Critical links between biodiversity and health in wild bee conservation

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Abstract

Wild bee populations are declining due to human activities, such as land use, which strongly affect the composition and diversity of available plants and food sources. The chemical composition of food (i.e. nutrition), in turn, determines health, resilience and fitness of bees. However, for pollinators, the term *health* is recent and 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, 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.

Keywords: Hymenoptera, biodiversity loss, plant-insect interactions, conservation, physiology, pollination, pollinators, ecosystem services

Bees decline because their food sources disappear

Animals pollinate more than 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 for plant productivity, food webs and ultimately for human well-being [1–3]. Bees (Apidae) are the most important group of pollinators with the vast majority of species 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 and acting 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 wild bee communities [12,13]. In fact, overall biodiversity typically decreases with increasing land-use intensity [14,15], which directly or indirectly leads to the 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 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 health, resilience to pathogens and fitness of animals [24], access to food resources enabling a diverse and balanced nutrition is one key driver of population stability [21]. In this context, we consider as nutrient any chemical compound, i.e., from chemical elements, through phospholipids, amino acids to "group components" like proteins, that are part of the food/nutrition of bees. Bees obtain most nutrients and several potentially medical active plant secondary metabolites from flowering plants through consuming mostly nectar and pollen [20,25,26]. Nectar primarily provides carbohydrates needed to maintain energetic and metabolic processes, while pollen is the main source of all other macro-nutrients (i.e., protein and fat) and micro-nutrients (e.g., vitamins, sterols) required for metabolic processes, tissue homeostasis and development (e.g., ovary development) as well as 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, i.e., 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 as 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 among 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 the nutritional landscape in which bees are foraging [21]. For more details on variation in nutritional quality in pollen and nectar, the effect of different diets on bee performance and fitness as well as on differences in foraging preferences among bees, see Vaudo et al. [21].

While much less understood, the nutritional needs of bee species are also expected to vary substantially between bee species [21]. The sustainability of bee populations thus depends on flowering plant communities that provide sufficient amounts and 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 nutritional landscape available and the health status of different wild bee species has hitherto received little attention (but see [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 of 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

While 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 population's health status should then be a direct consequence of the average health status of individuals, with population size likely being positively correlated 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 (Fig.1). We suggest recording and integrating all or several of the following physiological parameters to comprehensively capture individual bee health: 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 species' sensitivity to environmental modifications [45], because the physiology of individuals responds before changes in populations become visible [46]. For instance, diet quality correlates with increased levels of the storage protein and antioxidant vitellogenin in individual honey bees, which correlates with higher overwintering survival of the entire colony [19,47]. Energy storage is critical to 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 capacities, 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 or pathogen loads. For example, wing morphometry and wing fluctuating asymmetry were found to correlate with different stressors [49–51]. Also, floral composition and diversity are known to shape the bee microbiome composition, particularly in solitary bees, with consequences on 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 above are likely affected by multiple environmental parameters related to variation in floral resource diversity, abundance and quality, but also environmental pollutants (e.g., pesticides, antibiotics, heavy metals) and pathogens (Fig. 1). Measurement of multiple variables can therefore provide a more complete picture of pollinator health status than focus on a single one.

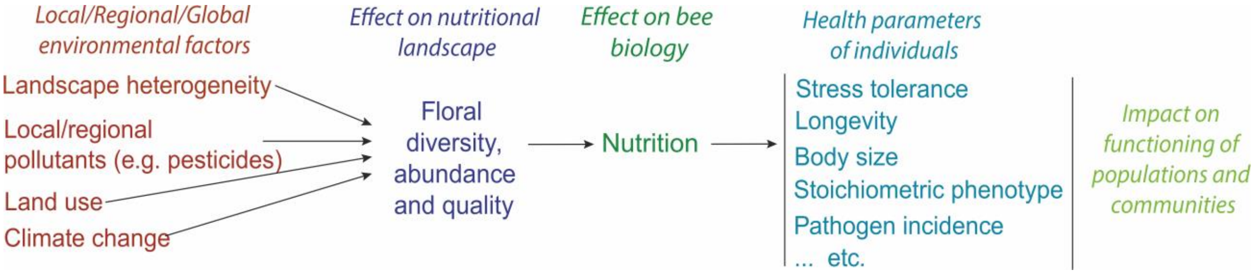

Fig. 1: The multifaceted nature of bee health. The main landscape-scale environmental factors, their effects on the floral community and thus nutritional landscape and bee diets, and consequences for bee nutrition and health. These can be observed by recording and integrating different parameters (right 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 for multiple seasons to infer changes in population densities across years.

