1 **Interacting stressors underlie pollinator declines; bees feel the squeeze**

2 Combined stress from parasites, pesticides and lack of flowers drives bee declines

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11 **Abstract**

12 Bees are subject to numerous pressures in the modern world. The abundance and diversity of

13 flowers has declined, bees are chronically exposed to cocktails of agrochemicals, and they are

14 simultaneously exposed to novel parasites accidentally spread by humans. Climate change is

15 likely to exacerbate these problems in the future. Stressors do not act in isolation; for example

16 pesticide exposure can impair both detoxification mechanisms and immune responses,

17 rendering bees more susceptible to parasites. It seems certain that chronic exposure to

18 multiple, interacting stressors is driving honey bee colony losses and declines of wild

19 pollinators, but such interactions are not addressed by current regulatory procedures and

20 studying these interactions experimentally poses a major challenge. In the meantime, taking

21 steps to reduce stress on bees would seem prudent; incorporating flower-rich habitat into

22 farmland, reducing pesticide use through adopting more sustainable farming methods, and

23 enforcing effective quarantine measures on bee movements are all practical measures that

24 should be adopted. Effective monitoring of wild pollinator populations is urgently needed to

25 inform management strategies into the future.

26

27 **Is there a 'pollination crisis'?**

28 Insect pollination is vitally important to terrestrial ecosystems and to crop production. The

29 oft-quoted statistics are that 75% of our crop species benefit from insect pollinators (*1*),

30 which provide a global service worth $215 billion to food production (*2*). Hence the potential

31 that we may be facing a "pollination crisis" (*3*, *4*) in which crop yields begin to fall because

32 of inadequate pollination has generated understandable debate and concern and stimulated

33 much research in recent decades. Nonetheless, knowledge gaps remain substantial, both with

34 regard to the extent and causes of pollinator declines. Indeed, for most regions of the globe

35 and for most wild pollinator taxa, we have no data as to whether there have actually been

36 declines. Our best estimates are for numbers of domesticated honey bee colonies, which can

37 be obtained for many countries with varying reliability. Overall, these suggest that numbers

38 of managed honey bee colonies have decreased in Europe (25% loss of colonies in central

39 Europe between 1985 and 2005 (*5*)), and markedly in North America (59% loss of colonies

40 between 1947 and 2005 (*6*, *7*)). However, overall global stocks actually increased by ~45%

41 between 1961 and 2008, due to a major increase in numbers of hives in countries such as

42 China and Argentina (*8*). Conversely, there are widespread reports of unusually high rates of

43 honey bee colony loss from many parts of the world, sometimes ascribed to a syndrome

44   known as Colony Collapse Disorder (CCD) (*9*). It seems that socioeconomic factors (such as

45   increasing demand for pollination or honey (*10*), are at present sufficient to incentivise

46   beekeepers to overcome problems with bee health, when examined at a global scale (but not

47   locally in North America and Europe).

48   If we turn to wild pollinators, the best data available are for bumblebees (*11*). In

49   Europe, many species have undergone substantial range contractions and localized extinction,

50   with four species going extinct throughout the continent (*11*, *12*) (Figure 1a). In North

51   America, some formerly abundant and widespread species such as *Bombus terricola* and *B.*

52   *occidentalis* underwent severe declines from the late 1990s onwards, and now occupy only a

53   small fraction of their former range (Figure 1b) (*13*, *14*). *Bombus franklini*, a species formerly

54   found in northern California and Oregon, has not been recorded since 2006 and is presumed

55   extinct. In a study of the bumblebee fauna of Illinois over the past 100 years, Grixti *et al.* (*15*)

56   describe substantial declines in species diversity, particularly in the period 1940-1960, with

57   the extirpation of four species during the 20th century. In South America, the recent invasion

58   by the European species *B. terrestris* is causing precipitous declines in the native *B.*

59   *dahlbomii* (*16*). There is some evidence of loss of species richness from lowland areas of

60   Sichuan in China (*17*, *18*), and a few reports of declines in Japan from the mid 1990s

61   onwards (*19*, *20*), but elsewhere in the world, few data are available. For the remaining wild

62   bees, data are exceedingly sparse, though they comprise the large majority of the world's

63   approximately 22,000 bee species. Analysis of historic records suggests that diversity of both

64   bumblebees and other wild bees declined in the UK, Netherlands and Belgium during the

65   twentieth century, but that these declines have decelerated since 1990 (*21*, *22*). In surveys in

66   Illinois, 50% of wild bee species went extinct over a 120 year period to 2010 (*23*). Given that

67   bee diversity has declined in both Europe and the Americas, it is probably reasonable to

68   assume that declines are also occurring elsewhere across the globe

69   The biggest knowledge gap is regarding bee abundance; although we have maps of

70   past and present distributions of bees for some well-studied countries such as the UK, we

71   have almost no data on how populations have changed over time. Hence we do not know

72   whether common species such as *Bombus terrestris* in Europe or *Bombus impatiens* in North

73   America are less abundant than formerly, or whether they are currently in decline. Most

74   pollination is delivered by a small number of these abundant species which tend to have large

75   distributions. Declines in their abundance would not be detected in distribution maps until

76 they become extinct in parts of their range, which is rather late to introduce conservation

77 measures.

78   Another way to examine the likelihood or proximity of a pollination crisis is to

79 examine delivery of pollination services. Although global honey bee stocks have increased by

80 ~45%, demand has risen more than supply, for the fraction of global crops that require animal

81 pollination has tripled over the same time period (*8*), making food production more

82 dependent on pollinators than before. It has also emerged that the majority of crop

83 pollination, at a global scale, is delivered by wild pollinators rather than honey bees. Yields

84 correlate better with wild pollinators abundance than with abundance of honey bees (*24–26*);

85 hence increasing honey bee numbers alone is unlikely to provide a complete solution to the

86 increasing demand for pollination. Reliance on a single species is also a risky strategy (*27*).

