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REVIEW PAPER

The risk of threshold responses, tipping points, and cascading failures in pollination systems

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Abstract

Growing evidence of global declines in pollinator abundance and diversity has raised concerns about the resilience of pollination systems. When subjected to stressors, each nested component of the pollination system (communities, populations, and colonies) can respond in either a smooth linear fashion, or in an abrupt nonlinear manner. Threshold and tipping point responses to stress are of particular concern because they result in sudden changes with little warning; such changes may lead to persistent non-functional states that are difficult to reverse. Here, we review evidence for threshold and tipping point responses at the colony, population and community levels of the pollination system. We find that while there are strong theoretical reasons to expect tipping point and threshold responses at all three levels of the pollination system, evidence in the field is lacking for all levels except the colony level. While this is encouraging, caution is still warranted as tipping point and threshold responses—by their very nature—may not be apparent until they are underway. Moreover, we propose that the interaction of nonlinear stress responses across different levels of the pollination system can increase the risk of cascading failures. We therefore suggest a cautious approach toward the management of pollination systems. Since environmental change will almost certainly continue to accelerate, understanding the potential for thresholds, tipping points and cascading failures is key to safeguarding global pollination systems.

Keywords Pollinator · Plant-pollinator community · Bee colony · Nonlinear · Interacting stress · Collapse

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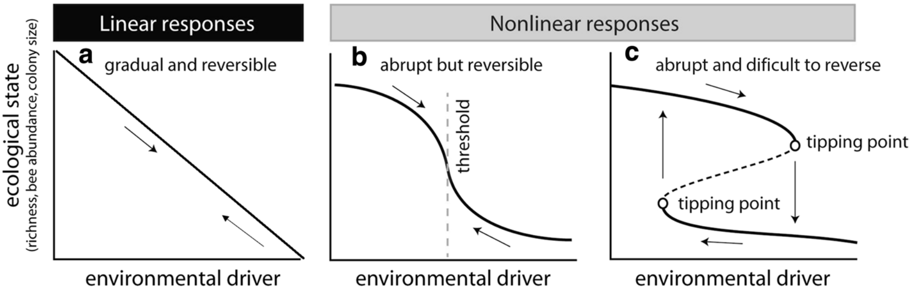

Fig. 1 Type of responses in ecological systems due to a change in an environmental driver. **a** Linear decline. **b** Nonlinear change of ecological state after the system passes a threshold. **c** Tipping point nonlinear response. At the tipping point, ecological systems shift from one state (upper branch) to the alternative state (lower branch). Black solid lines indicate stable equilibrium states, whereas black dotted lines represent the unstable threshold that separates the basins of attraction of different stable states. The open circles indicate the tipping points at which transitions between alternative states occur. Adapted from Scheffer et al. (2001)

Introduction

Pollinating animals have long been recognized for their ecological and economic importance. In temperate regions, 78% of flowering plants are animal pollinated; this number rises to 94% in tropical communities (Ollerton et al. 2011). The global economic value of animal pollination is estimated at 153 billion Euros annually (Gallai et al. 2009) with approximately 75% of the world's major crops being moderately to totally dependent on animal pollination (Klein et al. 2007). The past century has seen massive and accelerating levels of human-induced environmental change, much of which directly or indirectly impacts pollinators and the ecosystem services they provide. There is convincing evidence of ongoing global declines in many pollinator taxa (Biesmeijer et al. 2006; Carvalheiro et al. 2013; reviewed in Potts et al. 2010; Sánchez-Bayo and Wyckhuys 2019).

Pollinators are assailed by an array of interacting stressors from habitat loss and alteration to disease, invasive species, poor nutrition, exposure to agrochemicals and climate change (reviewed in Vanbergen 2013; Goulson et al. 2015; González-Varo et al. 2013). In the short term it is unlikely that these stressors will decrease; indeed, many (such as habitat loss and climate change) are on course to continue into the foreseeable future. Safeguarding our pollination systems against this backdrop of accelerating global change requires an understanding of how pollination systems may respond to environmental stressors.

From a conservation perspective, it is not only the speed and magnitude of system response that is important, but also the shape of the response function. Responses to environmental stressors can be broadly divided into three major groups: linear responses, threshold responses, and tipping point responses (Scheffer et al. 2001) (Fig. 1). If a response function is linear, incremental changes in environmental factors will affect the system in proportional and predictable ways (Fig. 1a). In linearly responding systems, reducing stressors can recover the system to its former state in the same way that a stretched rubber band will return to its initial shape once pulling is stopped.

In contrast, nonlinearly responding systems can change disproportionally to small changes in stressors with little or no warning. Threshold responses are a type of nonlinear response characterised by a sharp -but still reversible- change in system behaviour once a threshold stressor value is surpassed (Fig. 1b). Tipping point responses go one step further: they occur when a small change in the environmental stressor triggers a dramatic shift into an alternative state that is difficult to reverse (Fig. 1c). This means that a system that has shifted into an alternative state will not return to its previous state, even if conditions revert to pre-transition levels. This phenomenon is known as ‘hysteresis’ and encapsulates the idea that the pathway to system degradation may not be the same as the pathway to restoration (Scheffer et al. 2001).

