

Landscape alteration and habitat modification: impacts on plant-pollinator systems

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Highlights

1. Insect pollinators face multiple threats including landscape and habitat alteration.
2. Pollinator traits and network structure govern responses to environmental change
3. Changes in pollinator-mediated connectivity may alter plant mating systems
4. Disrupted mating systems may affect plant persistence and trophic interactions

1 **Summary**

2 Insect pollinators provide an important ecosystem service to many crop species and underpin the
3 reproductive assurance of many wild plant species. Multiple, anthropogenic pressures threaten
4 insect pollinators. Land-use change and intensification alters the habitats and landscapes that
5 provide food and nesting resources for pollinators. These impacts vary according to species traits,
6 producing winners and losers, while the intrinsic robustness of plant-pollinator networks may
7 provide stability in pollination function. However, this functional stability might be eroded by
8 multiple, interacting stressors. Anthropogenic changes in pollinator-mediated connectivity will alter
9 plant mating systems (e.g. inbreeding level), with implications for plant fitness and phenotypes
10 governing trophic interactions. The degree to which plant populations can persist despite, or adapt
11 to, pollination deficits remains unclear.

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15 **Introduction**

16 To advance understanding of global change impacts on the natural world requires an increased
17 focus on the changes that occur to the web of biotic interactions that underpin the functions of
18 populations, communities and ecosystems [1, 2]. Many flowering plant species have a facultative or
19 obligate dependence on insect pollination for reproductive success and ultimately population
20 persistence [3]. Furthermore, insect pollination provides an ecosystem service by increasing or
21 stabilizing yields and quality of many fruit, vegetable, oil, seed and nut crops [4, 5], which
22 contribute essential variety and nutrients to human diets [6]. Insect pollinators and the pollination
23 services they deliver face multiple, potentially interacting threats from climate change, pests and
24 pathogens, alien invasive species, and land-use change and intensification [7-9]. Moreover, there is
25 accumulating evidence that pollinator declines, range contractions and community homogenisation
26 have indeed occurred [10-15]. Land-use change and intensification alter the landscape extent and
27 quality of semi-natural habitats that provide the key forage and nesting resources supporting insect
28 pollinators and the pollination service they provide [16-20]. This opinion paper outlines the impact
29 of anthropogenic landscape alteration and habitat modification on pollinators and plant mating
30 systems and the implications for plant population persistence and community dynamics.

31 **Landscape alteration**

32 Pollinators rely on semi-natural habitat for a diversity of food sources and breeding sites [21, 22].
33 Land-use change and agricultural intensification has reduced the amount of such semi-natural
34 habitat and simplified landscape structure [23], and is one of many factors [7] linked to historic and
35 continuing losses of wild pollinator biodiversity [10-14, 24]. Forest fragmentation can lead to
36 declines in flower visitation by native pollinator species [25, 26] and the evenness of European wild
37 bee and butterfly communities was decreased by loss of habitat area [27]. A recent analysis revealed
38 that fragmentation of forested landscapes over the long-term resulted in degraded plant-pollinator
39 networks and substantial levels of pollinator extinction [24]. Extensive habitat loss and

40 fragmentation can isolate populations and reduce their persistence by erecting barriers to gene flow,
41 reducing gene diversity and leading to low effective population sizes [28, 29]. Agri-environment
42 interventions targeted at (re)creating pollinator habitats tend to have the greatest positive impact on
43 bee diversity and flower visitation in fields situated in spatially homogenous landscapes dominated
44 by agricultural monocultures and lacking good quality semi-natural habitat [30, 31]. The proportion
45 of semi-natural habitat in the landscape is therefore a strong predictor of pollinator diversity and
46 abundance [20, 25], stable population dynamics [32] and delivery of pollination services to plants
47 [17, 24].