87 Whilst Aizen *et al.* (*28*) concluded from a global analysis of changing crop yields over time

88 that there was not yet any clear evidence that a shortage of pollinators was reducing yield, a

89 subsequent analysis of the same data set by Garibaldi *et al.* (*29*) shows that yields of

90 pollinator-dependent crops are more variable, and have increased less, than crops that do not

91 benefit from pollinators, to the extent that a shortage of pollinators is reducing the stability of

92 agricultural food production. In a meta-analysis of 29 studies on diverse crops and contrasting

93 biomes, Garibaldi *et al.* (*30*) found that wild pollinator visitation and yields generally drop

94 with increasing distance from natural areas, suggesting that yields on some farms are already

95 impacted by inadequate pollination.

96   To summarize, in the past 50 years global honey bee stocks have increased, while

97 wild bees appear to have declined substantially, as evidenced by data for bumblebees, and

98 very scant data for other bee species. The demand for insect pollinators in farming has tripled

99 in the same period. There is clearly no major pollination crisis yet, but there is evidence for

100 localized limitation of crop yield as a result of inadequate pollination.

101

102 **Drivers of wild bee declines and honey bee colony losses**

103

104 Habitat loss

105 Bee declines have been attributed to many factors, some more plausible than others; however,

106 the clear consensus is that loss of habitat has been a long-term contributor to declines (*11*,

107 *31–33*). Bees require appropriate floral resources during the adult flight season, which may

108 be short for some solitary species or year-long for social species in tropical environments.

109   They also require undisturbed nest sites, with different species occupying diverse locations

110   (e.g.' cavities underground, hollow-stemmed twigs, burrows in the soil, even abandoned snail

111   shells). The conversion of natural and semi-natural flower-rich habitat to farmland has been a

112   major driver of long-term declines in bees. For example, in the UK, approximately 97% of

113   flower-rich grasslands were lost in the 20th century (*34*), and this has resulted in major range

114   contractions of bee species associated with this habitat, particularly long-tongued bumblebees

115   (*11*). Declines of similar magnitude have affected the grasslands of North America, although

116   these began in the early 19th century (*35*).

117   Urbanization also contributes to loss of natural habitat, but the net effect on bees is

118   less clear. Gardens can support high densities of wild bees, particularly bumblebees and some

119   solitary bee species, but highly urbanized environments have few bees (*36*, *37*), and the

120   building of roads and other infrastructure undoubtedly contributes to the ongoing

121   fragmentation and degradation of habitats. Increased traffic can also cause direct mortality

122   through collisions (*38*), although the numbers of bees killed in this way is not known. The

123   planting of road verges and traffic islands with wildflowers is often promoted as a means of

124   boosting urban pollinator populations, but it might increase mortality by vehicle collisions.

125

126   <u>Parasites and disease</u>

127   Bees naturally suffer from a broad range of parasites, parasitoids and pathogens, the latter

128   including protozoans, fungi, bacteria and viruses. By far the majority of research has focused

129   on those associated with honey bees and to a lesser extent with bumblebees, with very little

130   known about the pathogens of other wild bee species. Some bee diseases, such as Deformed

131   Wing Virus (DWV) and *Nosema ceranae*, have broad host ranges and are able to infect both

132   honey bees and bumblebees while others, such as *Crithidia bombi* or *Paenibacillus larvae*,

133   seem to be more host-specific (*39–41*). While natural pathogens undoubtedly play an

134   important but poorly-understood role in influencing the population dynamics of their bee

135   hosts, we will focus here on the impacts that non-native parasites and pathogens may have.

136   The spread of most honey bee parasites and pathogens has occurred inadvertently as

137   a result of transporting honey bees long distances. Much of this happened in historic times,

138   but it continues, despite some improvements in quarantine procedures. The best-known

139   example is the mite *Varroa destructor*, originally associated with the Asian honey bee *Apis*

140   *cerana*. Varroa has since jumped hosts to the European honey bee *Apis mellifera*, which has

141   little resistance to this pest. Since the 1960s Varroa has spread from Asia to Europe, the

142 Americas and most recently to New Zealand. The mite acts as a vector for pathogens such as

143 DWV, and the combined effect of the mite and the diseases it transmits is a major contributor

144 to honey bee colony losses in North America and Europe (*42*, *43*). Fortunately, the mite

145 appears unable to survive on bees outside the genus *Apis*.

146   A strikingly similar series of events has also seen the microsporidian *N. ceranae* jump

147 from *A. cerana* to *A. mellifera,* and in the past 20 years it has spread to Europe and the

148 Americas, where it is now prevalent at high frequency (Figure 2) (*44*, *45*). It has also been

149 detected in wild bumblebees in Europe, China and South America (*41*, *46*, *47*), and solitary

150 bees in Europe (*48*). In the lab *N.ceranae* appears to have higher virulence in bumblebees

151 than it does in honey bees (*41*), though the impact it has had on wild populations is unknown.

152 Asia is not the only source of non-native diseases; the African honey bee parasite *Aethina*

153 *tumida* (small hive beetle) recently invaded North America, Egypt, Australia and Europe, and

154 attacks *B. impatiens* colonies causing considerable damage (*49*, *50*). It seems highly likely

155 that it also attacks other wild bumblebee species that are not so readily cultured and therefore

156 less well studied.

