scientific community to identify constructive ways forward. On the topic of food security and biodiversity conservation, we believe that what is needed, most of all, is qualitative change – we need to think in an entirely different, more holistic, and more visionary way about how to achieve good outcomes for both food security and biodiversity conservation. It is with this overall outlook in mind that we respond to the concerns raised by Seppelt *et al.* [1].

First, Seppelt *et al.* [1] argue that biodiversity and food security are both multidimensional concepts, and that simplifying these to single dimensions is sometimes inappropriate. This point is correct in principle, but it does not invalidate our approach any more than it would invalidate any of a vast number of cases where heuristics are used to navigate an otherwise overwhelmingly complex reality. Indeed, if the social–ecological approach proposed by us is too simple, then surely this applies even more so to the dominant approaches of land sparing/sharing or sustainable intensification.

Biodiversity is indeed more than species diversity, but for many purposes, species diversity is a reasonable first proxy. In our paper, we argue that both farmland species and other species (e.g., forest specialists) need to be considered in conservation strategies.

For food security, the situation is more controversial. We disagree that yields versus nutrition are competing measures of food security. Food security implies sufficient quantity, quality, and access to food – not one at the expense of the other, but rather, the simultaneous satisfaction of multiple important conditions. In that sense, food security itself is perhaps not multidimensional, but rather the factors that determine it are manifold. This very point was made in our discussion on land grabbing: just increasing yields as an objective in its own right, without considering for whom (or similarly, of which crops), is meaningless. The variable 'yield gap' highlighted as an example by Seppelt *et al.* [1] thus is a classic distraction from a holistic analysis of food security, in that it is easily generated but says nothing about other important determining factors of food security. In short, (i) heuristics such as our framework need to be relatively simple or they stop being useful, and (ii) like many other concepts, the concept of 'food security' is not ambiguous, but rather has a multidimensional basis, and all of these multiple dimensions matter at the same time.

Second, are the archetypes presented in our paper realistic [1]? Our response here is that what dominates right now is never a good template to identify what might be possible in the future. Humankind would never have made it to the moon by only checking what was realistic at the time, simply because reaching the moon had never been done. In our paper, we drew the parallel to scenario planning, where the aim is to clarify and expand an option space, which can help to think creatively about the dynamics of complex systems and possible options to influence their trajectories. Such an approach is useful, most of all, to expand our thinking beyond 'status quo realism', which can easily lock us into path dependencies such as (not so) 'sustainable' intensification. If we want to get out of the patterns that got our planet into trouble in the first place, we need to allow ourselves to explore options that are not immediately apparent.

Finally, questions were raised about how to navigate between archetypes [1]. We are the first to admit that we have not worked this out in detail – but the general principle that drivers and feedback associated with certain dynamics need to be activated or overcome seems useful to us, because it offers a fresh perspective to the problems at hand. Additional nuance will come from further exploring this framework, and indeed, applying it empirically to real-world landscapes. It is always easy to criticize a new framework for not being complete, but it requires time and effort to gradually fill the gaps. The questions are whether the foundation we laid out is fundamentally different from the mainstream, and whether this might offer an alternative, useful way forward. If so, it is up to future research to empirically apply and further refine and improve the framework we laid out. What we put forward is not an end point, but hopefully a useful, alternative lens to investigate and resolve a problem that humanity widely agrees on needs to be tackled.

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Letter
The Multifaceted Nature of Vulnerability in Managed Bees: A Response to Klein *et al*.

Ryan J. Leonard[1,*] and Dieter F. Hochuli[1]

In their recent review in *TREE* [1], Klein *et al*. make an invaluable contribution to our understanding of why bees are

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particularly vulnerable to environmental stressors, bringing to wider attention the putative roles of neurobiology and foraging behavior. They discuss how the central-place foraging strategy used by most bees places particularly heavy demands on the cognitive capacities underpinning complex behaviors associated with learning, memory, and navigation. While we strongly agree these high cognitive demands influence vulnerability, we would like to expand on Klein *et al*.'s review and highlight additional important mechanistic drivers. Our hope is that this will stimulate further discussion on a topic that has emerged as a priority research area.