48 Differences in eco-evolutionary traits (e.g. mobility, feeding adaptations etc) govern the response of
49 pollinator species to habitat loss or landscape simplification. Overall, wild bee and hoverfly species
50 that are more specialised, nest above ground or have limited dispersal abilities are most vulnerable
51 to habitat loss and degradation [10, 24, 33-35]. For example, Western European bumblebee species
52 in decline tend to be those with late season phenology and possessing specialised long-tongued
53 mouthparts adapted to forage on plants typical of unimproved flower-rich grasslands (e.g. Fabaceae)
54 or legume crops, both habitats that declined in extent in this region during the late twentieth century
55 [36, 37]. Nesting habit is a strong predictor of bee species sensitivity to the loss of semi-natural
56 habitats because of the concomitant loss of particular nesting resources (e.g. stems of perennial
57 grasses, herbs and shrubs or dead wood cavities) [33]. Sociality is another trait affecting
58 vulnerability to landscape alteration. Social bees are central location foragers tied to the colony
59 location, consequently they are more sensitive to the distance to forage resource patches in the
60 surrounding landscape [20, 38] than non-social insects with free-living progeny, such as Diptera [38,
61 39]. Even within social bee taxa, species-specific differences in mobility and dispersal range will
62 govern responses to habitat loss and/or fragmentation. For instance, relatively common bumblebee
63 species (e.g. *B. pascuorum*, *B. lapidarius*) in Britain may be somewhat buffered against landscape
64 alteration due to their ability to forage and disperse over greater distances [40] than declining
65 congeners [28, 29]. Such dispersal by highly mobile, generalist species between habitat fragments

66 may ameliorate the effects of landscape fragmentation on pollinator community evenness [27].
67 Landscape alterations therefore are expected to filter species according to eco-evolutionary traits
68 with knock-on effects for ecological function. Creating and maintaining locally diverse, fine-grained
69 and well-connected habitat structure across the landscape will aid the stability of wild pollinator
70 populations and diversity.

71 **Habitat modification**

72 Aside from landscape alteration, anthropogenic perturbation (e.g. pollution, land-use change) and
73 modification (e.g. land management) of habitat structure can alter pollinator communities and
74 pollination processes. Conversion of semi-natural habitat to an agricultural or silvicultural land-use
75 is a prime driver of change to plant-pollinator biodiversity and interactions. Incorporation of semi-
76 natural habitat into livestock farming systems is one example common worldwide. Livestock
77 grazing through consumption of plant biomass, trampling and excreta can modify plant phenological
78 development, reproductive strategies and community structure [39, 41, 42]. Such plant community
79 changes can subsequently affect pollinator abundance or diversity [42] and plant-pollinator
80 interactions [39, 43, 44]. Cattle introduced to Patagonian forests altered the structure of plant-
81 pollinator networks by reducing the frequency of dominant interactions, mainly composed of
82 abundant generalist plant or pollinator species that interacted with many rarer species in the network
83 [43]. Whereas, moderate cattle grazing of birch (*Betula spp.*) habitat in Scotland increased the
84 connectance, via elevated floral species richness, but decreased the nestedness of pollinator
85 visitation networks [39]. Intensive cattle grazing of steppe vegetation, in contrast, eroded plant
86 diversity concentrating pollinator flower visitation onto the remaining few grazing-tolerant ruderal
87 plants [44]. In sum, habitat engineering by grazing livestock has the potential to alter pollinator
88 community structure [39, 43, 44], but the precise outcome likely depends on the habitat type, the
89 land management intensity and the pool of taxa and traits in the community [33, 34].

90 **Multiple, interacting drivers**

91 Insect pollinators face multiple, potentially interacting threats [7-9], yet our understanding of how
92 other global changes combine with landscape and habitat alteration to impact on pollinators is
93 relatively poor. Decreased genetic diversity of bumblebee populations isolated by habitat
94 fragmentation may increase their vulnerability to parasites that are implicated as a driver of bee
95 declines in America [15, 45]. Pollinator species living at the edge of their climatic limits have more
96 variable population sizes [46] and thus may be more vulnerable to the individual and combined
97 effects of habitat loss/fragmentation and climate change [12, 14]. Climate changes are shifting the
98 thermal limits of pollinator (e.g. butterflies) species distributions, but colonisation rates may be
99 restricted by limited availability of semi-natural habitat in intensively farmed landscapes [12].
100 Moreover, climate change may disrupt phenological synchrony between plants and pollinators
101 leading to gaps or curtailment in floral resource availability [47, 48] which, exacerbated by
102 deteriorating floral resources in intensively managed landscapes [36, 37], may lead to nutritional
103 deficits for pollinators. Thus there is the potential risk that pollinator populations and species may be
104 extirpated by the additive or synergistic effects of multiple anthropogenic threats.