157   Bee diseases are also being redistributed around the globe by the commercial trade in

158 bumblebee colonies, which are mainly used for pollination of greenhouse crops such as

159 tomatoes. This trade began in the 1980s in Europe, and now more than 1 million nests of the

160 European *Bombus terrestris* are reared each year and exported to various countries. In North

161 America, the eastern American species *Bombus impatiens* is reared for this purpose.

162 Unfortunately, it does not seem possible yet to rear colonies that are free of disease, not least

163 because the bees are reared on honey-bee collected pollen, providing a route for exposure to

164 many bee pathogens. Commercial colonies of *B. terrestris* are commonly infected with one or

165 more parasites, including *Nosema bombi, N. ceranae, Apicystis bombi* and DWV (*41*).

166   There is evidence that non-native pathogens or pathogen strains associated with these

167 colonies are having devastating impacts on wild bumblebee populations. In North America,

168 the accidental importation of a non-native strain of the parasite *Nosema bombi* via

169 commercial bumblebees has been implicated in the dramatic decline of several bumblebee

170 species, though convincing causal evidence remains elusive (*51*, *52*). The evidence from

171 South America is clearer; here, *B. terrestris* were deliberately introduced by the Chilean

172 government despite the presence of native *Bombus* species, with *terrestris* spreading rapidly

173 to occupy a vast area of southern South America. The arrival of *B. terrestris* appears to have

174 led to the rapid local extinction of the native *B. dahlbomii* at a speed only plausibly explained

175   by pathogen spillover (*16*). Although the parasite responsible has yet to be ascertained with

176   certainty, both *A. bombi* and *C. bombi* have been shown to be highly prevalent in the invasive

177   species (*16, 53*). There is a clear parallel with the devastating impact that the arrival of

178   European diseases had on the native Americans 500 years ago.

179   Even when commercial bees are free of disease on arrival, or are infected only with

180   indigenous parasites, they can still affect native pollinators. High-density populations of

181   managed bees may provide conditions for the rapid multiplication of parasites that then spill

182   over into wild populations (*54–56*). A combination of field observations and modelling

183   suggest that waves of *Crithidia bombi* infection travel outwards from greenhouses containing

184   commercial bumblebees. Prediction indicates that waves can spread at ~2 km per week, with

185   up to 100% of wild bees within the spreading radius becoming infected, although this is not

186   yet well supported by direct evidence (*55*).

187   In general we know little about the natural geographic range, host range, prevalence

188   or virulence of most bee pathogens, and so it would seem wise to take very careful

189   precautions to prevent further introductions of bee pathogens from outside their native range,

190   in addition to minimizing any spillover from commercial pollination operations (*52, 57*).

191

192   Pesticides

193   The most controversial and debated cause of bee declines are pesticides. When appropriately

194   used, pesticides can provide an economic benefit, but bring the welfare of bees into direct

195   conflict with industrial agriculture. Herbicides are highly effective at minimizing weed

196   problems in most cropping systems, enabling farmers to grow near-pure monocultures, but

197   their use inevitably reduces the availability of flowers for pollinators and can contribute

198   substantially to rendering farmland an inhospitable environment for bees (*11, 58, 59*).

199   Understandably, most attention has been paid to the direct toxic effects of pesticides on bees,

200   particularly the impacts of insecticides. One hundred and sixty one different pesticides have

201   been detected in honey bee colonies (*60, 61*) and based on their toxicity, frequency in hives

202   and the concentrations detected, Sanchez-Bayo and Goka (*61*) predict that three

203   neonicotinoids (thiamethoxam, imidacloprid and clothianidin), and the organophosphates

204   phosmet and chlorpyrifos pose the biggest risk to honey bees at a global scale. It is clear that

205   bees are often chronically exposed to cocktails of pesticides throughout their development

206   and adult life (*61–64*), but the effects of this are poorly understood and are not examined by

207   current regulatory risk-assessment procedures (*65*).

208   Neonicotinoids are the newest of the main classes of insecticide, and the group most
209   strongly implicated in bee declines (*65*, *66*). They are neurotoxins that target the insect
210   central nervous system, binding to postsynaptic nicotinic acetylcholine receptors and causing
211   over-stimulation, paralysis and death (*67*). These insecticides are commonly applied as seed-
212   treatments and are systemic within plants, spreading through plant tissues and into the pollen
213   and nectar of flowering crops such as canola. They are also water soluble but highly
214   persistent in soil and soil water, and as a result have been found at significant concentrations
215   in the pollen and nectar of wildflowers near crops (*63*). Thus there is a clear route for
216   ingestion by bees. Oral toxicity is high, with the short-term LD_{50} for the most commonly-
217   used neonicotinoids in the region of 4-5ng/honey bee (*68*) (LD_{50} = Lethal Dose 50%, the
218   dose that kills 50% of test organisms). Long-term chronic exposure results in mortality in
219   overwintering honey bees when feeding on food contaminated with concentrations as low as
220   0.25ppb (*69*). Sub-lethal effects of neonicotinoid exposure have also been observed in both
221   honey bees and bumblebees, including a reduction in learning, foraging ability and homing
222   ability, all of which are essential to bee survival (*70–74*). Yang *et al. (75)* recently showed
223   that even low exposure during the larval stage (0.04ng/larva equating to less than $1/100^{th}$ of
224   the LC_{50} for adult bees) can have a lasting impact on learning in adult honey bees (LC_{50} =
225   Lethal Concentration 50%, the concentration that kills 50% of test organisms).
226   It seems very likely that bees living in most arable farmland are routinely exposed to
227   sufficient neonicotinoids to suffer both lethal and sublethal effects. However, whether this
228   translates into a detrimental effect at the colony-level remains disputed. In bumblebees,
229   exposure of colonies to field-realistic concentrations of imidacloprid greatly impaired colony
230   growth and reduced queen production by 85% (*76*). In contrast, field studies with honey bee
231   colonies have proved more challenging to perform convincingly (*77*, *78*), not least because of
232   the huge areas over which honey bees forage, the lack of a clear end-point to colony
233   development, and their long-term storage of food reserves. This lack of clear evidence of
234   harm in the field is often misinterpreted as evidence that toxicological studies on individual
235   bees do not translate into colony losses in the field, rather than as the absence of evidence.
236
237
238   Monotonous diets
239   Intensively farmed areas provide few wildflowers, but do provide spatially and temporally
240   isolated gluts of flowers in the form of mass-flowering crops such as sunflowers and canola.