Floral diversity as 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] and so 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), likely due to access to adequate nutrition and beneficial plant secondary metabolites. In contrast, chronic intake of monotonous, non-suitable, 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 susceptibility to disease [67] and pesticides [68]. In fact, nutritional stress as a consequence of restricted access to adequate floral resources is considered one of the main drivers of bee pollinator decline [21,69,70]. While floral diversity may not provide an added value *per se* or automatically yield beneficial synergistic effects as compared to higher quality monofloral diets [34,71,72] it can clearly mitigate negative effects of poor diets and provide overall more choices to various bee species (Table 1).

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

Experiment	Bee species	Effects	Response variable	Citation

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 health (vitellogenin expression level)	Alaux et al., 2017 [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	Dance et al., 2017 [73]
Monofloral vs. polyfloral pollen diets	Honeybee *(Apis mellifera)*	When parasitized, bees fed with the polyfloral blend lived longer than bees fed with monofloral pollens	Longevity of adults	Di Pasquale et al., 2013 [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	Eckhardt et al., 2014 [75]
Royal jelly supplemented with mono- or polyfloral pollen diets	Honeybee *(Apis mellifera*	Larval resistance to *disease* was enhanced on a diet supplemented with either dandelion or polyfloral pollen	Larval resistance to disease	Foley et al., 2012 [76]
Landscapes differing in floral resource diversity, effect on colony performance and reproduction	Sugarbag bee *(Tetragonula carbonaria)*	Colony performance and reproduction was positively correlated with floral diversity in the landscape	Colony performance and reproduction (brood)	Kaluza et al., 2017 [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	Klaus et al. 2021 [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, effect increased on monofloral diet	Nesting success, queen mortality and activity levels, queen nectar consumption, colony development (brood)	Leza et al. 2018 [77]

Mixture of pollen in diet, effect on lifespan	Common eastern bumblebee *(Bombus impatiens)*	Survival of bees fed a pollen mixture with 50% unfavourable pollen *(Helianthus annuus*, Asteraceae) was as good as on a high quality monofloral diet	Lifespan of bees in captivity	McAulay et al., 2019 [78]
Mono-, di- and trifloral diets, effect on colony development	Buff tailed bumblebee *(Bombus terrestris)*	Colonies developed best on mixed pollen diets or high quality monofloral pollen diets	Colony development (brood)	Moerman et al., 2017 [38]
High pollen diversity and protein vs. low pollen diversity and protein diets combined with pesticide, effect on development of hypopharyngeal glands	Honeybee *(Apis mellifera*	Size and shape of hypopharyngeal acini was affected by pesticide and diet, while protein content in bee head was affected only by pesticide.	Physiological development	Renzi et al., 2016 [79]
Landscape gradient in floral resource abundance and diversity	Honeybee *(Apis mellifera*	Decline in pollen availability in summer led to decrease in pollen harvest, colony performance and to overwintering failure	Colony performance (brood, adult population size, honey reserve) and overwintering	Requier et al., 2017 [80]
Landscape gradient of semi-natural habitats	Buff tailed bumblebee *(Bombus terrestris)*	Higher abundance of seminatural habitats improved reproductive performance	Colony growth and reproductive performance (number of new queens produced)	Requier et al., 2020 [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	Stuligross and Williams 2020 [72]
Diets differing in floral composition, effect on resilience to heat stress	Buff tailed bumblebee *(Bombus terrestris)*	Colonies were less susceptible to heat stress when fed suitable/high quality diets	Colony resistance to stress	Vanderplanck et al., 2019 [81]

However, how floral resource diversity and nutritional quality interact and affect bee health is still largely unclear. This is particularly true for wild bees considered less resilient to environmental changes and more difficult to study than managed honeybees [72,82]. For example, it is little understood how different nutrients or nutrient groups contribute to bee health, and if bee species differ in their tolerance towards deviations from optimal nutritional profiles and thus 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 combat ongoing bee declines (see below). 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 a range of environmental conditions and resources 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 (Fig. 2a) [85–87]. Notably, precise values of the optimal niche can change with an animal’s internal state (e.g., larva vs. 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) functionally relevant to a species, i.e. required for development, survival and reproduction

[37,87,88] (Fig 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 consumer's optimal nutritional niche 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 bicornis*) regulate protein, lipid and/or carbohydrate intake depending on their age and the presence of brood [91,92]. For such important nutrients, species likely show little tolerance to deviations from those concentrations which best support their performance/fitness, while they are likely more tolerant to deviations from concentrations that are less important/regulated for performance/fitness (as shown for *B. terrestris* [93]).

