Land-Use Intensification on Plant–Pollinator Interactions

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Permanent grasslands are main habitats for many plant species and pollinators. Their destruction as well as their intensification has a major impact on plant and pollinator biodiversity, which has a cascading effect on pollination. However, we lack an understanding of these effects, thereby limiting our ability to predict them. In this review, we synthesised the literature on the mechanisms behind this cascade to provide new insights into the relationship between land-use intensification and pollination. By matching functional traits that mediate the relationship between the two trophic levels, we identified major knowledge gaps about how land-use intensification affects plant–pollinator interactions and how it favours plants with generalised floral traits, which are likely harmful to pollination.

Keywords: pollination function ; grasslands ; agricultural practices ; functional trait ; effect trait ; plant–pollinator interaction network ; floral traits ; pollinating insect traits

1. Introduction

Insect pollination on permanent grasslands relies on interactions between flowers and pollinators (hereafter, “plant–pollinator interactions”). An approach that includes the morphological, physiological and phenological features of organisms that affect their fitness [1] is useful because plant and pollinator features together drive plant–pollinator interactions. These functional features, called “matching traits” [2] mediate relationships between the two trophic levels [3]. Several plant traits (hereafter, “floral traits”) and pollinator-matching traits are involved in plant–pollinator interactions (**Table 1**). For example, flowers with deep corollas can only be accessed by pollinators with long mouthparts. Matching trait values can be calculated at the community scale, and the community weighted mean (CWM) is the mean value of traits weighted by the abundance of each species in a community. Functional diversity (FD) is the value, range, and relative abundance of functional traits in a given community [4]. In the mass-ratio hypothesis, an ecosystem’s functions depend on the CWM [4]. The hypothesis of niche complementarity suggests that greater FD values increase niche partitioning and lead to species complementary, which serves the ecosystem functions [5]. These hypotheses have been extensively tested for vegetative functional traits but much less so for the relationships between floral traits and pollination.

Table 1. Summary of known and theoretical effects of agricultural intensification on plant-pollinator matching traits. A negative effect is indicated by a -; a positive effect by a +. The level of knowledge about these effects can be: tested in the literature (T), not tested in the literature (NT), indirect (I) or direct (D).

Matching Traits Categories	Matching Traits	Function	Agricultural Practices or Land-Use Index	Effect	Number of Grasslands	Knowledge Level	Country	References
Signals		Allow communication between plants and pollinators and thus interaction between them. Signals generate sensory experiences for pollinators that are different from an animal species to another						[6][7]
	Colour (hue)	Detection from background [8]	LUI	Shift toward white	69	T—D	Germany	[9]
	Photoreceptors and visual system	Matching level between visual system and colour	LUI	-	119	NT—I	Germany	[10]
	VOC emitted	Detection of flower [6]	Grazing and fertilization	None	2	T—D	France	[11]
	ND	Odour preferences	Not tested	ND		NT—I		
Exploitation Barrier		Prohibit interaction with a pollinator if its own matching traits are not adapted						[12]
	Nectar tube depth	Threshold to be reached by pollinator mouthpart length [13]	LUI	-	40	NT—D	Germany	[14][15]
	Relative proboscis length	Depth of exploitable flowers	LUI	-	40	T—D	Germany	[16]

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Matching Traits	Matching Traits Categories	Function	Agricultural Practices or Land-Use Index	Effect	Number of Grasslands	Average Level	Country	References
Essential food for pollinators. They gather mainly nectar as source of carbohydrates and pollen as source of proteins. Rewards are linked with pollinator matching traits which inform for instance on their food needs.	Nectar production	Total quantity of sugar in a grassland [20]	Nitrogen deposition	-	768	T—I	Great-Britain	[21]
	Rewards, Livestock Unit/ha/year			-	561	T—D	Scotland	[22]
	Pollen production	Total quantity of pollen in a grassland	LUI	-	119	T—I	Germany	[23][24]
			Livestock Unit/ha/year	-	561	T—D	Scotland	[22]
	Body size	Quantity of pollinator food needs	LUI	-	40	T—D	Germany	[16]
	Phenology	Temporal availability of rewards [25]	Mowing, grazing, fertilization (i.e., advances) or none	-	33	T—D	France	[26]
			Livestock Unit/ha/year	1989	561	T—D	Scotland	[22]
	Sociability level	Duration of the breeding period	Not tested	-		NT—I		
	Nectar sugar concentration and nectar viscosity	Nectar feeding rate [27]	Not tested	-		NT—I		
	Anatomy of mouthpart	Adaptation to liquid viscosity	LUI	Shift toward sponging-sucking	40	NT—I	Germany	[16][28]
	Pollen amino acid concentration and protein content	Pollen quality [29]	LUI	-	40	NT—I	Germany	[15]
	Pollinator stoichiometric niche	Quality of pollinator food	Not tested	-		NT—I		

The generalisation of floral traits mainly affects the accessibility of floral rewards (pollen, nectar) for pollinators. However, it may also reflect a decrease in the quality of these rewards since many plants favoured by intensification belong to the family Asteraceae [23], which often has low pollen quality [30]. Intensification may also decrease rewards production on

Overall, these changes could have a major impact on pollination, as decreases in floral rewards quantity and quality is a major threat to pollinators [20].