241 If a human were to consume nothing but sardines one month, chocolate the next, turnips the
242 month after and so on, one could reasonably expect them to fall ill. This may seem a
243 frivolous example, but it is a reasonable parallel to the experience of some honey bee
244 colonies, particularly those in North America that are transported backwards and forwards
245 across the continent each year to provide pollination for major crops such as almonds in
246 California, blueberries in Maine and citrus in Florida. Where the nectar or pollen of crop
247 flowers contain toxins, such as the glycoside amygdalin found in almonds (*79*), bees might
248 potentially consume harmful concentrations of such substances.

249   More generally it seems certain that bees inhabiting intensive farmland have a more
250 monotonous diet than they would have experienced in their evolutionary past, but how this
251 impacts upon their fitness remains unclear. The pollen of different plant species varies greatly
252 in protein content, amino acid composition, lipid, starch, vitamin and mineral content. Nectar
253 commonly contains varying and low concentrations of a range of nutrients and other
254 compounds of largely unknown importance (*80–84*). Thus, we might expect the type and
255 range of flowers available will affect individual bee health and colony fitness in multiple
256 ways; for example in honey bees, both pollen quality and diversity influence longevity,
257 physiology and resistance/tolerance to disease (*85–88*). However, this topic has been little
258 investigated, particularly for wild bees. The perception that honey bees may be receiving an
259 inadequate diet has led to the development of protein supplements, but once again there has
260 been little research on the long-term effectiveness of such supplements on colony health (*89,*
261 *90*).

262   Interpreting the effects of availability of mass-flowering crops on bees and their
263 colonies is further complicated since visiting such crops often exposes bees to pesticide
264 residues, so that positive effects of increased food availability may be offset by negative
265 effects of the pesticide. Some studies have found positive effects of proximity to canola on
266 bumblebee colony growth and abundance (*91, 92*) and on numbers of nesting red mason bees
267 *Osmia bicornis* (*93, 94*) while others found no relationship for bumblebees (*58, 95*) nor for
268 solitary bees (*96*). Interestingly, none of these studies considered what role pesticides might
269 have played in mediating the effect of the crop, or even report which pesticides were applied
270 to crops in the study area, an omission that now seems naive given the recent focus on
271 impacts of neonicotinoid insecticides on bees.

272

273 Shipping fever

274 It seems reasonable to hypothesize that the long-distance transport of bees, as routinely

275 occurs for honey bees in North America and for commercial bumblebee colonies, places

276 stress on the colonies. For several days they may be confined and subject to vibration, high

277 temperatures, high levels of carbon dioxide and irregular disturbance. It has long been known

278 that such stress can activate bacterial and viral infections and generally reduce condition in

279 vertebrate livestock ([97]), but this has not been investigated in bees, although Bakonyi *et al.*

280 ([98]) suggest that shipping stress may have contributed to honey bee colony losses in

281 Hungary. This is clearly an area where further research is needed.

282

283

284 Competition

285 The role of competition in determining the relative abundance of species is notoriously hard

286 to ascertain in mobile organisms such as bees, but it seems likely that competition for floral

287 resources and perhaps also for nest sites does occur in natural communities, and that it can be

288 exacerbated by the introduction of non-native species, particularly when the latter are present

289 at high densities ([57]). For example, there is evidence that high concentrations of domestic

290 honey bee hives can displace wild bumblebees from their preferred foodplants and from

291 whole areas if hive densities are sufficiently high ([99], [100]). This can result in a reduction in

292 the size of bumblebee workers ([101]), and reduced reproductive success of bumblebee

293 colonies ([102]). Although in general the interests of honey bee keepers and wild bee

294 conservationists are aligned (all would agree on the benefits of increasing floral resources,

295 reducing exposure to pesticides and preventing invasions of alien pathogens), there may

296 occasionally be conflict where bee keepers wish to place hives in areas with significant

297 populations of rare wild bees ([57]).

298

299 Climate change

300 Climate change is widely accepted to pose one of the largest threats to biodiversity

301 worldwide, but likely impacts on pollinators and pollination are not well understood. One

302 danger is that the phenology of pollinators may diverge from that of the plants they pollinate,

303 with potentially disastrous consequences for both, but there is little evidence that this is

304 happening to a significant extent ([103]). Advances in flowering and bee emergence are

305 often broadly similar, and in any case few plants are dependent on a single pollinator so that

306 any mismatch with one pollinator is likely to be compensated by increased availability of
307 another (*103*, *104*).

308   Another potential effect of climate change is as a driver of range shifts, leading to a
309 spatial mismatch between plants and pollinators. Range shifts in response to climate have
310 been demonstrated in butterflies (*105*) and are to be expected in bees (*13*); for example there
311 is already evidence that the lower altitudinal limit of some montane bumblebees has shifted
312 uphill in Spain (*106*). We would predict declines in bumblebees at the southern edge of their
313 range since they tend to be poorly adapted to high temperatures.