Vulnerability is typically defined as the degree to which a system is susceptible to, or unable to cope with, injury or damage and is a function of exposure to a stressor(s), system sensitivity, and system resilience [2]. For the eusocial species that Klein *et al*. focus on (e.g., *Apis mellifera*), 'system' refers to the hive and vulnerability is typically measured at the individual level and extrapolated to the hive. Ultimately, the vulnerability of individuals is influenced not only by extrinsic factors, including the interaction between, and intensity of, environmental stressors, but also by intrinsic factors, including the biochemical, morphological, and behavioral traits of bees.

For managed bee populations, including some bumble- (e.g., *Bombus impatiens*) and stingless-bees (e.g., *Tetragonula carbonaria*), and several species within the Apidae group (e.g., *A. mellifera* and *Apis cerana*), the management practices used by beekeepers are critical extrinsic factors influencing vulnerability. In *A. mellifera*, for example, the almost universal practice of reusing wax combs allows contaminants to accumulate to highly toxic levels, especially when bee-keepers routinely use pesticides. Larvae of *A. mellifera* reared in old brood combs contaminated with pesticides experience significantly greater brood mortality, delayed larval development, and reduced adult emergence and longevity [3]. Additionally, rising demand for the crop pollination services provided by species such as *A. mellifera* and *A. cerana* is intensifying management practices, thereby increasing the stress experienced by, and vulnerability of managed bee populations [4]. Commercial beekeepers routinely ship bees great distances following crop blooms, meaning bees must continuously readapt to new climates and floral resources. This form of migratory management can increase levels of oxidative damage, thereby affecting colony health and productivity [4], factors that ultimately increase vulnerability. Contrastingly, beekeepers may also reduce vulnerability by, for example, selecting for and breeding resilient bee stock. This practice is increasingly used in Europe, where beekeepers are selecting for behavioral traits in *A. mellifera* such as adult grooming and brood cleaning, which increase resilience to the parasitic mite *Varroa destructor* [5].

Genetic background is a significant intrinsic factor influencing both intra- and interspecific vulnerability to environmental stressors. Genetic variants of *A. mellifera*, including Carniolan, Russian, and Italian bee stocks, exhibit different vulnerabilities to pesticides [6]. Similarly, *A. mellifera*, *Bombus terrestris audax*, and *Osmia bicornis* exhibit interspecific differences in vulnerability to certain heavy metals and pesticides [7]. Furthermore, compared with most insect genomes, bees, including both eusocial (e.g., *Bombus huntii*) and solitary species (e.g., *Megachile rotundata*) are deficient in detoxification genes [8]. This deficit is hypothesized to render bees more vulnerable to the synergistic effects of multiple pesticides compared with other insect groups [9].

Central-place foraging is a key factor influencing bee vulnerability, but is only one of several important behaviors requiring consideration. The underground nesting behavior of many non-*Apis* bees, including solitary species, such as *Colletes inaequalis*, increases their vulnerability by increasing exposure to xenobiotic residues in the soil. Furthermore, these non-*Apis* species are typically floral specialists, which could increase exposure to environmental stressors by increasing foraging time when host plants are limiting.

For eusocial bee colonies, the adult work force is divided between younger nonforaging hive bees that rear brood and maintain the hive and older, foraging bees that spend their time outside the hive collecting food. This division of labor coupled with age-dependent transitions in physiology, including metabolism and the activity of P450 enzymes [10], creates situations where vulnerability is age and developmental stage specific. Given that the proportion of nonforaging to foraging bees is plastic, varying in response to season and food availability [11], colonies with more foraging bees may suffer greater net vulnerability to environmental stressors. Vulnerability to environmental stressors is further influenced by feeding behaviors within these colonies, such as trophallaxis, where returning bees unload liquid food to hive mates, including larvae, via mouth-to-mouth contact. This behavior is a key factor increasing *N. ceranae* transmission within *A. mellifera* hives [12].

The extent to which bees are vulnerable to environmental stressors depends on a range of factors beyond the sensitive cognitive capacities that Klein *et al*. discuss. Ultimately, the key to understanding the mechanistic drivers of bee declines involves integrating myriad genetic, biochemical, behavioral, and anthropogenic factors.

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