In this paper, we synthesize theoretical and empirical evidence for nonlinear responses in pollination systems with emphasis on thresholds and tipping points. We conceptualise a pollination system as a hierarchical set of nested systems (‘a system of systems’) where pollinator-plant communities are made up of diverse and interacting pollinator and plant populations, which are, in turn, made up of interacting individuals that can adapt and exchange information. In the particular case of social insects, such as bumble bees, stingless bees and honeybees, an extra level of organisation is added as individuals are also organised into colonies, and colonies may interact with other colonies within a population. At each level of organisation there are a separate set of dynamics that create feedbacks across levels and result in emergent behaviours that cannot be anticipated if each part of the system is considered in isolation (Levin 1998). In our framework, we explicitly consider the potential that impacts on one level of the system can cascade through to other levels.

Our first goal was to identify empirical and theoretical examples of thresholds and tipping point responses at each level of the pollination system. Next, we explored the potential for threshold responses to propagate across levels of the pollination system, arguing that we need to explicitly consider their interactions and cascading effects. We conclude by highlighting several open research questions that could improve our understanding of the management and conservation implications of threshold and tipping point responses in pollination systems.

Threshold and tipping point responses in pollination systems: literature search

Evidence for strong nonlinear effects in pollination systems is likely scattered across many different literatures. We thus used a broad search strategy to capture the current state of evidence. We conducted searches of Web of Science using key words that describe strong nonlinear responses (“phase transition” or “bifurcation” or “tipping point” or “critical transition”) and at least one of the following additional terms: “pollinator”, “pollination”, “Hymenoptera” (bees, ants, wasps and sawflies), “Diptera” (true flies), “Lepidoptera” (moths and butterflies) and “Coleoptera” (beetles). We chose the search terms Coleoptera, Diptera, Lepidoptera and Hymenoptera as we wanted to find papers that dealt with aspects of pollinator life history or physiology that could be missed with the “pollination” and “pollinator” search terms. We choose these four orders in particular as they are responsible for the majority of insect pollination (Rader et al. 2016). In addition, we reviewed references obtained from the citation list of each paper. We also used knowledge of our respective fields to find additional examples that were not discovered using our search terms.

Empirical evidence for tipping points and thresholds in pollinations systems

We found only 1 empirical example of a tipping point or threshold response to stress at the colony level (Bryden et al. 2013), and no empirical examples at the population or community level. Although several studies investigated mechanisms that could plausibly lead to strong nonlinear declines (e.g. Whitehorn et al. 2009; Perry et al. 2015), they did not collect the time series data and/or do the analyses necessary to confirm thresholds or tipping points. Since a wide variety of terminology is used to describe nonlinear stress responses, we cannot rule out the possibility that empirical examples exist but were not discovered by our search terms. While we did not find strong experimental or observational evidence for tipping point or threshold stress responses, we did discover evidence from theoretical studies. We argue that the 'ingredients' needed for nonlinear responses, such as strong positive feedback mechanisms (see Glossary), exist at each level of the pollination system. In the sections below, we discuss the theoretical knowledge base for threshold responses at the colony, population and community level.

Threshold responses at the colony level: collapse of a pollinator society

Despite the fact that the majority of bee species are solitary, social species such as honeybees, stingless bees and bumble bees are often crucial pollinators in managed and natural ecosystems (e.g. Olesen et al. 2007; Geslin et al. 2017). Social bee species are sometimes considered more resilient to environmental stressors than solitary species due to their 'superorganism resilience', where the large number of non-reproductive workers acts as a buffer against stress (Straub et al. 2015). If an individual bee dies, another rapidly takes her place; indeed, in several species there are exquisite physiological and/or behavioural mechanisms that allow individuals to alter their developmental trajectory to replace lost nest mates (Robinson 1992). However, it is becoming increasingly clear that social bees may, under certain conditions, suffer from colony collapses due to positive feedback mechanisms within the colony (Bryden et al. 2013; Perry et al. 2015; Myerscough et al. 2017).

One of the clearest examples of a positive feedback leading to colony collapse comes from the European honeybee (*Apis mellifera*). In honeybees, the task a worker bee performs is dictated, in part, by her age. Younger workers typically perform in-nest tasks, while the oldest workers function as foragers (Huang and Robinson 1996). Up to a critical mortality rate, colonies can maintain a stable population size by replacing lost workers with sub-optimally performing precocious foragers (bees that accelerate their development to become foragers earlier than usual) (Khoury et al. 2011; Barron 2015; Perry et al. 2015; Myerscough et al. 2017). However, precocious foragers are not as proficient as normal-aged foragers and thus suffer from a higher mortality rate. Once the threshold mortality rate is surpassed, the colony population declines precipitously as the workforce becomes increasingly young and ineffective. This leads to a subsequent decline in food levels, which in turn stimulates the recruitment of even younger bees into the foraging force (Perry et al. 2015). This death spiral continues until the colony's adult workforce is depopulated and the colony ceases to function (Fig. 2a). While compelling modelling strongly suggests the existence of tipping points or thresholds in stressed honeybee colonies, strong empirical verification is lacking.