314   Of course climate change is not solely associated with warming; extreme weather
315 events such as storms, floods and droughts are predicted to increase, and we would expect
316 these to have major impacts on local bee communities. For example, flooding is likely to be
317 harmful to the many bee species that nest or hibernate underground.

318   Overall, although there is little strong evidence that climate change has yet had any
319 great effect on bees, it is likely to provide a growing source of stress in the future that would
320 exacerbate the impact of other factors, such as habitat loss.

321

322 **Interactions between stressors**
323 Unfortunately the public debate on bee health has often become polarized, with claims that,
324 for example, *Varroa* or neonicotinoid insecticides are the sole or primary cause of bee
325 declines or honey bee colony losses. If a middle-aged man who is overweight, does little
326 exercise, and smokes and drinks heavily were to die of a heart attack, we would not be
327 surprised and we might not spend too long arguing over which single risk factor was most
328 important in bringing about his untimely demise. Similarly, wild bee declines and honey bee
329 colony losses are clearly due to multiple, interacting and sometimes synergistic factors, and
330 the combination of factors involved no doubt varies in time and space.

331   In general, the combined effect of multiple stressors are likely to be more harmful than
332 one stressor alone (*107–109*) (Figure 3). In the worst-case scenario, sublethal stressors that do
333 not incur any significant harmful effects in isolation could, in combination, result in lethal
334 effects. As we have already seen, bees are often exposed chronically to mixtures of pesticides
335 and other chemicals. Some, such as ergosterol biosynthesis inhibitors (EBI) fungicides, have
336 very low toxicity in themselves but may increase the toxicity of some neonicotinoids and
337 pyrethroids up to 1,000-fold (*110–112*). Piperonyl butoxide is often added to pesticide
338 formulations and also acts synergistically with some neonicotinoids, increasing toxicity up to

339 244-fold (*111*). Intriguingly, whilst imidacloprid alone has been shown to impair olfactory
340 learning (*113*), combined exposure to imidacloprid and coumaphos has been shown to result
341 in a slight increase in learning in honey bees (*114*). So while regulatory processes examine
342 the effects on bees of exposure to a single pesticide at a time, in reality bees are
343 simultaneously exposed to many pesticides, some of which have combined effects that cannot
344 be predicted from studies of their effects when used in isolation.

345 Several recent studies indicate that interactive effects between pesticides and
346 pathogens could be especially harmful for bees (*115–121*). For instance, developmental
347 exposure to neonicotinoid insecticides renders honey bees more susceptible to the impact of
348 the invasive pathogen *N. ceranae* (*122*). Imidacloprid can act synergistically with *Nosema*
349 spp. by increasing the prevalence of *Nosema* infections in hives (*116*) and increasing
350 *Nosema*-induced mortality (*115*). Similarly, Aufauvre *et al.* (*118*) showed that mortality of
351 honey bees was greater when bees were exposed to the insecticide fipronil and infected by *N.*
352 *ceranae* than when only a single stress factor was present. There is evidence that exposure to
353 pesticides may impair the immune function of insects, which would explain these effects (*43*,
354 *123–125*). For example, Di Prisco *et al.* (*126*) recently showed that exposure to
355 neonicotinoids (clothianidin or imidacloprid) leads to immunosuppression in honey bees,
356 which, in turn, promotes the replication of the deformed wing virus in insects with covert
357 infections. This effect was found at very low concentrations, well below those that bees are
358 likely to encounter in the field.

359 Interactions between stressors are not confined to pesticides and pathogens. The
360 ability of bees to survive parasite infections is compromised by nutritional stress. For
361 example, *Crithidia bombi* causes little mortality in well-fed bumblebees, but becomes
362 virulent in bumblebees with a restricted diet (*127*). Activating the immune response has a
363 metabolic cost; bumblebees increase their food consumption when immune responses
364 areupregulated (*128*), and artificially stimulating the immune response by injecting latex
365 beads caused mortality in starving bumblebees but not in those that were well fed (*129*).
366 Increased food consumption in infected bees could also increase exposure to pesticides.
367 Activating immunity has been shown to impair learning in both honey bees (*130*) and
368 bumblebees (*131*, *132*), and impaired learning will reduce the bees' ability to locate floral
369 resources and extract rewards, so exacerbating nutritional stresses.

370 Although to our knowledge this has not yet been examined, it seems highly likely that
371 nutritional stress may also modulate the ability of bees to cope with pesticides, and this may

372 explain in part why the observed LD50 of toxins in bees is highly variable across studies

373 (*65*).

374   In summary, stressors do not act in isolation. Bees of all species are likely to

375 encounter multiple stressors during their lives, and each is likely to reduce the ability of bees

376 to cope with the others. A bee or bee colony that appears to have succumbed to a pathogen

377 may not have died if it had not also been exposed to a sublethal dose of a pesticide and/or

378 been subject to food stress (which might in turn be due to drought or heavy rain induced by

379 climate change, or competition from a high density of honey bee hives placed nearby).

380 Unfortunately, conducting well-replicated studies of the effects of multiple, interacting

381 stressors on bee colonies is exceedingly difficult. The number of stressor combinations

382 rapidly become large, and exposure to stressors is hard or impossible to control with free-

383 flying bees. Nonetheless, a strong argument can be made that it is the interaction between

384 parasites, pesticides and diet that lies at the heart of current bee health problems.

