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1
2 **The risk of threshold responses, tipping points, and cascading**
3 **failures in pollination systems**
4

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6

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39 **Abstract**

40 Growing evidence of global declines in pollinator abundance and diversity has raised
41 concerns about the resilience of pollination systems. When subjected to stressors, each nested
42 component of the pollination system (communities, populations, and colonies) can respond in
43 either a smooth linear fashion, or in an abrupt nonlinear manner. Threshold and tipping point

44 responses to stress are of particular concern because they result in sudden changes with little
45 warning; such changes may lead to persistent non-functional states that are difficult to
46 reverse. Here, we review evidence for threshold and tipping point responses at the colony,
47 population and community levels of the pollination system. We find that while there are
48 strong theoretical reasons to expect tipping point and threshold responses at all three levels of
49 the pollination system, evidence in the field is lacking for all levels except the colony level.
50 While this is encouraging, caution is still warranted as tipping point and threshold responses
51 – by their very nature- may not be apparent until they are underway. Moreover, we propose
52 that the interaction of nonlinear stress responses across different levels of the pollination
53 system can increase the risk of cascading failures. We therefore suggest a cautious approach
54 toward the management of pollination systems. Since environmental change will almost
55 certainly continue to accelerate, understanding the potential for thresholds, tipping points and
56 cascading failures is key to safeguarding global pollination systems.

57

58 **Keywords:** pollinator, plant-pollinator community, bee colony, nonlinear, interacting stress,
59 collapse

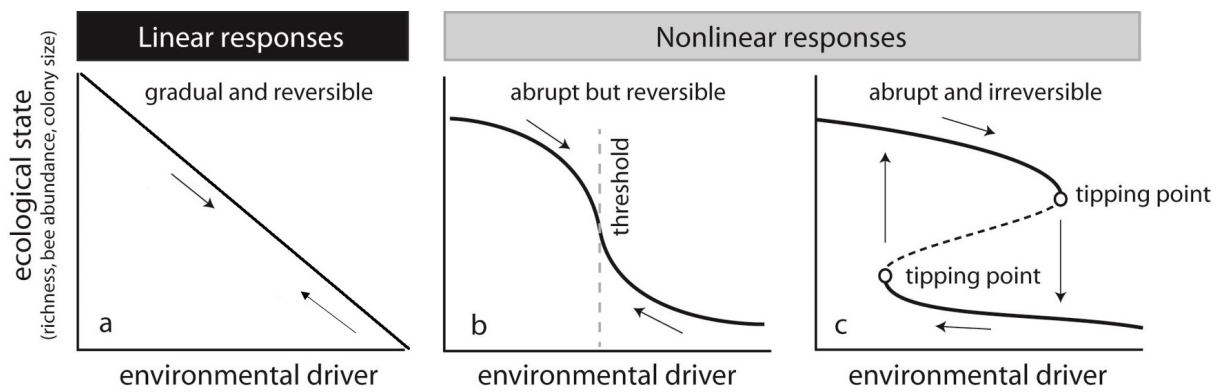
60 **Introduction**

61 Pollinating animals have long been recognized for their ecological and economic importance.
62 In temperate regions, 78% of flowering plants are animal pollinated; this number rises to 94%
63 in tropical communities (Ollerton et al. 2011). The global economic value of animal
64 pollination is estimated at 153 billion Euros annually (Gallai et al. 2009) with approximately
65 75% of the world's major crops being moderately to totally dependent on animal pollination
66 (Klein et al. 2007). The past century has seen massive and accelerating levels of human-
67 induced environmental change, much of which directly or indirectly impacts pollinators and
68 the ecosystem services they provide. There is convincing evidence of ongoing global declines
69 in many pollinator taxa (Biesmeijer et al 2006, Carvalheiro et al 2013, reviewed in Potts et al
70 2010 and Sanchez-Bayo and Wyckhuys 2019).

