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Increasing plant functional diversity is not the key for supporting pollinators in wildflower strips

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ABSTRACT

Intensification of agriculture has been one of the major drivers for biodiversity loss in recent decades. Pollinators, which serve an important role in pollinating crops as well as wild plants, have shown a decline in species richness. Flower strips can be used to support pollinators in agro-ecosystems, however the question remains as to how their design can be optimized in order to best benefit pollinators. Increasing plant species diversity has been shown to be beneficial for pollinators, and it is often suggested that functional traits are driving this relationship. Therefore, increasing plant functional diversity could be a tool to support pollinator abundance and diversity. As experimental evidence on this relationship is scarce, we developed a field study with experimental sown flower strips with four functional diversity levels, based on multiple flower traits and with equal plant species richness. We monitored vegetation development, as well as the flower-visiting pollinator community and their interaction networks with flowers. We were able to create a functional diversity gradient while controlling for plant species richness and evenness. However, in contrast to our expectations, pollinator species richness and evenness were not influenced by functional diversity, and increasing functional diversity even resulted in lower flower visitation rates. Network stability metrics showed no effect or negative relationships with functional diversity. We conclude that increasing functional diversity was not the key for supporting pollinators in wildflower strips. Our results also suggest that, for a constant amount of flower resources, increasing plant functional diversity and thus decreasing redundancy of potential pollinator feeding niches, decreases the amount of flower resources present per feeding niche. As pollinator species tended to have less overlap in their feeding niches in flower strips with increased functional diversity, this may lead to a reduction of flower resources available for pollinator species with a more specialized feeding niche.

1. Introduction

Intensification of agriculture has been one of the major drivers for biodiversity loss in recent decades (Stoate et al., 2001; Tilman et al., 2001). Among others, pollinators, which play a critical role in delivering pollination services to crops and wild plants (Klein et al., 2007; Potts et al., 2010), have seen declines in species richness and abundance (Biesmeijer et al., 2006; Potts et al., 2010; Winfree et al., 2009). The provision of food sources, shelter, and nesting sites in agro-ecosystems, by creating and managing ecological infrastructure, has been suggested as an important way to support pollinators (Klein et al., 2007; Nicholls and Altieri, 2012). One example is wildflower strips (Wratten et al., 2012), of which the main goal is to enhance biodiversity, while also attracting useful insects such as crop pollinators as well as natural enemies of crop pests (Haaland et al., 2011). Creating flower strips is in most cases beneficial for pollinators (Uyttenbroeck et al., 2016), however the question remains as to how to optimize their design to support pollinator abundance and diversity. Next to the intrinsic biodiversity conservation value, a higher abundance and diversity of pollinators can also enhance pollination services (e.g. Albrecht et al., 2007; Hoehn et al., 2008; Klein et al., 2003; Morandin and Winston, 2005).

Increasing the number of plant species in flower mixtures has been suggested to improve the effectiveness of flower strips for pollinator support (Scheper et al., 2015). Indeed, it has been reported that pollinator abundance and species richness are positively related to plant species richness (e.g. Ebeling et al., 2008; Hudewenz et al., 2012; Potts

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et al., 2003; however, see Grass et al., 2016). Also pollinator functional group richness (Hegland and Boeke, 2006) and pollinator functional diversity (based on pollinator feeding niche, i.e. the plant families they are reported to visit; Orford et al., 2016), were found to be positively related to plant species richness. Next to plant species richness, increasing flower abundance is often found to increase pollinator abundance and species richness (e.g. Hegland and Boeke, 2006; Ebeling et al., 2008). Increasing plant species richness offers more feeding niches to pollinators, which can allow more pollinator species to find floral resources (Blüthgen and Klein, 2011).

Whereas increasing plant species diversity is beneficial for pollinators, they perceive their host plants by their functional traits (Campbell et al., 2012; Fontaine et al., 2006; Junker et al., 2013). The shape of flower corolla for instance, determines the accessibility of floral nectar for flower visitors, while pollinators, depending on the length of their mouthparts, may prefer different corolla shapes (Fontaine et al., 2006). Flower functional traits can act as attractive features or as barriers for flower visitors. Traits related to flower phenology, morphology and visual cues have been reported to contribute more in defining the pollinator species feeding niche, compared to other traits, like flower nectar and pollen mass and display size (Junker et al., 2013). As these functional traits may be the underlying mechanism, increasing not plant species diversity *per se*, but increasing plant functional diversity (FD), i.e. the value and range of plant functional traits (Tilman et al., 2001), has been suggested as a tool to support pollinators and pollination services (Campbell et al., 2012; Fontaine et al., 2006; Junker et al., 2013). Increasing plant FD is expected to increase the number of feeding niches available for pollinators, and thus to support more pollinator species (Junker et al., 2013).

