675
72. Stuligross, C. and Williams, N.M. (2020) Pesticide and resource stressors additively impair wild bee reproduction. *Proc. R. Soc. B Biol. Sci.* 287, 20201390
73. Dance, C. *et al.* (2017) The combined effects of a monotonous diet and exposure to thiamethoxam on the performance of bumblebee micro-colonies. *Ecotoxicol. Environ. Saf.* 139, 194–201
74. Di Pasquale, G. *et al.* (2013) Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? *PLoS One* 8, e72016
75. Eckhardt, M. *et al.* (2014) Pollen mixing in pollen generalist solitary bees: a possible strategy to complement or mitigate unfavourable pollen properties? *J. Anim. Ecol.* 83, 588–597
76. Foley, K. *et al.* (2012) Nutritional limitation and resistance to opportunistic Aspergillus parasites in honey bee larvae. *J. Invertebr. Pathol.* 111, 68–73
77. Leza, M. *et al.* (2018) Effects of neonicotinoid insecticide exposure and monofloral diet on nest-founding bumblebee queens. *Proc. R. Soc. B Biol. Sci.* 285, 20180761
78. McAulay, M.K. and Forrest, J.R.K. (2019) How do sunflower pollen mixtures affect survival of queenless microcolonies of bumblebees (*Bombus impatiens*)? *Arthropod-Plant Interact.* 13, 517–529
79. Renzi, M.T. *et al.* (2016) Combined effect of pollen quality and thiamethoxam on hypopharyngeal gland development and protein content in *Apis mellifera*. *Apidologie* 47, 779–788
80. Requier, F. *et al.* (2017) The carry-over effects of pollen shortage decrease the survival of honeybee colonies in farmlands. *J. Appl. Ecol.* 54, 1161–1170
81. Vanderplanck, M. *et al.* (2019) Ensuring access to high-quality resources reduces the impacts of heat stress on bees. *Sci. Rep.* 9, 12596
82. Straub, L. *et al.* (2015) Superorganism resilience: eusociality and susceptibility of ecosystem service providing insects to stressors. *Neurosci. Spec. Sect. Insect Conserv.* 12, 109–112
83. Polechová, J. and Storch, D. (2019) Ecological niche. In *Encyclopedia of Ecology* (2nd edn) (Fath, B. , ed.), pp. 72–80, Elsevier
84. Descamps, C. *et al.* (2021) Climate change-induced stress reduce quantity and alter composition of nectar and pollen from a bee-pollinated species (*Borago officinalis*, Boraginaceae). *Front. Plant Sci.* 12, 2264
85. Simpson, S.J. and Raubenheimer, D. (2012) Beyond nutrients. In *The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity*, pp. 71–87, Princeton University Press
86. Stabler, D. *et al.* (2015) Nutrient balancing of the adult worker bumblebee (*Bombus terrestris*) depends on the dietary source of essential amino acids. *J. Exp. Biol.* 218, 793
87. Machovsky-Capuska, G.E. *et al.* (2016) The multidimensional nutritional niche. *Trends Ecol. Evol.* 31, 355–365
88. Sperfeld, E. *et al.* (2017) Bridging ecological stoichiometry and nutritional geometry with homeostasis concepts and integrative models of organism nutrition. *Funct. Ecol.* 31, 286–296
89. Filipiak, M. (2019) Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. *J. Appl. Ecol.* 56, 1410–1418
90. Behmer, S.T. (2009) Insect herbivore nutrient regulation. *Annu. Rev. Entomol.* 54, 165–187
91. Austin, A.J. and Gilbert, J.D.J. (2021) Solitary bee larvae prioritize carbohydrate over protein in parentally provided pollen. *Funct. Ecol.* 35, 1069–1080
92. Kraus, S. *et al.* (2019) Bumblebees adjust protein and lipid collection rules to the presence of brood. *Curr. Zool.* 65, 437–446
93. Ruedenauer, F.A. *et al.* (2019) Bumblebees are able to perceive amino acids via chemotactile antennal stimulation. *J. Comp. Physiol. A.* 205, 321–331
94. Sverdrup-Thygeson, A. *et al.* (2017) Habitat connectivity affects specialist species richness more than generalists in veteran trees. *For. Ecol. Manag.* 403, 96–102
95. Crumière, A.J.J. *et al.* (2020) Using nutritional geometry to explore how social insects navigate nutritional landscapes. *Insects* 11, 53
96. Ruedenauer, F.A. *et al.* (2018) Do honeybees (*Apis mellifera*) differentiate between different pollen types? *PLoS ONE* 13, e0205821