Such differences in tolerance to deviations is captured by the *tolerated nutritional niche* which is a deviant of the optimal niche and captures the range that is still physiologically manageable by organisms and results in a positive growth, development and fitness[87]. If the realized nutritional niche as 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]. The degree of variation in niche space tolerated, in turn, denotes the tolerance of a specific animal for suboptimal diets. Different species likely vary not only in the position of their optimal niche (i.e., the specific proportions and ratios required), but also their tolerance for deviations from the optimum, resulting in species-specific nutritional niche shapes and sizes (Fig. 2b). Determining the tolerated nutritional niche of species can thus provide valuable information to predict the spatial and temporal distribution of that species and its responses to environmental change [87,94].

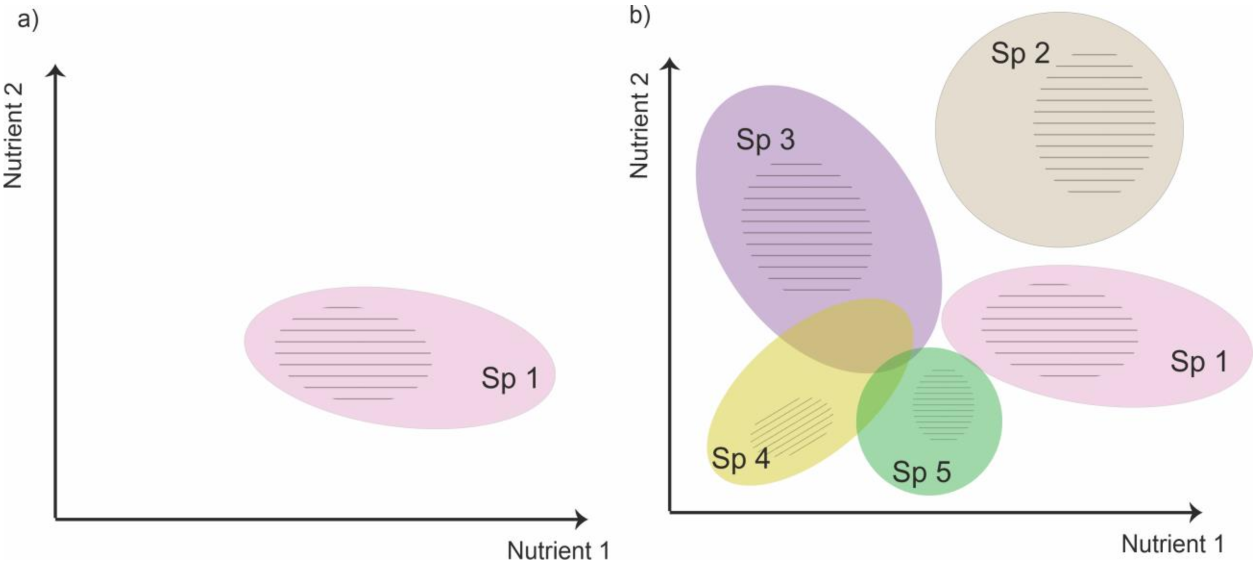

Fig. 2: Nutritional niches of bee species in a multidimensional nutritional space. The optimal niche space (shaded) and the tolerated niche space (lighter color) of a species (Sp) and species-specific nutritional niches. Each shaded space represents the combinations and concentration ranges of nutrients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

As a consequence of the complex and variable chemistry encountered in different plant species, animals need to perform nutrient selective foraging in order to ensure healthy offspring development [95]. In the case of bees, this means that they should choose pollen with nutritional composition that match 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 bee larvae of *O. bicornis* that prefer high carbohydrate content diets [91]. The chemical profile of pollen jointly collected by individual (female) bees of a population can therefore be considered a proxy for their species-specific nutritional niche.

