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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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Introduction

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

Landscape alteration

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

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

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

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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**

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

Stability and collapse of pollinator communities

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

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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

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

Conclusions

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

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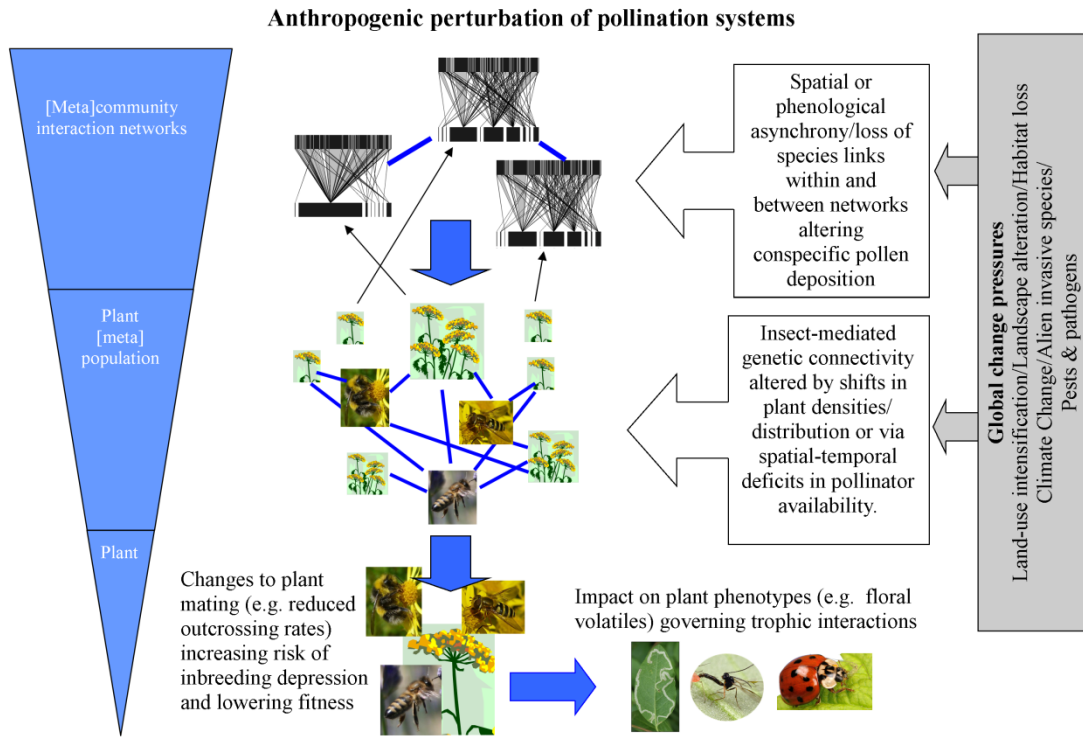391   **mutualism**. Ecology Letters, 2012. **15**: 227-234.

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

organisation