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Plant–flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient

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Abstract

Although most plants benefit from pollen vectors, very little information exists about how plant diversity structures the interactions between plants and their flower visitors. The structure of such interaction webs holds information about specialization and effectiveness of flower visitors in flower resource use. Here, we analyzed 52 plant–flower visitor interaction webs along a gradient of experimentally manipulated plant species richness in a European grassland. The gradient allows testing for effects of the number of flowering plant species per se. Linkage density and interaction diversity between flowering plant species and their visiting insect species increased with higher richness of flowering species. Increased interaction diversity led to smaller temporal variability in the frequency of flower visits. These results suggest higher temporal stability of pollination provided for plants integrated in complex interaction webs with a high number of flowering plant species.

Flower resource specialization of solitary bees, but not of honey and bumble bees, increased with increasing flowering plant species richness. Conservation of diverse grasslands can result in high flower specialization and may promote effectiveness of pollination services.

Zusammenfassung

Die meisten Pflanzen werden durch Pollenüberträger begünstigt, jedoch ist wenig bekannt über die Auswirkungen von Pflanzendiversität auf die Interaktionen zwischen Pflanzen und ihren Blütenbesuchern. Die Struktur dieser Interaktionsnetze liefert wichtige Informationen über Spezialisierung und Effektivität der Blütenbesucher in ihrer Resourcennutzung. Wir untersuchten 52 Pflanze–Blütenbesucher-Interaktionsnetze eines europäischen Graslandes entlang eines experimentellen Gradienten in der Anzahl von Pflanzenarten. Der experimentelle Gradient bietet uns die Möglichkeit den Einfluss der Anzahl der blühenden Pflanzenarten per se zu untersuchen. Linkdichte (linkage density) und Interaktionsdiversität (interaction diversity) zwischen den blühenden Pflanzenarten und ihren Blütenbesuchern nahmen mit der Anzahl der blühenden Pflanzenarten zu. Ein Anstieg in der Interaktionsdiversität führte wiederum zu einer Abnahme in der zeitlichen Variabilität. Die Ergebnisse lassen auf höhere zeitliche Stabilität in der Bestäubung von Pflanzen schließen, die von einer hohen Anzahl an blühenden Pflanzenarten umgeben

Keywords: Biodiversity experiment; Bumble bees; Grassland; Solitary bees; Honey bees; Temporal stability

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sind und somit in ein komplexes Interaktionsnetz integriert sind. Die Spezialisierung auf Blütenresourcen nahm bei den solitären Bienen mit zunehmender Anzahl an blühenden Pflanzenarten zu, nicht jedoch bei Honigbienen und Hummeln. Der Schutz von diversen Graslandflächen führt demnach zu höherer Resourcenspezialiserung, und kann somit eventuell eine Zunahme in der Bestäubungsleistung fördern.

Introduction

Plant reproduction may not only be influenced by the number and density of pollinating species but may depend also on the number and type of interactions between plants as the primary producers and pollinators as the primary consumers. Metrics, describing the structure of these interaction webs, are sensitive indicators for slight changes in entire communities.

The present study is based on a data set that had already been used by Ebeling, Klein, Schumacher, Weisser, and Tscharntke (2008). While the previous study investigated species number and diversity patterns, the present study looks at plant–pollinator interaction webs. In contrast to common metrics like species richness (e.g. of flower visitors in relation to plant species richness), interaction structure also accounts for species identity and link intensity, and therefore shows changes before diversity loss becomes visible (Tylianakis 2008; Bascompte 2009; Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch 2010). Plant–flower visitor interaction webs and their metrics such as linkage density, interaction diversity or flower resource specialization hold important information for network stability (e.g. May 1972; Bascompte 2009; Parrott 2010). For example, the proportion of weak versus strong plant–pollinator interactions (flower visits) can influence resistance of plant–flower visitor networks to the extinction of a single species (Bascompte, Melian, & Sala 2005; Kaiser-Bunbury et al. 2010). Further, food web theory predicts a decline in the complexity (linkage density) of biotic interactions with decreasing species richness and abundance, which makes a system more sensitive to extinctions of important key species or elements shown for example by low values of linkage density (Melian & Bascompte 2002; Ives & Cardinale 2004). Interaction metrics such as linkage density or interaction diversity can also be used to study the variability of density of flower visitor species over time, giving information about the temporal stability of pollinator communities (Dyer, Walla, Greeney, Ill, & Hazen 2010).

Bee species greatly differ in their feeding niches (Bluethgen & Klein this issue). The majority of pollinating species are polylectic and forage on pollen of many different plant species (Eickwort & Ginsberg 1980; Waser, Chittka, Price, Williams, & Ollerton 1996; Fontaine, Thébault, & Dajoz 2009). The degree of flower visitor resource specialization within an interaction web may be an indicator of the effectiveness of the pollination service provided. Resource specialization gives us information, if species are able to utilize a wide variety of food resources (generalists) or if they are relatively restricted in their food resources (specialists). In the case of largely specialised oligo- and monolectic bees robbing pollen from their preferred plant species resource specialization could lead to reduced effectiveness of the pollination service. In the case of our study, where only polylectic bee species belong to the bee community, higher resource specialization implies behavioural changes in resource specialization. Higher resource specialization was shown to increase flower constancy of the bees, which may turn into a better pollination benefit (Larsson 2005; Perfectti, Gómez, & Bosch 2009; Bluethgen & Klein this issue).

Recently, methods have been developed to allow the quantification of flower visitor resource specialization (Dormann, Gruber, & Fruend 2008; Dormann, Fruend, Bluethgen, & Gruber 2009). An interaction web-wide measure of specialization, and a species- or guild-specific measure of specialization can be calculated, which is independent of the total number of species in the interaction web (Bluethgen, Bluethgen, & Menzel 2006; Bluethgen, Menzel, Hovestadt, Fiala, & Bluethgen 2007).

Many real-world studies have investigated mutualistic interaction webs (e.g. Memmott 1999; Bluethgen et al. 2006; Kaiser-Bunbury, Memmott, & Müller 2009; Albrecht, Riesen, & Schmid 2010; Fruend, Linsenmair, & Bluethgen 2010; Kaiser-Bunbury et al. 2010; Weiner, Werner, Linsenmair, & Bluethgen this issue; Gotlieb, Hollender, & Mandelik this issue) by analysing differences in food availability (blossom cover) and flowering species richness (but see Fontaine, Dajoz, Meriguet, & Loreau 2006). In this study, however, we controlled for additional influences occurring in natural ecosystems (soil fertility), and could clearly identify the flower visitor response to plant species richness or changes in richness and blossom of flowers.

The present study is part of the Jena-Experiment (Roscher et al. 2004), and we analyzed the structure and the specialization of 52 plant–flower visitor interaction webs along an experimental gradient of flowering species richness. We used highly replicated experimental grassland plots, where plant species richness had been manipulated and species composition was randomly selected out of a species pool of 60 grassland species. It is known that small-scale changes in the vegetation can determine bee and wasp communities – due to their high mobility and their active selection of the most suitable plants (e.g. Tylianakis, Klein, & Tscharntke 2005). Lazaro and Totland (2010) showed that foraging behaviour was mainly driven by the availability of attractive plant species in small flower patches, and by patch diversity and density. Pollinators are attracted differently by differently composed plots albeit the small plot size and the small dis-