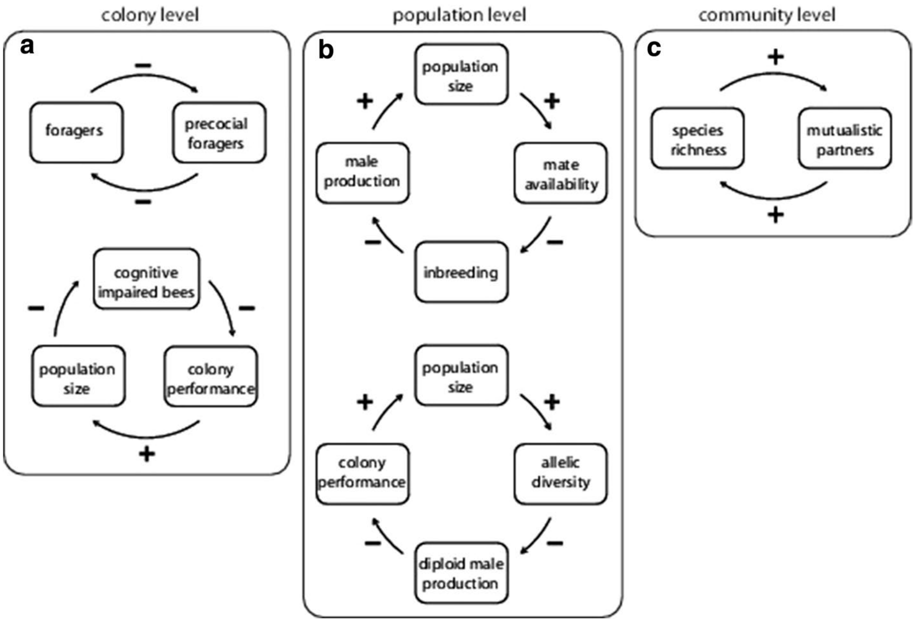

Fig. 2 Known and suggested positive feedbacks that can possibly cause threshold and tipping point responses in pollination systems. Boxes contain system components, while arrows indicate interactions between components. Minus signs depict negative relationships between components, while plus signs indicate positive relationships. The product of the signs along the direction of the arrows results in a positive feedback process that may constitute a mechanism for causing threshold behaviour at each level of the pollination system

Models suggest that a high rate of forager loss (upwards of 30% of foragers dying per day) would be needed to push honeybee colonies over the threshold (Perry et al. 2015). While this is an extreme mortality rate (more than double the background mortality rate), it is not unreasonable, especially when we consider that bees (and other central-place foragers) are thought to be particularly sensitive to stressors that impair their cognitive function (Klein et al. 2017). Cognitively impaired bees suffer high mortality because they cannot effectively navigate, orient, communicate and/or learn. A wide range of stressors are known to impact the cognitive function of bees including pesticides, heavy metals, parasites and pathogens, malnutrition and low temperatures during development (Tautz et al. 2003; Gegear et al. 2006; Jin et al. 2015; Burden et al. 2016; Klein et al. 2017). At least one study has found experimental evidence that cognitive impairment alone is enough to trigger colony collapse in bumblebees, where chronic exposure to sub-lethal doses of neonicotinoid insecticides resulted in colony collapse when the number of cognitively impaired bees exceeded a critical threshold (Bryden et al. 2013).

Threshold responses at the population level: Allee effects and extinction vortices in pollinators

In 1930, Allee observed that many species suffer from low or negative population growth when their population size is small (Allee et al. 1949; Courchamp et al. 1999). Populations of small size would then suffer 'Allee effects' which drive them abruptly to extinction. At least six mechanisms underlying Allee effects have been identified so far, including mate limitation, cooperative defence, predator satiation, cooperative feeding, dispersal, and habitat alteration (Kramer et al. 2009). Most of these mechanisms could affect the population dynamics of pollinators. Butterflies, for example, may experience Allee effects due to mate limitation because individuals become reproductively active at different times of the year (Calabrese and Fagan 2004). At low population densities, more individuals find themselves reproductively isolated thus reducing the population growth rate and further decreasing the mating probability of individuals, ultimately leading to a spiral toward extinction.

It is also possible for a population to be subject to multiple simultaneous Allee effects (Berec et al. 2007). It is easy to imagine situations where an environmental driver (e.g. insecticide use) causes an increase in mortality rate which then sets off an extinction spiral as Allee effects become more pronounced. Although the prevalence and magnitude of Allee effects amongst pollinators is unknown, it seems likely that they could increase the risk of extinction in pollinator populations at low densities.