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

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

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



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97

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

105

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

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

126

127 **Threshold and tipping point responses in pollination systems: literature**
128 **search**

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

142

143 **Empirical evidence for tipping points and thresholds in pollinations systems**

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

157

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

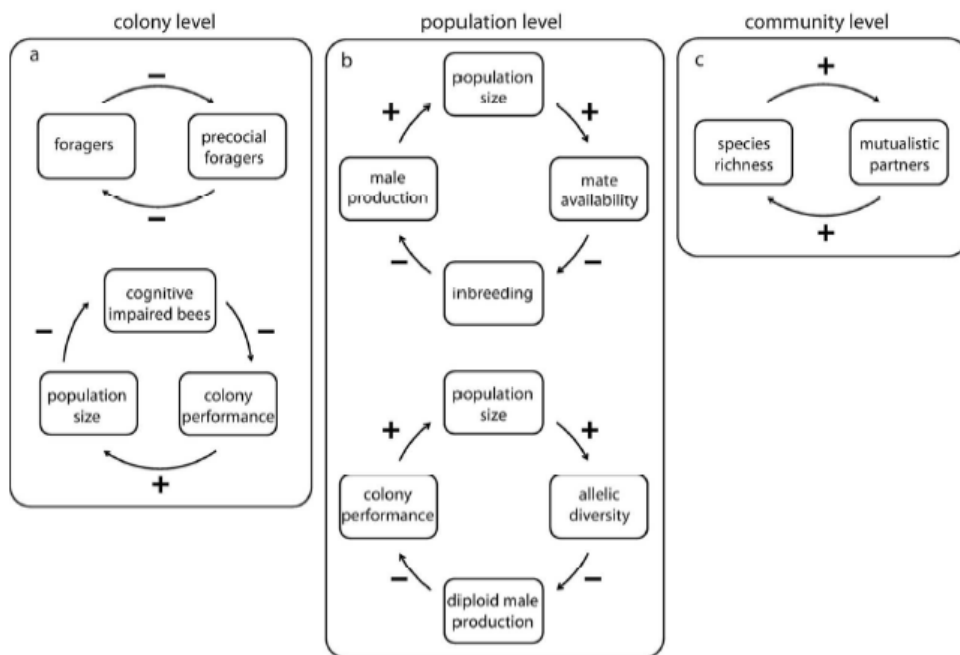
159 Despite the fact that the majority of bee species are solitary, social species such as honeybees,
160 stingless bees and bumble bees are often crucial pollinators in managed and natural
161 ecosystems (eg. Olesen et al. 2007; Geslin et al 2016). Social bee species are sometimes
162 considered more resilient to environmental stressors than solitary species due to their
163 'superorganism resilience', where the large number of non-reproductive workers acts as a
164 buffer against stress (Straub et al. 2015). If an individual bee dies, another rapidly takes her
165 place; indeed, in several species there are exquisite physiological and/or behavioural

166 mechanisms that allow individuals to alter their developmental trajectory to replace lost nest
167 mates (Robinson 1992). However, it is becoming increasingly clear that social bees may,
168 under certain conditions, suffer from colony collapses due to positive feedback mechanisms
169 within the colony (Bryden et al. 2013, Perry et al. 2015, Myerscough et al. 2017).

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

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

198 threshold (Bryden et al. 2013).



199
200

201 **Figure 2.** Known and suggested positive feedbacks that can possibly cause threshold and
202 tipping point responses in pollination systems. Boxes contain system components, while
203 arrows indicate interactions between components. Minus signs depict negative relationships
204 between components, while plus signs indicate positive relationships. The product of the
205 signs along the direction of the arrows results in a positive feedback process that may
206 constitute a mechanism for causing threshold behaviour at each level of the pollination
207 system.
208

209 **Threshold responses at the population level: Allee effects and extinction** 210 **vortices in pollinators**

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

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

229 In addition to Allee effects, a nonlinear shift to extinction at low densities can be
230 enhanced by the combined effects of genetic diversity loss, environmental stochasticity, and
231 demographic stochasticity. These elements create an ‘extinction vortex’ (Fig. 2b) that can
232 cause accelerating decline leading to extinction (Gilpin 1986). Extinction vortices have been
233 implicated in the extinction of ENREF_1810 vertebrate species (Fagan and Holmes 2006).