385

386 **Sustainable pollination into the future**

387 There is universal agreement that we must ensure adequate pollinator populations into the

388 future if we wish to continue to grow a diversity of insect-pollinated crops and also ensure the

389 integrity of natural ecosystems. It is also clear that moving towards heavy reliance on a few

390 species of managed pollinators, such as honey bees or one or two species of bumblebee, runs

391 the risk of supply failure; for example, should honey bee stocks in North America fall much

392 further, the viability of almond production in California would be threatened (*133*). Wild

393 pollinators provide a service that is largely free, and globally already contributes the majority

394 of crop pollination (*24*, *25*, *134*, *135*). Maintaining a diversity of pollinator species improves

395 crop success via functional complementarity; different species visit different parts of the crop

396 or crop plant, at different times of the day or year, and respond differently to environmental

397 perturbations (*1*, *136–141*). A diversity of pollinators can buffer impacts of climate change

398 which might otherwise result in a mismatch in phenology of pollinators with the flowering of

399 crops (*104*). It is thus essential that we take steps to conserve a broad community of

400 pollinators in farmland.

401   Fortunately, although the causes of pollinator ill-health may be complex and multi-

402 causal, conserving pollinators need not be difficult or expensive. If we accept that declines

403 are due to interacting stressors, then it follows logically that removing or reducing any of the

404 stressors we have described is likely to benefit bee populations. Measures can be taken that

405 are likely to simultaneously benefit a broad suit of species, both domesticated and wild:

406

407   1) Increase abundance, diversity and continuity of floral resources. Schemes such as the

408   sowing of flower-rich field margins or hedgerows, or retaining patches of semi-

409   natural habitat among or near farmland provide clear benefits to bee diversity and

410   abundance (*30*, *141–148*) (Fig. 4A). This in turn increases pollination to nearby crops

411   and provides an economic incentive to farmers growing insect-pollinated crops (*149*).

412   Many countries also offer financial incentives to farmers for taking measures to boost

413   biodiversity that help to offset implementation and opportunity costs. However, take-

414   up of schemes to boost pollinators remains low in most countries, perhaps reflecting a

415   lack of understanding of the economic and environmental benefits, or a lack of

416   familiarity with implementation of such measures. Education and outreach in this area

417   could pay great dividends for pollinator conservation.

418   Planting of appropriate flowers in gardens and amenity areas can also

419   contribute to pollinator conservation (*150*, *151*) (Fig. 4B). There is evidence that

420   urban areas can support higher populations of some pollinators than farmland e.g.,

421   (*36*) and boost bee numbers in adjacent farmland (*58*). Many lists of bee or wildlife-

422   friendly flowers are available on the internet but they tend to be based on anecdote

423   rather than evidence, and there is a need to develop regionally appropriate, evidence-

424   based advice as to the best plants to grow (*152*).

425

426   2) Provide nest sites. Wild bees use a diversity of habitats for nesting, including

427   burrowing into bare soil, using existing cavities underground, holes in wood, or

428   hollow plant stems. Semi-natural habitats, hedgerows and permanently uncropped

429   field margins cater for many of these, meaning that schemes to boost floral diversity

430   are also likely to boost nesting opportunities (*141*). Additional nest sites can also be

431   provided by providing bundles of hollow reeds or canes, or patches of bare soil (*153*).

432

433   3) Reduce exposure to pesticides. Bees are currently chronically exposed to a cocktail of

434   pesticides some of which act synergistically. Since the late 1990s, the cost of

435   pesticides has fallen markedly relative to labor and fuel costs and the value of the

436   crops (*154*). As a result, current levels of pesticide use are generally high, and not

always justified by evidence that they are necessary to maintain yield (*66*, *155*). The widespread, prophylactic use of systemic insecticides, such as neonicotinoids as seed dressings, exposes bees and other non-target wildlife, results in accumulation of pesticides in the environment, and places strong selection pressure on pests to evolve resistance. A return to the principles of Integrated Pest Management (*156*), which utilizes preventative methods, such as crop rotation, and views the use of pesticides as a last resort in the battle against insect pests, could greatly reduce exposure of bees, benefit the environment, and improve farming profitability. Some European countries have independently developed national pesticide reduction programs (*156*), and the European Union Sustainable Use of Pesticides Directive (Anon 2009) required member states to implement national action plans to minimize pesticide use by January 2014. In most EU states this directive appears to have had little or no impact on farming practices.

Current risk assessment procedures, which examine the short-term impact of a single pesticide in isolation, are clearly not adequate to encapsulate the true scenario faced by bees living in farmland. Improvements are needed to make them more realistic, whilst keeping the cost of regulatory tests affordable, posing a considerable challenge to the ingenuity of scientists and regulators.

The EU moratorium on the use of three neonicotinoids (which started in December 2013) is an attempt to use policy change to reduce exposure of bees to stressors, following a review by the European Food Standards Agency (*157–159*) which declared that neonicotinoids pose an "unacceptable risk" to bees. However, if this simply leads farmers to replace neonicotinoids with other pesticides this may not be of great benefit to bees or the environment. Funding for research and for the provision of clear, independent advice for farmers with regard to how to reduce pesticide use generally by adopting IPM practices might provide a better and more sustainable long-term solution.

4) <u>Prevent further introductions of non-native bees, parasites and pathogens.</u> The careless disregard with which we ship bees from country to country has resulted in the irreversible spread of many serious parasites and pathogens. Strict quarantine controls should be implemented on the movement of all commercial bees, and there is an urgent need to develop means of rearing commercial bumblebees that are free from

15

470   disease. Deliberate introductions of non-native bee species (such as the recent

471   introduction of the European *Bombus terrestris* to South America) should of course be

472   prevented. The companies that rear commercial bees should bear some responsibility

473   here, and refuse to sell bees to regions where they are not native. There is clear

474   hypocrisy in the policies of countries that prevent importation of non-native species

475   but allow exportation of species to places where they do not naturally occur.