In addition to Allee effects, a nonlinear shift to extinction at low densities can be enhanced by the combined effects of genetic diversity loss, environmental stochasticity, and demographic stochasticity. These elements create an 'extinction vortex' (Fig. 2b) that can cause accelerating decline leading to extinction (Gilpin 1986). Extinction vortices have been implicated in the extinction of 10 vertebrate species (Fagan and Holmes 2006).

Pollinating insects in the order Hymenoptera may be at risk of a type of extinction vortex caused by their haplo-diploid sex-determination mechanism. In hymenopterans, sex is determined by the fertilization status of the egg; males are haploid and result from unfertilised eggs while females result from fertilized eggs and are diploid. In single locus complementary sex determination (sl-csd) (widespread in the Hymenoptera and believed to be ancestral), sex depends on the allelic composition of a single gene known as the csd (Van Wilgenburg et al. 2006). If a fertilized egg is heterozygous at the csd, it will develop into a normal diploid female (Hedrick et al. 2006). However, if the offspring is homozygous at the csd, the result is an inviable or sterile diploid male (Hedrick et al. 2006). A female that mates with a male with whom she shares one of her sex determination alleles will produce 50% inviable diploid males.

The production of diploid males results in mate limitation for fertile females, leading to decreased population size. If the population size continues to decline, genetic diversity at the csd also declines (Fig. 2b). As a consequence, the probability that a female will mate with a 'matched male' increases, thereby increasing the frequency of diploid males (Chapman and Bourke 2001). The resulting positive feedback loop, termed 'the diploid male vortex', ultimately drives the population to extinction at rates more than an order of magnitude higher than that caused by other forms of inbreeding depression (Zayed and Packer 2005).

Studies of inbred bumblebee colonies found that increased diploid male production was associated with a slower colony growth rate, shorter survival time and decreased offspring production suggesting the presence of an incipient diploid male vortex (Whitehorn et al. 2009). Darvill et al. (2012) found that the presence of infertile triploid male bumble bees (the product of a mating between a diploid male and a normal female) was negatively correlated with patch size, suggesting that environmental degradation caused an increase in triploid males as predicted by the diploid male vortex.

The risk of entering a diploid male vortex is influenced by several parameters. Modelling suggests that the number of diploid males in a population is driven more strongly by male flight radius than by the number of sexual alleles (Faria et al. 2016). The impact of male flight radius on allelic diversity is more pronounced in small patches than in larger patches (Faria et al. 2016). These results suggest that populations of smaller hymenopterans, which tend to have smaller flight ranges (Greenleaf et al. 2007), living in fragmented environments may be at increased risk of the diploid male vortex. The risk of diploid male vortices is exacerbated in social hymenopterans such as honeybees, stingless bees and bumble bees because only one or a few individuals within the colony actively engage in reproduction. As a result, effective population size can be orders of magnitude lower than the number of individuals observed in the field (Chapman and Bourke 2001).

Despite the dire implications of the diploid male vortex, some studies suggest that inbred populations can escape extinction. For example, Boff et al. (2014) found no relationship between island isolation and diploid male production in an orchid bee species even though genetic diversity was lower on islands. Similarly, Elias et al. (2010) found no evidence for extinction proneness in parasitoid wasp populations containing high numbers of diploid males. Despite a massive population bottleneck, invasive *Apis cerana* honeybees apparently avoided the diploid male vortex because balancing selection prevented the loss of rare csd alleles, thus restoring high levels of heterozygosity (Gloag et al. 2016).

A modelling study by Hein et al. (2009) suggested that in order for the diploid male vortex to start, four conditions needed to be met: (i) extreme fragmentation (i.e., populations are small and isolated), (ii) fixed sex ratio, (iii) low reproductive rate, and (iv) an inability on the part of females to detect the genotype of potential mates. Relaxing any of these conditions allows the population to escape the diploid male vortex. While these theoretical results may reduce the set of conditions under which a diploid male vortex can develop, the combination of even a weak diploid male vortex with unknown (so far) Allee effects might still lead to nonlinear responses to extinction in pollinator populations.

Threshold responses at the community level: extinction cascades and the collapse of pollinator communities

Pollinator communities are made up of interacting flowering plants and their pollinators whose interactions form ecological networks. Ecological networks provide a powerful conceptual tool for understanding the influence of environmental change on communities (Pascual and Dunne 2006). Such influence can take place due to changes in species composition, due to changes in realised species interactions, or to changes in the co-evolutionary processes that shape species interactions (Tylianakis and Morris 2017).

A characteristic property of pollination networks is their ‘nested’ structure, which means that specialist species tend to interact with a core composed of their most generalist partners (Bascompte et al. 2003; Bascompte and Jordano 2007). There is a substantial amount of theoretical literature that aims to understand the role of this nested topology on the stability and maintenance of biodiversity in mutualistic communities such a plant-pollinator networks.