Recent advances in analytical methods facilitate the 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 atoms of chemical elements [89]. The chemical/nutritional profile of the overall pollen diet composed by a bee individual can thus be calculated through integrating information on the proportional contribution of 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 to determine the optimal nutritional niches of species, which would require cage (semi-field) experiments with manipulated artificial diets. However, through linking measured (realized) nutritional niches and animal health the nutritional niches measured at sites where populations show a generally good health status and high population density can be a good proxy for the species' tolerated nutritional niches.

Dietary vs. 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 & Sipes [108] and Müller & Kuhlmann [105]. This classification, however, does not consider pollen nutrients, thus is not based on the species' nutritional niches [105,108].

We propose that bee species differ not only in the specific nutrient amounts and ratios required for optimal survival and reproduction (see above), but also in the degree of variation in nutrient space tolerated, i.e., the tolerated nutritional niche, and thus in the nutritional landscape in which they can thrive. Nutritional specialists are thus species with comparatively narrow nutritional niches, and generalists are species with a comparatively wide nutritional niche (Fig. 3). Nutritional niche breadth and dietary breadth can be, but do not necessarily have to be correlated. While 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, e.g., bee species collecting pollen from Asteraceae. These are mostly specialized bees foraging on many different Asteraceae species, while 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]). While the reasons for this Asteraceae paradox remain unresolved, the abundance of specific chemical compounds, e.g. Δ7-sterols, found in 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, on the other hand, 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 micro-nutrient requirements can be met [24,109]. We therefore predict that nutritional specialists with a comparatively small nutritional niche are more common in florally diverse habitats and thus nutritionally diverse landscape, where they have access to a broader spectrum of resources and thus of potential nutritional niches, including their own [110] (Fig. 3).