Intensification could also change pollinator community composition. First, total abundance of pollinators, which provides quantitative information about pollination, may fall due to the lower (reward) attractiveness of the grassland and lower food availability. Second, intensification is expected to lead to a decrease in the mean values of pollination effect traits [32], which provide information about the effects of organisms on ecosystem functions [33] (i.e., qualitative information about pollination). Even though traits such as pollinator body size have not been found to be relevant in all ecosystems [34], they are essential to understand ecological processes [35].

Here, we aim to consider both quantitative and qualitative components of pollination because they are rarely considered together despite their high complementarity [2].

2. Effects of Intensification on Plant–Pollinator Matching Traits

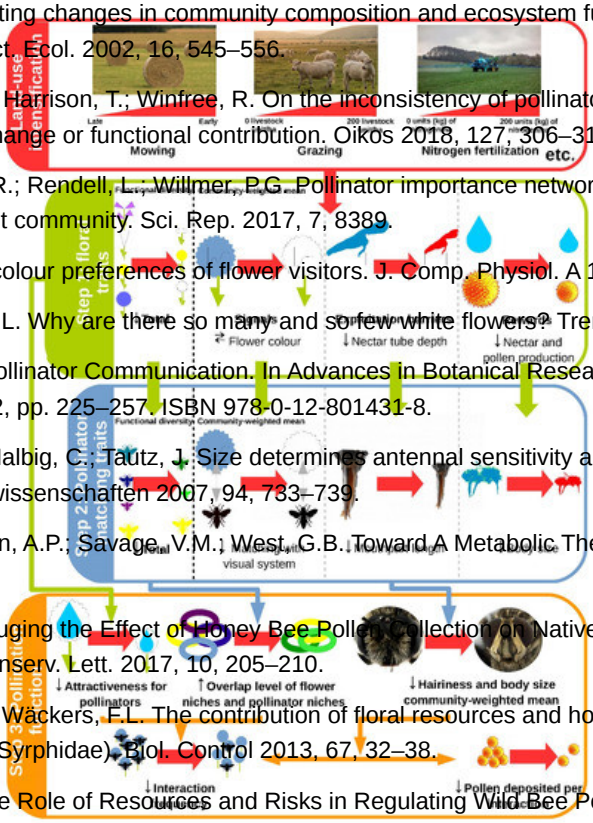

Figure 1. Examples of theoretical cascading effects from land-use intensification to pollination function. The diagram shows only certain expected relationships, but not all were tested. The thick red arrows represent the potential direct or indirect effects of agricultural intensification. The medium-sized colored arrows represent the effects between boxes or within a box (i.e., between steps or within a step in the case of the pollination function). The thin black arrows represent the direction of the expected relationships (upward arrow: increase; downward arrow: decrease; left or right arrow: shift). Agricultural intensification, represented by the red box, combines different parameters (defoliation earliness, duration of pasture or density of livestock, nitrogen fertilization) and could have an effect in step 1 on floral traits (green box). A distinction was made between the three main categories of traits involved in plant–pollinator interactions (signal, exploitation barrier, rewards). In addition, the effects on the total functional diversity and the community weighted mean of traits are distinguished. The shift of flower visitors has a cascading effect on pollinator matching traits in step 2 (blue box). A distinction was made between functional diversity and community weighted mean of traits but also between pollinator matching traits corresponding to signal, exploitation barrier and rewards. These cascading effects could have an impact on pollination function on the grasslands in step 3 (orange box). Two components of the pollination function are distinguished: the quantitative component with the frequency of plant–pollinator interactions and the qualitative component, represented by the quantity of pollen deposited per interaction. The frequency of interactions can decrease with a decrease in the attractiveness of the grassland due to an overall decrease in floral rewards, or with an increase in their diversity drive pollinator visitation. Oikos 2017, 126, 1020–1030.

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3. Potential Effects of Intensification on Pollination Function on Grasslands

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One way to study the relationships between ecosystem functioning and plant–pollinator interactions is to analyse the latter's degree of specialisation. Indeed, the more an interaction network is specialised, the higher the complementarity of its interactions and the differentiation of species niches [45]. An increase in complementarity implies that more functionally complementary species are needed to fulfil the ecosystem function [46]. Matching traits are useful for describing the niches of plants and pollinators [47] and providing mechanistic explanations for the degree of complementarity of plant–pollinator interactions. [48] showed that a plant community with higher floral diversity had higher plant–pollinator interaction network complementarity (measured by H2′, an index that describes the complementarity of interaction, [49]). In our review, we suggest that the CWM of nectar tube depth may decrease with intensification. Hence, flowers may be exploitable by a larger pool of pollinators, which reflects a plant community with more generalised exploitation-barrier traits. Moreover, intensification decreases forb richness [31] and thus may likely decrease flower functional diversity [50] due to its positive relationship with taxonomic diversity. Hence, intensification should generate networks with low functional complementary because of high niche overlap in floral traits among plant species. However, [23] found that intensification decreased plant species diversity but did not decreased H2′, which remained high overall. [51] observed the same lack of correlation without looking at the effect of intensification.