Nested plant-pollinator communities have been shown to sustain high biodiversity (Bastolla et al. 2009) and to remain stable to random disturbances (Grilli et al. 2016) when compared to their random counterparts. On the other hand, nested pollination networks are more prone to nonlinear community-wide collapses compared to random networks without a nested structure (Lever et al. 2014). The increased susceptibility to collapse occurs because in highly nested communities a strong positive feedback can develop between pollinators that interact with the same plant. Simply put, in a nested pollination network there are more pollinator species that interact with the same plant species. These multiple shared interactions translate into a higher number of pollinator visitors for the plant. Since the mutualistic benefit to the pollinators is proportional to plant biomass, pollinators can survive high levels of stress because they are benefiting from indirect positive effects from their nested pollinator partners. The positive indirect effect sustains the existence of the pollinators up to a threshold stress level. Once the stress threshold is surpassed the indirect effects are no longer sufficient at which point all nested partners collapse to extinction.

Nonlinear species loss is expected to occur predominantly in communities where plants depend strongly on their pollinators and vice versa (obligate mutualism) (Lever et al. 2014; Dakos and Bascompte 2014). The nonlinear response is usually a sequence of cascading tipping point events where subsets of species go extinct from the community. In addition to nestedness, higher degree of connectance (i.e. the realised number of interactions over the total possible number in a network) results in a higher probability that these tipping point events become synchronised; this synchronicity ultimately leads to a single strong response affecting most of the community (Lever et al. 2014).

However, the pattern of community extinction in pollination systems under stress is not necessarily nonlinear. Species extinctions in plant-pollinator communities may follow a sequential pattern occasionally triggering cascading secondary extinctions, but where the overall pattern of species loss will appear gradual rather than abrupt. Whether or not the pattern of extinction is linear or nonlinear is influenced by each species' tolerance to extinction which in turn depends on the species' number of interactions and on its contribution to network nestedness (Saavedra et al. 2013). Memmott et al. (2004) found that removing pollinators from the most specialist to the least specialist species led to nonlinear response only after the majority of pollinators had been lost. However, when pollinators were removed in the reverse order (least specialist to most specialist) plant species went extinct more rapidly but in a linear manner.

Which extinction pattern (least specialist to most specialist or vice versa) is more likely to occur empirically? Aizen et al. (2012) found evidence that specialist pollinator species with a small number of interactions were more likely to disappear from isolated hills in Argentina. Using a 120 year-long dataset, Burkle et al. (2013) found that specialist pollinators were more likely to be extirpated, even when their host plants were still present. These empirical findings suggest that specialist pollinators are more likely to go extinct than generalists.

Other empirical studies show that invasive species can also alter the structure of pollination networks (Aizen et al. 2008) thus altering the probability of nonlinear collapses. For instance, exotic plants are often generalists, attracting a large number of pollinator species (Aizen et al. 2008; Stouffer et al. 2014) which can cause invaded communities to become significantly more nested (Bartomeus et al. 2008). If such patterns are generally true, the loss of specialist species or the invasion of generalist species may lead to strongly connected or nested networks that will be more likely to suffer strong, sudden synchronised collapses.

The prediction that networks may become prone to synchronised collapses neglects the potential buffering effect of 'interaction rewiring', which has been empirically shown to contribute to maintaining a constant network structure (Petanidou et al. 2008;

Timóteo et al. 2016). Interaction rewiring refers to a pollinator's ability to switch to alternative, less-preferred flowers if a preferred flower is unavailable; this behaviour might prevent a pollinator population from collapsing long enough for a preferred plant species to recolonise the site. Removal experiments conducted on simulated Mauritian pollination networks found that network stability can be maintained if species 're-wire' themselves by shifting to new plants when their preferred species becomes extinct (Kaiser-Bunbury et al. 2010).

More generally, adaptive foraging by pollinators can increase community persistence and robustness to species loss (Valdovinos et al. 2013). The potential of adaptive responses to stabilise communities will depend partly on the amount and conservation of trait variation within populations that could counteract phenological mismatches between plants and pollinators (Revilla et al. 2015) or the sensitivity of specific species to chemical pollution (reviewed in Leonard and Hochuli 2017). In addition, the effect of network rewiring via adaptive foraging will depend on the temporal and spatial variability of interactions (Tylianakis and Morris 2017). Climate-induced phenological shifts in plant-pollinator communities (Rafferty et al. 2013) can leave plants and pollinators without interactions even if the phenological shifts are small (Memmott et al. 2007) and could potentially increase the risk of a community collapse. So far there is insufficient empirical evidence and an incomplete theoretical understanding of the extent to which behavioural changes, flows between metacommunities, and trait variation act in concert to minimize the risk of threshold responses in pollination networks.

Open research questions

Our synthesis of theoretical and empirical evidence for nonlinear effects at different levels of the pollination system revealed several missing links and open questions. Below we address several areas where further knowledge could improve our understanding and management of thresholds and tipping points in pollination systems.

How prevalent are threshold and tipping point responses?