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

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

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

259 The risk of entering a diploid male vortex is influenced by several parameters.
260 Modelling suggests that the number of diploid males in a population is driven more strongly

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

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

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

286
287

288 **Threshold responses at the community level: extinction cascades and the** 289 **collapse of pollinator communities**

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

296 A characteristic property of pollination networks is their ‘nested’ structure, which
297 means that specialist species tend to interact with a core composed of their most generalist
298 partners (Bascompte et al. 2003, Bascompte and Jordano 2007). There is a substantial amount

299 of theoretical literature that aims to understand the role of this nested topology on the stability
300 and maintenance of biodiversity in mutualistic communities such a plant-pollinator networks.

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

315 Nonlinear species loss is expected to occur predominantly in communities where
316 plants depend strongly on their pollinators and vice versa (obligate mutualism) (Lever et al
317 2014, Dakos and Bascompte 2014). The nonlinear response is usually a sequence of
318 cascading tipping point events where subsets of species go extinct from the community. In
319 addition to nestedness, higher degree of connectance (i.e. the realised number of interactions
320 over the total possible number in a network) results in a higher probability that these tipping
321 point events become synchronised; this synchronicity ultimately leads to a single strong
322 response affecting most of the community (Lever et al 2014).

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

334 Which extinction pattern (least specialist to most specialist or vice versa) is more
335 likely to occur empirically? Aizen et al (2012) found evidence that specialist pollinator
336 species with a small number of interactions were more likely to disappear from isolated hills
337 in Argentina. Using a 120 year-long dataset, Burkle et al (2013) found that specialist

338 pollinators were more likely to be extirpated, even when their host plants were still present.
339 These empirical findings suggest that specialist pollinators are more likely to go extinct than
340 generalists.

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

349 The prediction that networks may become prone to synchronised collapses neglects
350 the potential buffering effect of ‘interaction rewiring’, which has been empirically shown to
351 contribute to maintaining a constant network structure (Petanidou et al 2008, Timoteo et al
352 2016). Interaction rewiring refers to a pollinator’s ability to switch to alternative, less-
353 preferred flowers if a preferred flower is unavailable; this behaviour might prevent a
354 pollinator population from collapsing long enough for a preferred plant species to
355 recolonise the site. Removal experiments conducted on simulated Mauritian pollination
356 networks found that network stability can be maintained if species ‘re-wire’ themselves by
357 shifting to new plants when their preferred species becomes extinct (Kaiser-Bunbury et al.
358 2010).

359 More generally, adaptive foraging by pollinators can increase community persistence
360 and robustness to species loss (Valdovinos et al. 2013). The potential of adaptive responses to
361 stabilise communities will depend partly on the amount and conservation of trait variation
362 within populations that could counteract phenological mismatches between plants and
363 pollinators (Revilla et al. 2015) or the sensitivity of specific species to chemical pollution
364 (reviewed in Leonard and Hochuli 2016). In addition, the effect of network rewiring via
365 adaptive foraging will depend on the temporal and spatial variability of interactions
366 (Tylianakis and Morris 2017). Climate-induced phenological shifts in plant-pollinator
367 communities (Rafferty et al 2013) can leave plants and pollinators without interactions even
368 if the phenological shifts are small (Memmott et al 2007) and could potentially increase the
369 risk of a community collapse. So far there is insufficient empirical evidence and an
370 incomplete theoretical understanding of the extent to which behavioural changes, flows
371 between meta-communities, and trait variation act in concert to minimize the risk of
372 threshold responses in pollination networks.