476

477   5) Develop monitoring programs. We have good distribution maps for pollinators in

478   some countries, particularly for bumblebees, and citizen science schemes such as

479   "Bumble Bee Watch" in North America and "Beewatch" in the UK can help to track

480   changes in these distributions. However, the lack of long-term data on pollinator

481   abundance is a glaring knowledge gap that urgently needs to be filled. It will probably

482   never be possible to monitor all pollinator species at a global scale, but it would be

483   practical to systematically collect data on the abundance of a subset of the more

484   abundant and economically important pollinators. Citizen science surveys can provide

485   a cost effective means for large-scale population monitoring; for example the UK

486   butterfly monitoring scheme employs volunteers to walk regular transects using a

487   standard methodology to count the butterflies seen, and has generated a large and

488   long-term data set which has provided powerful insights into insect population change

489   (*160*, *161*). "Beewalks", a similar scheme to count bumblebees, has been launched by

490   the Bumblebee Conservation Trust to obtain population data for bumblebees in the

491   UK, although it is still in its infancy. In the USA, "The Great Sunflower Project" asks

492   volunteers to count pollinators in flower patches in their local area. However, such

493   schemes are limited by the taxonomic skills of volunteers, particularly for the many

494   pollinator taxa that are hard or impossible to identify in the field. LeBuhn *et al.* (*162*)

495   argue that a pan-tapping network, which could employ citizen scientists to place out

496   the traps but experts to identify the catch, would be the most cost-effective means for

497   monitoring a large cross-section of pollinator species on a large geographic scale.

498   Indeed, for a relatively modest sum it would be possible to set up an international pan-

499   trapping network to monitor pollinators following a standard methodology. Until

500   good population data become available, we cannot identify species or regions under

501   most threat and hence we cannot prioritize management.

502 In the absence of pollinator monitoring, we have no early warning system to tell us how close

503 we may be to a pollination crisis. With a growing human population and rapid growth in

504 global demand for pollination services, we cannot afford to see crop yields begin to fall, and

505 we would be well advised to take pre-emptive action to ensure that we have adequate

506 pollination services into the future.

507

508 **Acknowledgements**

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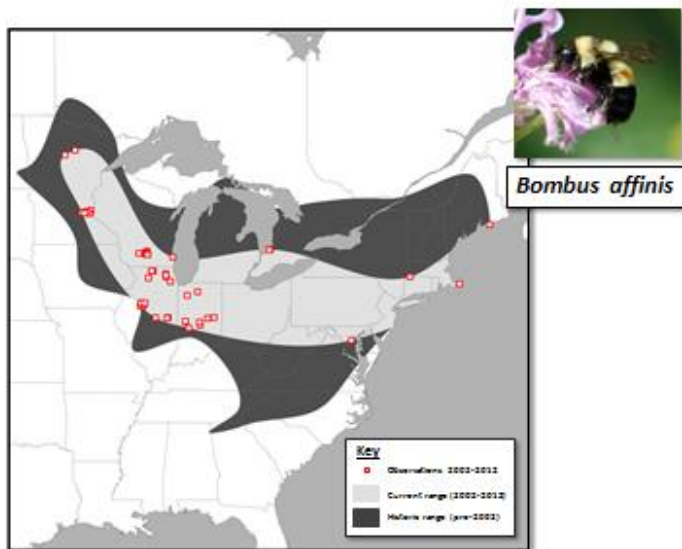940

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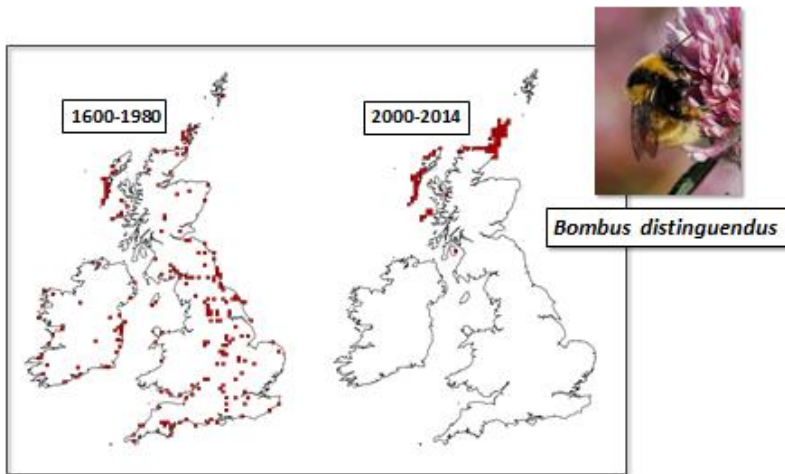
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954 **Figure 1. Some wild bee species have undergone major range contractions**. Shown here

955 for A the bumblebee *Bombus distinguendus* in the UK (data from the National Biodiversity

956 Network, UK, https://data.nbn.org.uk/ and (B) *Bombus affinis* in North America (Map

957 produced by the Xerces Society, list of data providers can be found at:

958 http://www.leifrichardson.org/bbna.html). Photo credit: Dave Goulson, Johanna James-