The existence of positive feedback loops at all levels of the pollination system lead us to the prediction that nonlinear stress responses should be common. Yet our literature search failed to find either experimental or observational evidence for nonlinear phenomenon at the population or community level and only one clear example from the colony level. Why is there a mismatch between prediction and experimental results? One possibility is that real pollination systems have a number of resilience mechanisms (discussed below) that allow for greater-than-expected tolerance to stressors. Nonlinear effects are also, by their very nature, difficult to observe until collapse is already underway. It is also possible that more examples of nonlinear responses exist but were not captured by our search terms. We suspect that researchers may not always frame their results in terms of thresholds and tipping points, even when studying systems that display these dynamics. Thus we suggest that future work focus on characterising the shape of stress responses at all levels of the pollination system; this would allow us to determine the actual prevalence of nonlinear effects.

Are there mechanisms that safeguard the stability of pollinator systems and reduce the risk of threshold and tipping point responses?

It is possible that resilience mechanisms (such as network rewiring, flexible caste determination, demographic rescue from nearby populations, conservation of genetic variation) are sufficient to delay or prevent the kind of nonlinear responses we describe throughout this manuscript. However the extent and nature of these mechanisms is still largely unknown. With further research, it may be possible to harness the stabilising ability of resilience mechanisms to buffer systems that are close to tipping points. In the case of urban and agricultural environments, this could take the form of selective planting of key plant species, or the provision of nesting habitat targeted at pollinator species known to play key roles in maintaining network resilience. On the conservation side, a thorough understanding of resilience mechanisms may allow us to prioritise the conservation of particularly important plant or pollinator species. At the colony level, understanding resilience mechanisms could lead to new interventions for preventing colony collapse in managed pollinators.

What kind of experiments and models can we develop to identify thresholds and tipping points at the colony, population and community level?

A key step towards safeguarding pollination systems is to identify which systems (if any) have a high risk of threshold or tipping point responses. This will require studies aimed at identifying key stressors, positive feedback mechanisms, nonlinear responses in observational data, and, if possible, experiments for establishing the existence of thresholds (Scheffer and Carpenter 2003). Here, we have tentatively identified places where there is potential for threshold or tipping point responses (Fig. 2), but further work is needed to confirm and expand our list. This is no easy task as experimental evidence is difficult to gather (Schröder et al. 2005). So far, studies using space-for-time substitution document gentle rather than nonlinear decreases in abundance of bee populations along disturbance gradients (Winfree et al. 2009). Nonetheless, such observed response patterns are few, remain difficult to obtain, and do not preclude the potential for threshold or tipping point responses. A meta-analysis of studies focused on long term population trends in pollinating species might be helpful in determining whether population declines tend to be linear or nonlinear. Unfortunately, longer term studies at the required resolution remain few and far between.

At the colony level, experiments that carefully apply varying stressors to bee colonies could be used to determine the shape of the colonies' response function. It would be particularly interesting to determine if different stressors result in different types of decline (e.g. threshold, tipping point, linear). The data needed to address these questions might already exist within data sets collected from the increasing number of sensor-enabled honeybee hives. In addition, modelling of bee colony demography and behaviour can be used to narrow down the list of potential stressors (and their interactions) that are likely to cause nonlinear declines; once candidate stressors have been identified in silico they can then be tested in the field (Henry et al. 2017).

Systems with tipping points can appear gradual in their responses to stress due to time lags (Hughes et al. 2013). Slowly responding populations under rapid environmental change, assisted by subsidies between metacommunities, can create temporal and spatial heterogeneities that may mask the nonlinear response of a bistable system. Indeed, threshold responses at the colony, population and community level will most likely be identified after terminal collapse processes are underway because timescales of ecological responses often do not match monitoring timescales. In addition, traditional census techniques (e.g. pollinator sampling) which do not take into account the potential for nonlinear responses might overestimate the true health of pollination systems. What is needed is a reliable way to identify the conditions that can increase the potential fragility of pollination systems (see Foley et al. 2015; Hunsicker et al. 2016). Research that combines modelling and field experiments can help achieve this goal.

Could interacting threshold and tipping point responses lead to cascading failures across scales in a pollination system?

Thus far we have described real and potential threshold or tipping point responses at colony, population and community levels in isolation (Fig. 2). However, levels of the pollination system can interact with one another, potentially accelerating global collapse (Fig. 3). It is well-recognised that different environmental stressors can interact with one another leading to synergistic effects on pollinator decline (e.g. Vanbergen 2013; Goulson et al. 2015; González-Varo et al. 2013). What is less well-studied is the potential for interactions between *different levels* of the pollination system to cause cascading effects that could increase the risk of pollination system collapse. Consider, for instance, that exposure to sublethal doses of insecticides could result in the collapse of wild bumblebee colonies if a threshold number of bees experience cognitive impairment. A local increase in the rate of colony failure could reduce population-level genetic diversity, initiating a diploid male vortex. This would trigger a decrease in the number of social bees, which are often important, highly connected components of the pollination network (Olesen et al. 2007). The loss of social bees could in turn initiate a series of plant extinctions, resulting in a cascade of secondary extinctions and, ultimately, community collapse.