105 **Stability and collapse of pollinator communities**

106 Filtering and loss of species due to anthropogenic modification of landscapes and habitats may
107 change community structure to the point where pollination function is lost [16, 24]. Simulation
108 modelling of plant-pollinator networks has revealed that if species losses continue to the point that
109 the most generalised species - i.e. those most connected to other species via direct or indirect species
110 interactions in the network - are eliminated, then a sudden cascade of secondary extinctions could
111 arise [49, 50]. However, the most highly linked and common pollinators may be the least sensitive
112 to extinction [35, 51] and networks of plant-pollinator interactions appear relatively robust to
113 species loss because of the stability derived from network topology (e.g. nestedness), the presence
114 of very abundant and connected species, species redundancy and behavioural flexibility [50-53]. For
115 example, adaptive foraging by generalist species may confer network stability, while ‘rewiring’ of
116 the network by remaining species adopting extirpated species niches may compensate for species

117 loss [52, 53]. However, greater specialisation of plant-pollinator interactions or networks increases
118 vulnerability to perturbation and extinction [10, 24, 33, 35]; this might have implications in
119 temperate regions where plant-pollinator networks tend to be more specialised [54]. Finally, recent
120 theoretical and empirical modelling work suggests that if environmental stresses reach a certain
121 level, then individual bee colonies/populations and even inherently robust pollinator community
122 networks could collapse [50, 55]. As pollinators face multiple anthropogenic threats [7, 8], a
123 potential risk is that this multiplicity of stresses may increase the probability of such sudden
124 population or community collapse, although there have been few experimental tests of this to date
125 [38, 56].

126 **Consequences for plant diversity, fitness and multitrophic interactions**

127 Insect pollination is a vital ecosystem process supporting plant diversity, with an estimated 87% of
128 flowering plant species globally [3] reliant on animal (mostly insect) pollination for mating and
129 reproductive success [57]. Some studies in northern Europe have linked pollinator and plant decline,
130 with facultative or obligate dependence on insect pollination partly explaining observed declines in
131 wild plant species richness or occurrence [10, 36, 58]. It should be noted, however, that another
132 analysis revealed plant species declines occurred irrespective of the level of plant dependence on
133 pollinators [11], suggesting another common driver (e.g. nitrogen pollution).

134 Outcrossing plant species often carry high loads of potentially deleterious recessive alleles [57].
135 Hence modification of plant mating systems by environmental changes (Fig.1) has the potential to
136 elevate the risk of inbreeding depression, affecting plant fitness negatively and potentially driving
137 population evolutionary change [57, 59, 60]. Anthropogenic modification of landscape or habitat
138 structure will drive changes in the densities or dispersion of conspecific plants that change
139 pollinator-mediated connectivity within a plant population (Fig.1) [61]. This can lead to altered
140 pollen flow impacting on the ability of plant individuals to achieve outcrossed mating and avoid

141 biparental inbreeding (i.e. mating among close relatives) and can increase self-fertilisation rates
142 [57].

143 Large areas of contiguous forest are required for minimum viable population sizes of insect-
144 pollinated tree species [62] and trees isolated by fragmentation can experience altered patterns of
145 visitation by native pollinator species [25, 63]. This can potentially lead to disrupted mating
146 systems, altered phenotypes and reduced plant fitness (Fig.1) [59, 60], although the level of this
147 impact is likely to be dictated by the extent of the habitat fragmentation and the pool of pollinator
148 species and traits in the locale [63]. For example, reduced visitation by native pollinators to forest
149 trees isolated by fragmentation was partly compensated by increased visitation of highly mobile
150 introduced honey bees, leading to some reproductive assurance [64, 65]. Plant reproductive success
151 has also been assured by linear features (e.g. hedgerows) facilitating bee-mediated connectivity of
152 plants in fragmented landscapes [66].

153 Similarly, habitat modification by land management (e.g. grazing livestock) may directly (e.g.
154 trampling, consumption) or indirectly (e.g. altered pollinator foraging in disturbed community)
155 affect pollen deposition and seed set by changing the densities and dispersion of conspecific plants
156 [67]. It has also recently been shown that grazing management of woodland was associated with
157 increases in the outcrossing rate and the number of different pollen donors in a focal understory
158 plant species, partly reflecting the increased connectivity of insect visitation networks, driven by the
159 greater floral resources in the grazed habitat [39].