373

374 **Open research questions**

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

379

380 **How prevalent are threshold and tipping point responses?**

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

394

395 **Are there mechanisms that safeguard the stability of pollinator systems and** 396 **reduce the risk of threshold and tipping point responses?**

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

410

411 **What kind of experiments and models can we develop to identify thresholds** 412 **and tipping points at the colony, population and community level?**

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

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

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

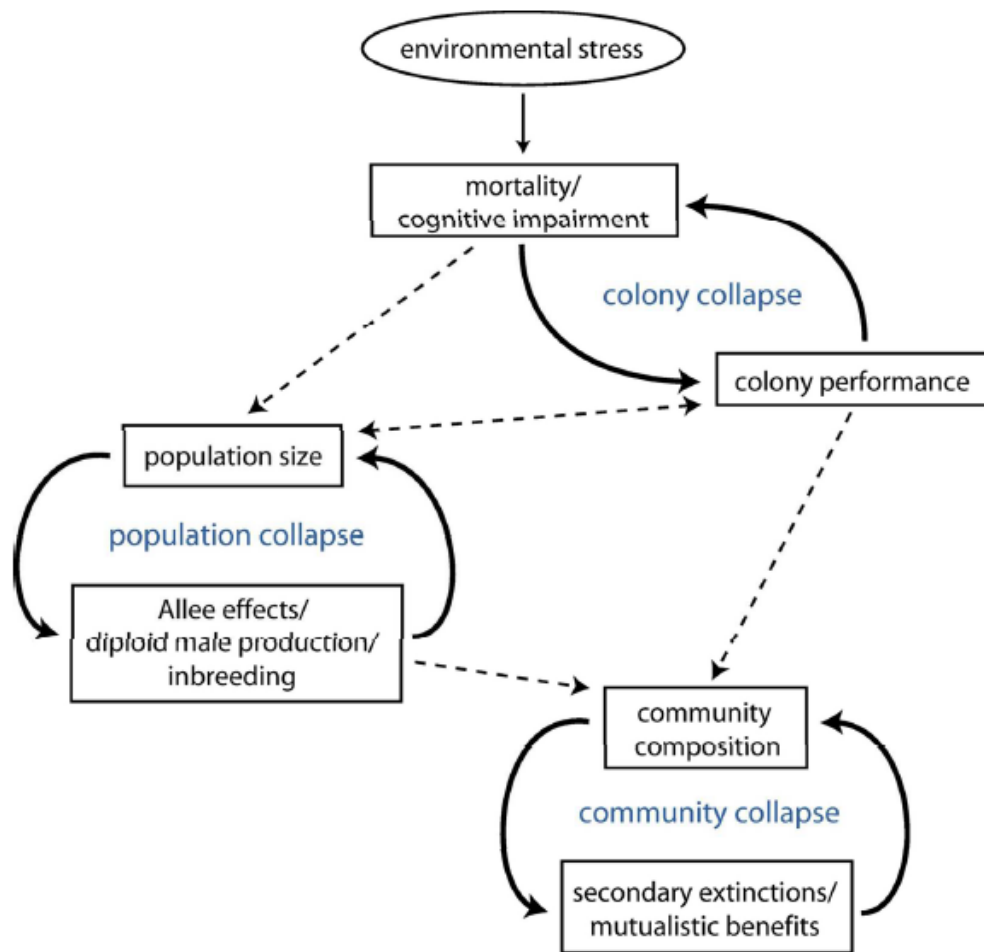
448

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

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

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

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

490

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

493 Ideally, species or populations at risk of non-linear declines would be identified as potential
494 targets for monitoring and conservation efforts. The hymenopteran sex determination system
495 and the fact that hymenopterans are central place foragers could potentially make them more
496 vulnerable than other insect groups to non-linear declines. However, we currently have little
497 knowledge on how common extinction vortices and diploid male vortices are in nature nor do
498 we know whether there are strong Allee effects in non-hymenopteran pollinators. At the
499 colony level, experimental evidence for non-linear declines in colony health comes only from
500 bumble bees; examples from other eusocial bee species are lacking although there is strong
501 anecdotal evidence of rapid, nonlinear collapse in honeybees. Future research should
502 determine if non-linear decline is a common feature of colony failures or if it is associated
503 with particular stressors.

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

509

510 **Can we develop indicators for detecting impending pollinator collapse?**

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

528 in combination, could serve as response variables, which could be analysed for early warning
529 indicators

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

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

559

560 **How do we manage threshold responses in pollination systems?**

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

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

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

578

579 **Concluding remarks**

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

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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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