How likely is this scenario? Although there are mechanisms that can buffer responses in the pollination system (like the ones described in the previous section), the extent to which resilience mechanisms can prevent collapse in the face of rapidly increasing environmental change remains unknown. Thus, research is needed to understand how different nonlinear responses of the pollination system at different scales might interact to cause global systemic collapses (Fig. 3).

Which pollinator species are most susceptible to threshold and tipping point responses at the population level?

Ideally, species or populations at risk of non-linear declines would be identified as potential targets for monitoring and conservation efforts. The hymenopteran sex determination system and the fact that hymenopterans are central place foragers could potentially make them more vulnerable than other insect groups to non-linear declines. However, we currently have little knowledge on how common extinction vortices and diploid male vortices are in nature nor do we know whether there are strong Allee effects in non-hymenopteran pollinators. At the colony level, experimental evidence

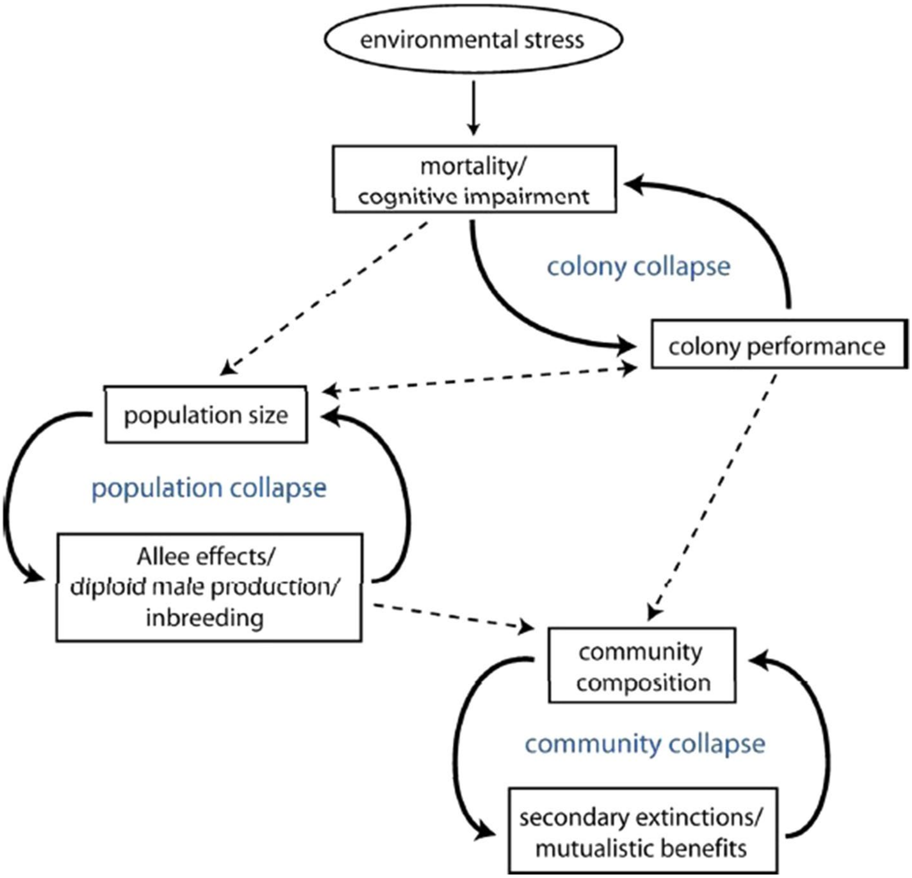

Fig. 3 Potential interconnections between positive feedbacks across different levels of organisation in the pollination system. Potential pathways are depicted via which environmental stresses can create a series of cascades that could increase the risk of collapse in a pollination system. Straight dotted arrows indicate interactions between different components. The solid curved arrows depict positive feedback processes. Allee effects, diploid male effects, and inbreeding are grouped together for ease of representation. Colony collapse occurs at the colony level, extinction vortices occur at the population level, and extinction cascades occur at the community level

for non-linear declines in colony health comes only from bumble bees; examples from other eusocial bee species are lacking although there is strong anecdotal evidence of rapid, nonlinear collapse in honeybees. Future research should determine if non-linear decline is a common feature of colony failures or if it is associated with particular stressors.

Another unresolved question is the extent to which eusocial species are more sensitive to environmental change than are solitary species. The potential fragility of social species is suggested by several recent analyses which found that sociality in bees is associated with a lack of resilience to land use changes (Williams et al. 2010; De Palma et al. 2015 although see Bartomeus et al. 2013 for a counter example).

Can we develop indicators for detecting impending pollinator collapse?