160 Increased self-fertilisation of facultatively outcrossing plants can lead to loss of heterozygosity and
161 increased selection of deleterious alleles, which can reduce plant fitness [57, 59]. Consequently,
162 environmental perturbation that lowers insect-mediated pollen flow can affect the plant phenotype,
163 such as floral traits or volatile emissions, and hence its interspecific interactions across the wider
164 food web [60, 68, 69] (Fig.1). Recent work using experimentally inbred plant lines has shown that
165 inbreeding depressed gene expression in pathways (e.g. jasmonic acid, ethylene) that regulate the

166 induction of defensive compounds and organic volatiles [70]. This altered trophic interactions with
167 inbred plants emitting more constitutive volatiles, which attracted greater numbers of herbivores,
168 but fewer herbivore-induced volatiles leading to reduced natural enemy recruitment [68]. Whether
169 the anthropogenic impacts on pollinator communities, plant mating systems and floral phenotypes
170 [39, 59, 60, 62] lead to similar alteration of multi-trophic interactions has yet to be tested (Fig.1).

171 **Conclusions**

172 Pollination is a key ecosystem process that directly and indirectly supports wider biodiversity and
173 ecological function. Recent research initiatives around the world
174 (e.g. www.insectpollinatorsinitiative.net) are advancing our knowledge about the anthropogenic
175 pressures affecting pollinators and pollination [7]. Nonetheless, further research is needed to
176 understand better the threat to this ecosystem service. For example, we need to improve basic
177 understanding of pollinator [meta]population and [meta]community dynamics in anthropogenic
178 landscapes (Fig.1). We should also assess multifactorial impacts (e.g. landscape modification, alien
179 species, disease) on pollinator networks and plant reproduction (Fig.1) and compare species
180 persistence along gradients of habitat degradation. As plants underpin food-webs in most
181 ecosystems, a particular challenge is to investigate the consequences of human-induced changes to
182 pollination for the multitrophic interactions connecting plants and consumers (Fig.1), both above
183 and below ground. Such an integrated approach will further our capacity to predict the resilience of
184 ecosystems to global environmental changes.

185

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190

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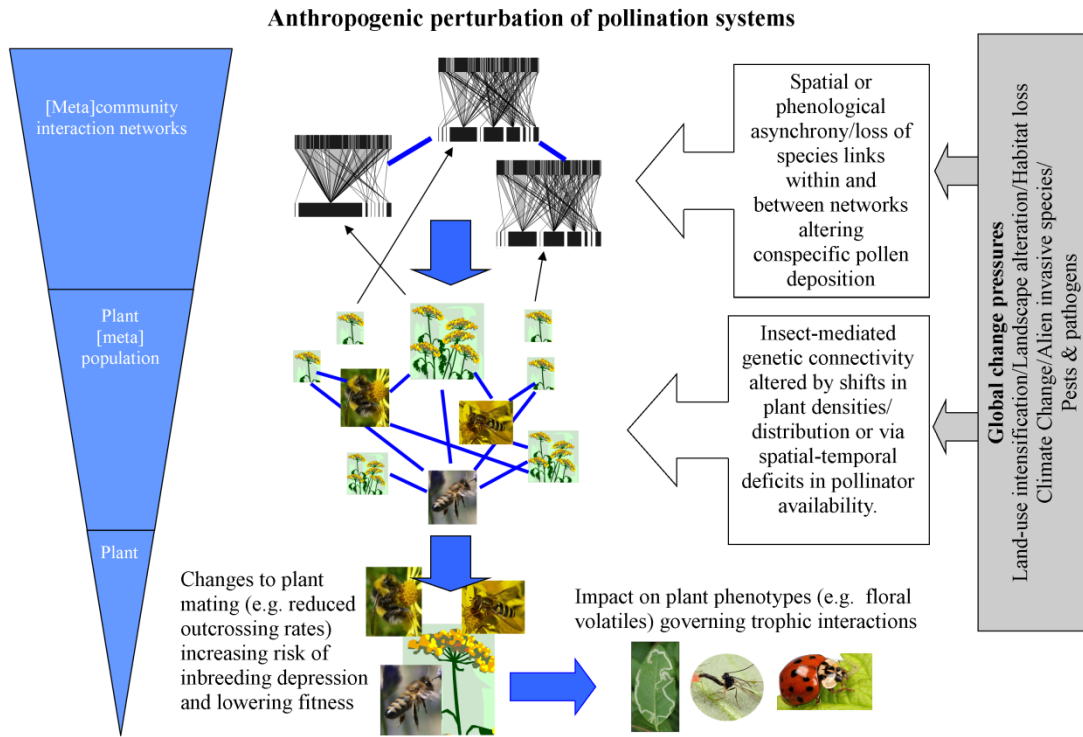
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440 Figure 1. Global change impacts on pollination and trophic interactions across levels of ecological
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