97. Weiner, C.N. *et al.* (2010) Pollen amino acids and flower specialisation in solitary bees. *Apidologie* 41, 476–487
98. Vanderplanck, M. *et al.* (2011) Micro-quantitative method for analysis of sterol levels in honeybees and their pollen loads. *Anal. Lett.* 44, 1807–1820
99. Vanderplanck, M. *et al.* (2020) Sterol addition during pollen collection by bees: another possible strategy to balance nutrient deficiencies? *Apidologie* 51, 826–843
100. Zu, P. *et al.* (2021) Pollen sterols are associated with phylogeny and environment but not with pollinator guilds. *New Phytol.* 230, 1169–1184
101. Stevenson, P.C. *et al.* (2017) Plant secondary metabolites in nectar: impacts on pollinators and ecological functions. *Funct. Ecol.* 31, 65–75
102. Devictor, V. *et al.* (2010) Defining and measuring ecological specialization. *J. Appl. Ecol.* 47, 15–25
103. Goulson, D. *et al.* (2005) Causes of rarity in bumblebees. *Biol. Conserv.* 122, 1–8
104. Roulston, T.H. and Cane, J.H. (2000) The effect of diet breadth and nesting ecology on body size variation in bees (Apiformes). *J. Kansas Entomol. Soc.* 73, 129–142
105. Müller, A. and Kuhlmann, M. (2008) Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biol. J. Linn. Soc.* 95, 719–733
106. Murray, T.E. *et al.* (2009) Conservation ecology of bees: populations, species and communities. *Apidologie* 40, 211–236
107. Westrich, P. (2018) *Die Wildbienen Deutschlands*, Verlag Eugen Ulmer
108. Cane, J.H. and Sipes, S. (2006) Floral specialization by bees: analytical methodologies and a revised lexicon for oligolecty. In *Plant–Pollinator Interactions: From Specialization to Generalization* (Waser, N. and Ollerton, J., eds), pp. 99–122, University of Chicago Press
109. Sterner, R.W. and Elser, J.J. (2002) *Ecological Stocihiometry: The Biology of Elements from Molecules to the Biosphere*, Princeton University Press
110. Guzman, A. *et al.* (2019) On-farm diversification in an agriculturally-dominated landscape positively influences specialist pollinators. *Front. Sustain. Food Syst.* 3, 87

111. Ambika Manirajan, B. *et al.* (2016) Bacterial microbiota associated with flower pollen is influenced by pollination type, and shows a high degree of diversity and species-specificity. *Environ. Microbiol.* 18, 5161–5174
112. McNeil, D.J. *et al.* (2020) Bumble bees in landscapes with abundant floral resources have lower pathogen loads. *Sci. Rep.* 10, 22306
113. Goulson, D. *et al.* (2008) Diet breadth, coexistence and rarity in bumblebees. *Biodivers. Conserv.* 17, 3269–3288
114. Erler, S. and Moritz, R.F.A. (2016) Pharmacophagy and pharmacophory: mechanisms of self-medication and disease prevention in the honeybee colony (*Apis mellifera*). *Apidologie* 47, 389–411
115. McArt, S.H. *et al.* (2017) Landscape predictors of pathogen prevalence and range contractions in US bumblebees. *Proc. R. Soc. B Biol. Sci.* 284, 20172181
116. Palmer-Young, E.C. *et al.* (2016) Bumble bee parasite strains vary in resistance to phytochemicals. *Sci. Rep.* 6, 37087
117. Crone, M.K. and Grozinger, C.M. (2021) Pollen protein and lipid content influence resilience to insecticides in honey bees (*Apis mellifera*). *J. Exp. Biol.* 224, jeb242040.
118. Hill, M.P. *et al.* (2017) A global assessment of climatic niche shifts and human influence in insect invasions. *Glob. Ecol. Biogeogr.* 26, 679–689
119. Wilson Rankin, E.E. *et al.* (2020) Reduced water negatively impacts social bee survival and productivity via shifts in floral nutrition. *J. Insect Sci.* 20, 5
120. Descamps, C. *et al.* (2021) Warm temperatures reduce flower attractiveness and bumblebee foraging. *Insects* 12, 493
121. Cane, J. (2021) Global warming, advancing bloom and evidence for pollinator plasticity from long-term bee emergence monitoring. *Insects* 12, 5
122. Bartomeus, I. *et al.* (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci.* 108, 20645