959 Heinz.
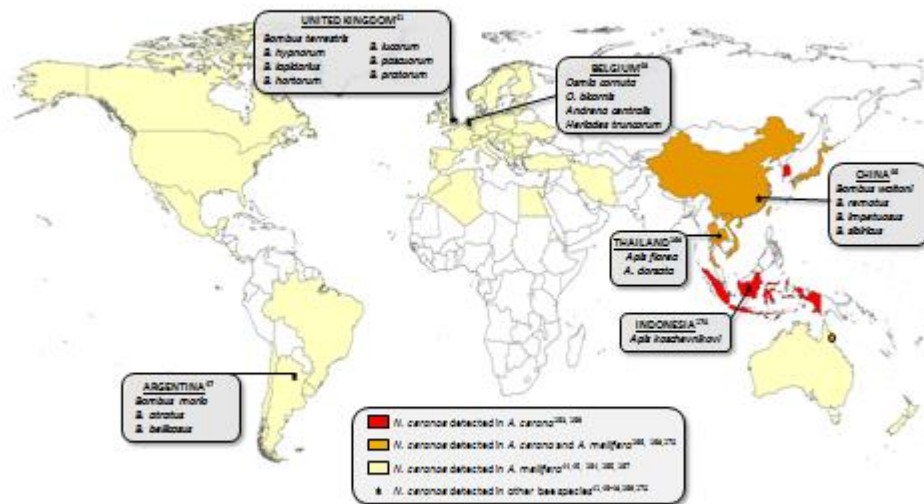
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962   **Figure 2. World distribution of the microsporidian pathogen *Nosema ceranae* in**

963   **different bee hosts.** This parasite was first isolated from the Eastern honeybee (*A. cerana*)

964   collected in China in 1996 (*163*), and was subsequently found infecting Western honey bees

965   (*A. mellifera*) in Europe in 2005 (*164*). Soon after *N.ceranae* was detected in *A. mellifera* in

966   many regions of the world including Africa, Asia, the Americas and Oceania (*44*, *45*, *165*–

967   *168*), and more recently in other bee species including several Asian *Apis* species (*169*, *170*)

968   and wild bumblebees species from Europe, China and South America (*41*, *46*, *47*). *N.*

969   *ceranae* has also now been detected in solitary bees from Europe (*48*), confirming a very

970   wide range of hosts and high dispersal rate. Although the origins and primary host of *N.*

971   *ceranae* are yet to be accurately established, the apparent late and gradual invasions of *N.*

972   *ceranae* into different *A. mellifera* populations have led some authors to suggest that *A.*

973   *cerana* may be the primary host of *N. ceranae* and that it may have only recently emerged as

974   a parasite of Western bees (*170*). The mechanism by which *N. ceranae* broadened its host

975   range from an Asian bee species to other bee species across the world is unknown, but there

976   has been human-mediated contact between Asian and Western bees for at least a century. It

977   should be noted that regions in the figure where *Nosema* appears to be absent (white) may be

978   due to a lack of sampling in these areas.

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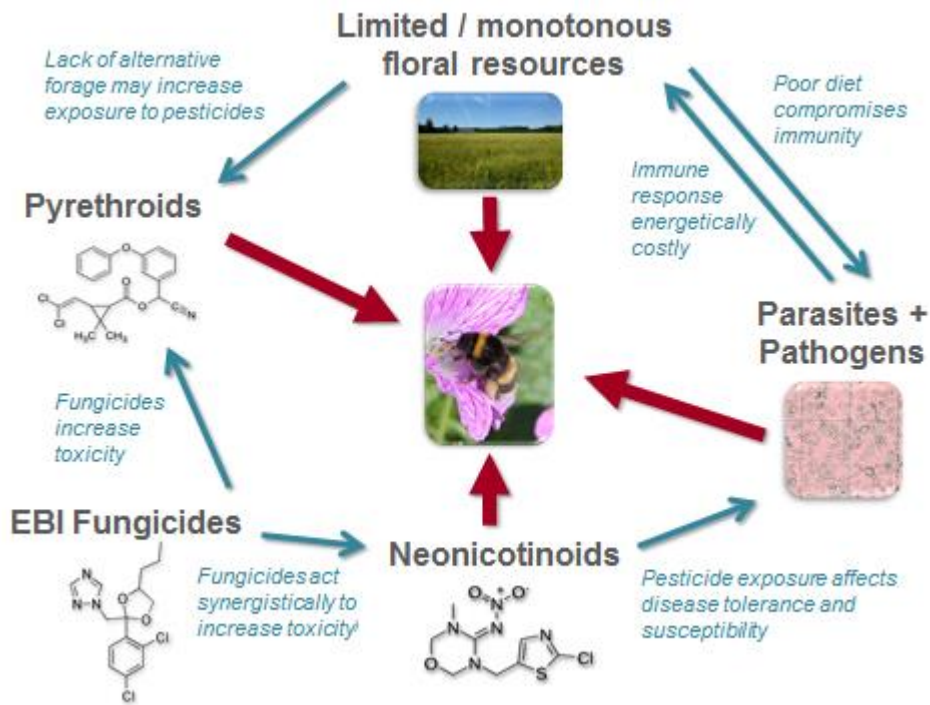
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984 **Figure 3. Both wild and managed bees are subject to a number of significant and**

985 **interacting stressors.** For example, exposure to some fungicides can greatly increase toxicity

986 of insecticides (*110–112*), whereas exposure to insecticides reduces resistance to diseases

987 (*115–123*, *125*, *126*). Dietary stresses are likely to reduce the ability of bees to cope with both

988 toxins and pathogens (*127–129*). Photo credit: Beth Nicholls; Flickr Commons, *AJC1*, *David*

989 *Martyn Hunt.*

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1004 **Figure 4. Increasing floral abundance in the landscape is very likely to benefit**
1005 **pollinator populations**. A Schemes to boost flower abundance in farmland, such as this
1006 wildflower strip along a field margin, have been demonstrated to provide clear benefits for
1007 wild bee populations (e.g. *140–145*); B Urban areas can support high populations of
1008 pollinators, which may spill over into neighboring farmland. Conversion of amenity
1009 grasslands in urban areas to wildflower patches has been shown to greatly boost numbers of
1010 wild pollinators (*151*).
1011