The degree of network specialisation may be explained in part by the matching traits but also by other processes, such as resource competition between pollinators. Hence, two competing pollinators with the same matching traits values may lead to fidelity for a flower [52] that they match less well. This highlights the need to define specialisation of plant–pollinator

interactions carefully [53]. However, on intensively managed grasslands, despite the loss of pollinator species, the stability of pollination function loss may increase, because pollinators are more interchangeable than on less intensive grasslands.

Intensification is likely to decrease the flower functional diversity (e.g., flower colour FD in [9]). Two assumptions can be made concerning the relationship between the FD of floral traits and interaction frequency. First, this relationship may be negative because a higher FD may blur the visual signal, leading to an increase in search time (serial processing; [54]). This assumption was confirmed in the studies of [50] and [55], which recorded a low taxonomic diversity of pollinators with a few generalist pollinator species representing most of interactions. Secondly, we expected a positive relationship between the functional diversity of floral traits and interaction frequency due to a better distribution of pollinators and a greater complementarity of pollinator niches [46]. Ref. [56] confirmed this hypothesis on permanent grasslands with 247 pollinator species. The highly diverse pollinator community recorded in this study may have increased the interaction frequency and the complementary between pollinator niches. Hence, more studies are needed to understand how floral trait functional diversity affects interaction frequency, and to confront niche theory with cognitive ecology, as the latter is based mostly on experiments performed under non-natural conditions [57]. Lastly, to improve understanding of how niche complementarity shapes the relations between floral functional diversity and interaction frequency, studies that include functional indices on each component of functional diversity (e.g., functional evenness, functional richness, functional divergence; [5]), not aggregative indices like functional entropy, Ref. [58] are needed.

Besides interaction frequency, information about the quality of interactions is needed [2][35]. Quality per interaction is often measured as the quantity of pollen deposited by a pollinator during a single visit to a freshly opened flower. This seems to be positively correlated with pollinator hairiness [59][60]. However, these two studies only focused on three cultivated plants species with easy access to the reproductive organs. Ref. [61] showed that pollinators' facial pollen load increased with facial area and hairiness on 127 bee and fly species and 36 wild plants. Ref. [16] found that intensification led to a decrease in the CWM of both relative hairiness and body size of pollinators. An increase in the relative abundance of Diptera, which are less hairy [16][61] and smaller than bees [15] and have different pollination behaviour [62] may explain this result. This shift in pollinator community highlights the need to consider the phylogenetic signals between pollinator effect traits such as hairiness, body size and behaviour, and their respective effects independently.

4. Conclusions

Grassland intensification on floral traits has a cascading effect on the matching traits of pollinators and likely leads to the selection of plant species with generalised floral traits while decreasing the production of floral rewards. A decrease in mouthparts length and body size, two correlated traits, is consistent with the above-mentioned changes in floral traits. Furthermore, shifts in the taxonomic composition of pollinator communities toward Diptera-dominated communities can also be explained by generalised floral traits and the decrease in rewards production. We advocate for more studies to examine relationships between pollinator community composition and intensification to determine if the increase in the relative abundance of Diptera because of intensification is a common pattern.

Second, the data on how grassland intensification affects quantitative floral and pollinator traits are lacking. Indeed, while some of the matching traits that explain plant–pollinator interactions are well known—e.g., flower colour and insects' visual systems have been studied for more than 100 years [63]—others, like flower odours, have received little attention or remain to be studied because they belong to different ecological fields. In particular, the impact of grassland intensification on floral rewards quality has rarely been studied.

Overall, little is known about the effect of intensification on grassland pollination function despite its importance in the current global pollination crisis. Most studies reviewed here addressed this issue with a quantitative dimension by using interaction frequency as a proxy of pollination function. We highlighted possible relationships between intensification and several qualitative dimensions of plant–pollinator interactions by focusing on pollinator hairiness and body size. In addition, although intensification leads to decreased pollination function, it selects for generalised plant species, but plants with generalised floral traits may be less pollen-limited than those with specialised floral traits [64].

Lastly, while the landscape scale has been recognised elsewhere as a main driver of plant–pollinator interactions [65], we showed that local factors may also change them drastically, despite having little knowledge about the ecosystem scale. This review places these gaps of knowledge into a clear framework, which we hope will motivate researchers to study them, especially because a holistic view of the human impact on pollination function and pollinators is needed to understand the current global pollination and pollinator crisis.