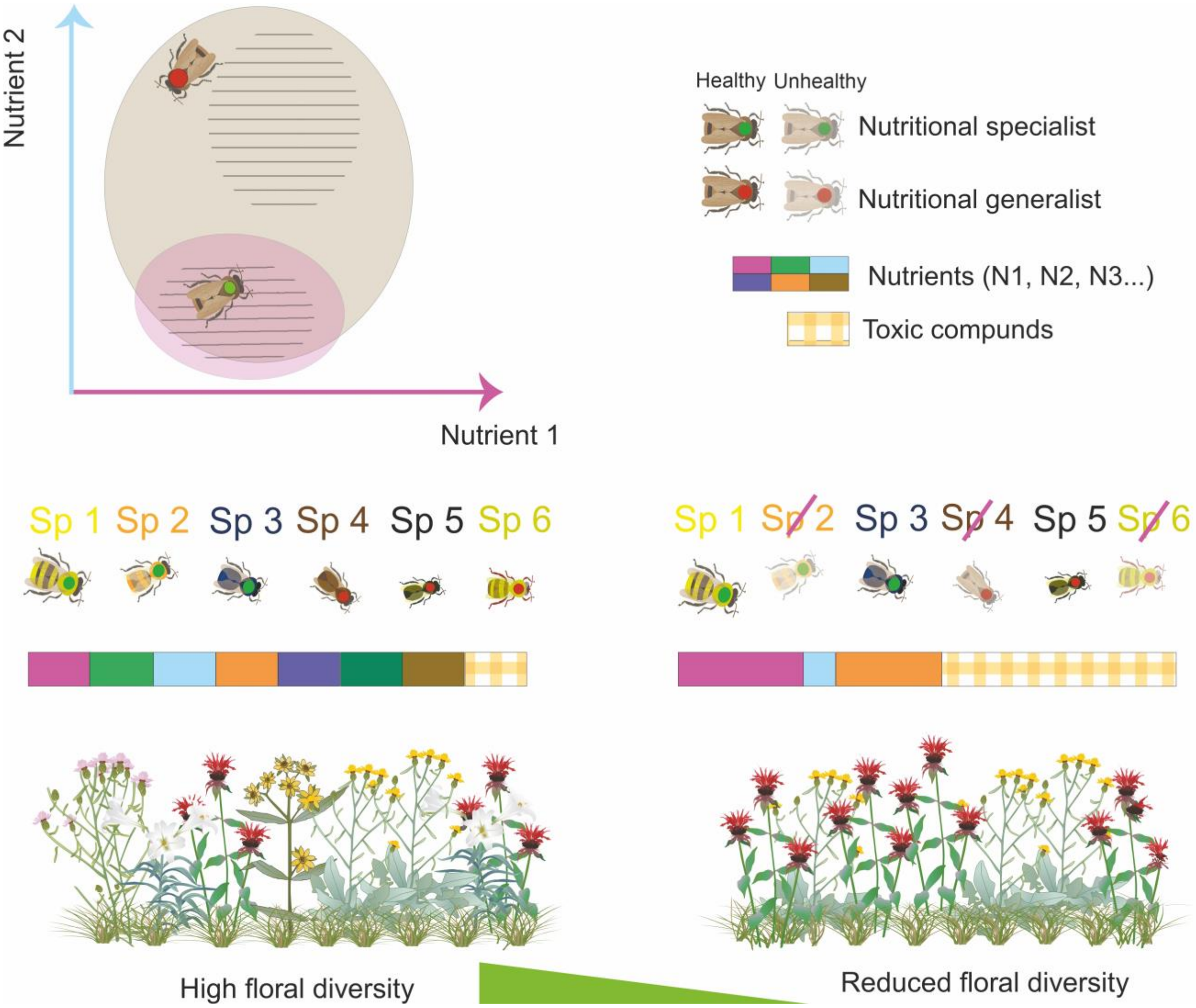

Fig. 3: Link between floral diversity, nutritional landscapes and nutritional niches. Bee species (Sp) with narrow nutritional niches (nutritional specialists, green dotted marked bees) and thus little tolerance for changes in the nutritional space (purple area in nutritional space) are likely to be more susceptible to changes in the floral diversity than bee species with broad nutritional niches (nutritional generalists, red dotted marked bees) and a higher tolerance (brown area in nutritional space). The nutritional landscape of each environment is reflected by different colours of nutrients (bars in the centre). It is more diverse, balanced and thus provides more nutritional niches in florally diverse environments (left) compared to environments with reduced floral diversity (right). Florally diverse environments also enable bees to dilute toxic compounds (e.g., harmful plant secondary metabolites or pesticides) exposing them to overall less harmful compounds than environments with reduced floral diversity.

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 (Fig. 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 harbour 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, e.g., through increasing the proportion of protein in diets [114,115] or collecting resources with antimicrobial plant secondary metabolites [25,33,116]. In fact, the bees' resilience to diseases, but also 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 rather predict a three-way-interaction between nutrition, health and stressors, such as pathogen loads, which may result in different scenarios, such as linear and non-linear shifts in nutritional niches (Fig. 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 different stressors, which will result in altered nutritional niche spaces (Fig. 4). Consequently, floral/nutritional diversity may convey health benefits to generalist and specialist bee species through providing a variety of nutritional niches, which can increase nutritional flexibility and resilience when facing additional stressors.