Experimental evidence for the relationship between plant FD and pollinator abundance and diversity, however, is scarce. Balzan et al. (2016, 2014) created a gradient of flower strips by increasing plant functional group richness. They found a positive effect of the presence of flower strips on the abundance of flower visitors, but in general no clear effect of a higher plant functional group richness. Campbell et al. (2012) created flower strips with one or two plant functional groups, based on corolla depth, and with similar total flower abundance. They found that flower strips with two plant functional groups attracted similar numbers of bumblebees (Hymenoptera: Apidae: *Bombus* sp.) and syrphid flies (Diptera: Syrphidae) as flower strips with one functional group, while the number of parasitoids (super-family Hymenoptera: Parasitica) was reduced in plots with two plant functional groups. The functional diversity gradient in these studies was however simplified to varying either a single trait (Campbell et al., 2012) or the number of functional groups (Balzan et al., 2016, 2014), and both studies did not control for plant species richness. To the best of our knowledge, an experiment with a plant FD gradient based on several functional traits and without increasing plant species richness, had not been conducted prior to this study.

When plant species richness is increased in a plant community, each additional species can add either complementary or redundant trait values to the functional trait spectrum of that plant community. This may result in a saturating increase of plant functional diversity and potential feeding niches, and thus a saturating increase of pollinator diversity, as simulated by Junker et al. (2013). When plant FD is increased with constant plant species richness, i.e. by replacing plant species by other plant species with more complementary trait values, the number of complementary feeding niches available for pollinators should also be higher. However, this may also imply that there is less overlap and thus less redundancy in these niches, as the same number of plant species has to provide more different functional trait values. Consequently, non-generalist pollinators are less likely to have several plant species providing their feeding niche in plant communities with high functional diversity. By consequence, they may visit fewer plant species, resulting in a less connected interaction web between plants and pollinators. Analyzing plant-pollinator interactions as a mutualistic network can deliver useful information on stability and structure of these interaction webs (Tylianakis et al., 2010). A change in network structure can decrease the resilience of the plant-pollinator interaction network and can be measured with network structure metrics such as connectance and nestedness (Devoto et al., 2012; Thébault and Fontaine, 2010; Tylianakis et al., 2010).

To use the plant FD approach in wildflower strips, these strips can be sown with a seed mix to create a desired level of FD. However, sowing a seed mix may not automatically result in the desired vegetation composition (De Cauwer et al., 2005; Lepŝ et al., 2007; Uyttenbroeck et al., 2015). Other plant species can settle spontaneously from seeds in the soil seed bank or from dispersing seeds, while sown species may not always successfully settle (Münzbergová and Herben, 2005).

To test whether increasing FD is a key factor for supporting pollinators, we developed a field study with experimental flower strips establishing a FD gradient based on multiple flower traits and without increasing plant species richness. We monitored vegetation development, as well as the flower-visiting pollinator community and their interaction networks with flowers, aiming to explore the effect of increasing FD on (i) the community composition of the flower-visiting pollinator species, (ii) the species richness and evenness of pollinators, (iii) the visitation rate of pollinators, (iv) the structure of the plant-pollinator network, more specifically on network resilience metrics connectance and nestedness, and (v) the overlap in the feeding niches of the pollinators.

2. Materials and methods

2.1. Experimental setup

To test the use of FD in the establishment of wildflower strips for pollinators, we set up an experimental functional diversity gradient in wildflower strips in an arable field. The field setup is briefly described here. For a more detailed description, see Uyttenbroeck et al. (2015).

The FD gradient was made by composing four mixtures of herbaceous species with contrasting levels of FD and equal species richness and evenness. From a list of 20 commercially available forb and legume species commonly found in grasslands and used in perennial flower strips (agri-environment scheme MC8c; Natagriwal asbl, 2017) in Wallonia, Belgium, we simulated all possible mixtures of seven species. To calculate the functional diversity of these mixtures, we selected seven functional traits related to flower morphology, flower visual cues and flower phenology, as these floral traits are expected to influence flower-visiting insect communities in wildflower strips and their interaction networks with plants (Hegland and Totland, 2005; Junker et al., 2013). The selected traits are (1) flower color (three classes: 'white', 'yellow' and 'violet/purple' with the last one containing red, pink, purple, violet, lilac and blue), (2) flower type according to Müller (1881) (categorical: 'Hymenoptere flowers', 'Bee flowers', 'Bumblebee flowers', 'Flowers with open nectar', 'Flowers with totally hidden nectar', 'Flower associations with totally hidden nectar'), (3) UV reflection in the periphery of the flower (categorical, 5 class means: 3.5%, 11.5%, 21.5%, 33.5%, 53%, 76%), (4) presence of a UV pattern (categorical: 'yes', 'no'), (5) the month of the initiation of flowering (numerical), (6) flowering duration in months (numerical) and (7) the maximal height of the plant. For these functional traits, trait values of the 20 selected species were retrieved from the TRY database (Kattge et al., 2011; trait 1–4) and from Lambinon et al. (2008. With these trait values, FD of all simulated mixtures was calculated using Rao quadratic entropy index based on Gower distance (Botta-Dukát, 2005), with equal abundance of the seven plant species in a mixture. The mixtures with lowest and highest FD were selected, as well as the mixtures with functional diversity closest to the 33rd and 67th percentile of the FD range. This resulted in four plant species mixtures with contrasting FD: very low (VL), low (L), high (H) and very high (VH). For these mixtures,

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