A possible method for assessing the risk of nonlinear responses in pollination systems comes from a set of methods called resilience indicators. Resilience indicators are based on statistical properties in the dynamics of a system that are symptomatic of an impending tipping point (Scheffer et al. 2009). The most prominent of these indicators are a rise in variance and autocorrelation, both of which are consequences of the slow response capacity of a system close to a tipping point (Wissel 1984). General frameworks for the application and use of these indicators are well-developed (Dakos et al. 2012), and they have been increasingly tested in lab and field experiments (Carpenter et al. 2011; Dai et al. 2012; Veraart et al. 2012; Gsell et al. 2016). In fact, these indicators have been shown to be generic for a range of ecological responses which makes them universal signals of degradation and loss of ecological resilience (Kéfi et al. 2013). Although so far there is no empirical testing of early warning indicators in pollination systems, these indicators have been theoretically shown to provide warning of impeding collapse both at the species and community level in simulations of empirically described plant pollinator networks under increasing environmental stress (Dakos and Bascompte 2014). At the colony level, recent advances in high frequency monitoring via sensor arrays inside managed bee colonies could be used to collect a large amount of data about colony health and performance. These metrics, alone or in combination, could serve as response variables, which could be analysed for early warning indicators.

It may be particularly difficult to adapt generic early warning indicators to the community and population levels of pollination systems because they require long and highly resolved records of population abundances; while such data may exist for some taxa in some places, it is difficult to collect and unavailable for the majority of pollinator species. Theoretical work suggests that it may be possible to decrease this complexity by reducing multispecies community dynamics to aggregated dynamics of plant and pollinators functional groups (Jiang et al. 2018). It remains, however, a challenge to achieve this simplification as it requires information on both the structure and the intensity of mutualistic interactions between plants and their pollinators.

Alternatively, response variables such as crop yield, fruit quality or farmer profit could be attractive targets for analysis with early warning indicators because they are relatively easy to collect and are likely linked to the functioning of the pollination system. Theoretically, it has been shown that changes in variance and autocorrelation of profit made by the exploitation of a harvested resource (e.g. fisheries) could better reflect the risk of collapse compared to changes in the same indicators of the state of the system itself (Richter and Dakos 2015). However, the use of yield, profit or quality might be complicated in agricultural systems because of human management. For example, growers might compensate for decreased crop yields due to the loss of wild pollinators by renting honeybee colonies; this would mask early warning signals in crop yield data. Indeed, it has been suggested that human adaptive management tends to keep agricultural systems close to their tipping points (Yletyinen et al. 2019), which might dampen the effectiveness of early warning indicators (Bauch et al. 2016). For this reason, a combination of ecological and socioeconomic response variables might be more useful (Yletyinen et al. 2019). For instance, in the case of agricultural pollination, monitoring could include the amount of money growers allocate to renting honeybee hives as well as floral visitation rate and/or pollinator species richness. Progress toward identifying suitable response variables will require simulation studies to explore scenarios of how the combination of abundance dynamics, structural community properties and human responses could create synthetic indicators for the risk of abrupt community responses that could be tested in the real-world.

How do we manage threshold responses in pollination systems?

Insight into how to best manage threshold effects in pollination systems could come from the experiences of managers in other ecological systems. In their analysis of 51 case studies, (Kelly et al. 2015) found that ecological systems with strong nonlinear responses could be best managed when the systems were relatively small (so that inputs and outputs could be more closely controlled), when routine monitoring programs were in place, and when systems were specifically managed with nonlinearity, thresholds and tipping points in mind.

Long term pollinator monitoring programs are urgently needed especially in poorly studied regions of the world such as Australia, Africa and Asia. A precautionary attitude should be taken when setting conservation targets for pollination systems, since declines may happen suddenly and, in the case of bistable systems, may be irreversible. Primary industries such as agricultural systems may be at particular risk for tipping points and the economic impacts of such collapse could be very high (Yletyinen et al. 2019). Thus, we suggest there is an urgent need for research into nonlinear responses in pollination-dependent crops.

The finding that management outcomes were most successful when managers specifically managed with thresholds and critical transitions in mind is promising; it is our hope that the present manuscript will encourage managers and researchers to think about potential threshold responses within pollination systems.

Concluding remarks

Tipping points and thresholds are, by their nature, difficult to detect until they have been passed. As such, the lack of direct field evidence for nonlinear effects at the community and population level should not lead to complacency. While pollination systems can be resilient against environmental change, collapse of these systems would be economically and ecologically catastrophic. Since environmental change will almost certainly continue to accelerate, understanding the mechanisms that can provoke collapses and developing techniques to prevent them may be key to safeguarding our pollination systems.

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Glossary

Allee effect	Allee effects occur when populations suffer from low or negative population growth when their population size is small
Alternative stable states	Different states of a system that can occur under the same external conditions
Bistability	The presence of two alternative stable states under the same conditions
Extinction vortex	A self-reinforcing process that drives population size downward to extinction
Hysteresis	The lack of reversibility in bistable systems; hysteresis refers to the phenomenon where the pathway to system degradation may not be the same as the pathway to restoration
Threshold response	A strong nonlinear response of a system to small changes in environmental conditions or stressors
Pollination system	Community composed of interacting pollinators (animals) and plants
Positive feedback	A self-amplifying process between two or more system components
Resilience indicators	Indicators of increasing instability in system dynamics that are used to detect proximity to tipping points (also referred to as early-warning signals)
Tipping point	A point where a runaway process (usually due to a positive feedback) pushes a system to flip into a different state

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