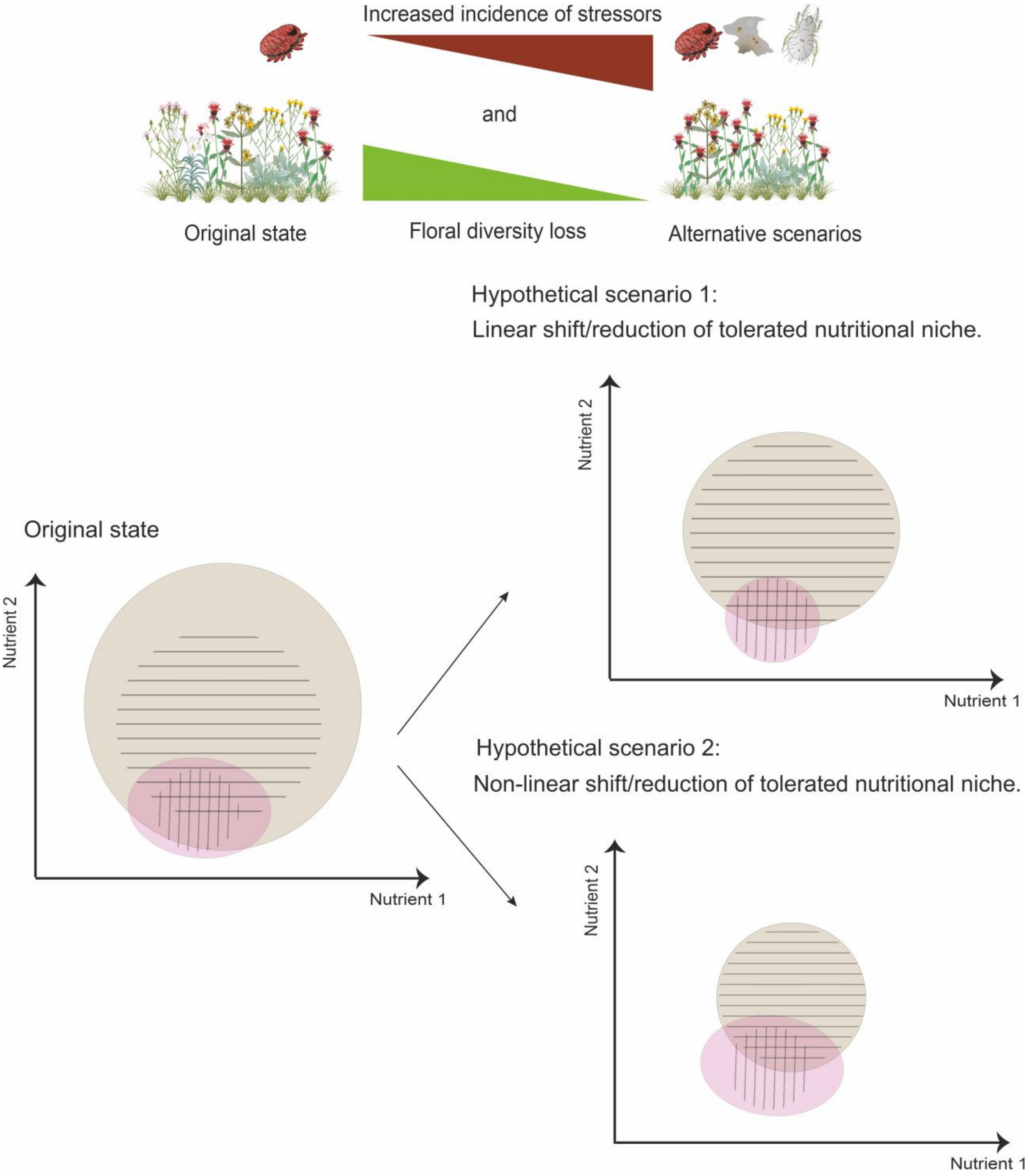

Fig 4: Interaction between nutrition, health and stressors altered in addition to florally impoverished landscapes. Hypothetical scenarios depict linear and non-linear changes in nutritional niches of nutritional specialists (purple area) and generalists (brown area) following loss of floral diversity plus additional stressors (e.g. increased pathogen prevalence). Stressors may simply decrease the bees' tolerated nutritional niche space without affecting their optimal nutritional niches (scenario 1). Alternatively, it may result in a non-linear 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, while the optimal and tolerated nutritional niche of another species may remain unaffected in the presence of additional stressors (scenario 2). This may in turn result in a species-specific likeliness of becoming (locally) extinct under stressed conditions. To our knowledge there is hitherto no study that assessed nutritional niche shifts in different bee species exposed to different stressors.

Concluding Remarks and Outstanding Questions

Through integrating different physiological health measures and nutritional niches with floral diversity and composition, we can reveal meaningful interactions between nutritional landscapes and bee health (Fig. 3, Fig. 4). We can also investigate hitherto unknown interactive effects between different physiological health parameters, such as stoichiometry, physiology and disease loads.

This integrative approach will enable better tailored management recommendations for bee conservation. Until now, most conservation measures implicitly assumed that wild bee populations can be enhanced by increasing floral diversity [8]. This can however lead to shortages in 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 e.g. 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, with strong links indicating 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, e.g. 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 little understood how such global change induced shifts in phenology or resource use interact with bee health. Can we use knowledge on links between species-specific nutritional niches (breadth) and health to predict which bees will be able to forage in specific landscapes? How can we adjust floral enhancement schemes to take into consideration additional factors besides 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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Author contributions

M.A.P. drafted the manuscript, developed figures and tables and coordinated co-authors 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.

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