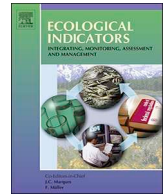




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Original Articles

The vulnerability of plant-pollinator communities to honeybee decline: A comparative network analysis in different habitat types

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ABSTRACT

The populations of most pollinators, including honeybees, are declining that heavily affects both crop and wild plant pollination. Wild bee diversity and habitat type may modulate these effects. We addressed the question how the structure of plant-pollinator networks in different habitat types may influence the vulnerability of pollinator communities to the hypothetical loss of honeybees. We performed network analysis based on plant-visitation data in a traditional agricultural landscape and quantified the structural vulnerability (i.e. the effect of the loss of honeybee) of the plant-pollinator networks by a topological index (distance-based fragmentation). We found that very different plant-pollinator communities inhabited the studied different agricultural habitat types. The early summer arable fields had the most, pastures in mid-summer had the less vulnerable structure and, in general, an intermediate plant/pollinator ratio was associated with high vulnerability in the absence of honeybees. We suggest that increased plant species richness can ensure higher wild bee diversity and more stable plant-pollinator networks without honeybee, where flower-visitation can rely more on wild bees. Decreased management intensity in agricultural landscapes can therefore contribute to the maintenance of diverse plant-pollinator communities in agricultural landscapes and to sustainable farming.

1. Introduction

Ecosystem services like pollination (Daily, 1997; Ollerton, 2017) may be better managed if the evolutionary ecology of the underlying processes is better understood (Bronstein, 2001). In the age of the pollination crisis (Ghazoul, 2005; IPBES, 2016; Potts et al., 2016), it is a major challenge to better understand the ecological and economical aspects of pollination as an ecosystem service. The decline of pollinators seems to be strongly related to agricultural activities at both local and landscape scales (Carvell et al., 2017; Kovács-Hostyánszki et al., 2017). Such disturbance, however, might have no visible effect on the number of foraging bee species, while disturbance can reduce the number or frequency of bee and flower interactions, and consequently foraging and pollination success (Carman and Jenkins, 2016). This calls for an explicit analysis of plant-pollinator communities along a gradient of human influence.

Western honeybee (*Apis mellifera*) is widely used, managed pollinator, responsible for pollination of highly commercial crops (e.g. almond, cherry, apple, etc.; Abrol et al., 2012), but it is also important

supergeneralist pollinator in wild plant communities (Giannini et al., 2015; Hung et al., 2018). The exclusive dependence on honeybees, however, has several risks. On the one hand honeybees show massive decline in several parts of the world (Goulson et al., 2015; IPBES 2016) that can be balanced by beekeepers in a certain extent dividing existing colonies, but still the number of honeybee colonies cannot keep up with the even faster growing of insect-pollination demand of agricultural crops (Aizen et al., 2009). On the other hand, honeybees are capable for effective pollination only among favourable weather conditions (Brittain et al., 2013), and only for certain plant species at limited extent (Garibaldi et al., 2013), while their pollination service is often well supplemented, substituted by wild pollinators or even exclusively provided by them (Aslan et al., 2016). Furthermore, the presence of honeybees within agricultural and (semi-) natural habitats is strongly influenced by beekeeper activities (e.g. location and number of colonies), and in natural habitats in 33% of plant-pollinator networks honeybee visit was not even observed (Hung et al., 2018), which consequently rely on only wild pollinator species. To conclude, the decline or lack of honeybees in agricultural and (semi-) natural habitats can be a realistic

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scenario among different circumstances that can have a considerable but still partly unknown effect on plant-pollinator communities. Looking at from the wild pollinators point of view, wild bees and others face also the detrimental effects of land-use change, land management and other effects such as pathogens, climate change, invasion (Goulson et al., 2015; IPBES 2016), therefore the stability of managed and semi-natural ecosystems against wild bee decline is also questionable.

A systems approach to understand land use and land management effects and the reliance of plant-pollinator communities on honeybee and wild bees is the analysis of plant-pollinator networks that have been extensively studied in the last decades (Jordano, 1987; Memmott, 1999; Olesen et al., 2002; Bascompte et al., 2003; Vamosi et al., 2006; Waser and Ollerton, 2006; Bascompte, 2009; Guimarães et al., 2017; Kaiser-Bunbury et al., 2017; Soares et al., 2017). The analysis of these mutualistic bipartite networks may help in quantifying either their local (e.g. hubs, Biella et al., 2017) or global (e.g. nestedness, Podani et al., 2014) properties, characterizing particular species or the whole community, respectively. Since plant-pollinator interaction networks encompass the characteristics of species, their interactions, and the evolutionary processes (Bascompte, 2007), they may be better indicators of environmental change effects than species diversity (Tylianakis et al., 2010; Carman and Jenkins, 2016; Soares et al., 2017).

In this paper, (1) we describe a large-scale, total plant-pollinator network for a traditional agricultural landscape in Transylvania, Romania, (2) we analyse and compare its 16 subnetworks representing different habitat types (according to land use and land management) and (3) we study the vulnerability of these networks to honeybee loss, using a network measure imported from social sciences to ecology. We hypothesised that the structure of plant-pollinator networks is different in different habitat types based on their land-use, sown crop type or management in the case of grasslands, which may also influence the vulnerability of their flower-visitation networks to the hypothetical loss of honeybees. We expected higher vulnerability of those networks that are comprised by fewer plant and/or pollinator species, whereas flower-visitation networks of floristically diverse habitats were hypothesised to be more stable and based more on wild bees as flower visitors. Such differences can be also expected within land-use or crop types depending on the season and the availability of flowering plant species between months.

2. Data: Network construction

We collected flower-visitation data in Southern Transylvania, Romania in 2012 (see map in Kovács-Hostyánszki et al., 2016, S1. Fig), in 19 village catchments characterised by a traditionally managed agricultural landscape of small parcels of low-intensity arable fields (15%), pastures (40%) and deciduous forests (33%). In each catchment typically two arable fields and two grasslands (land-use types) were chosen, which varied along different crop and/or management types, including alfalfa ($N = 15$), cereal (winter wheat and barley; $N = 8$), corn ($N = 8$), fallow ($N = 4$), grassland with shrubs ($N = 7$), pasture (grazed by cattle or sheep; $N = 24$), hay meadow ($N = 10$) and mowed grasslands or harvested arable fields (hereafter stubbles; $N = 14$). (for further details see Kovács-Hostyánszki et al., 2016). Landscape composition around the study sites was considered by the calculation of percentage area of semi-natural habitats (vineyards; fruit trees and berry plantations; pastures; complex cultivation patterns; land principally occupied by agriculture, with significant areas of natural vegetation; natural grasslands; transitional woodland-shrub) and Shannon index of land cover diversity (land cover categories: urban, arable, semi-natural, forest, water) within 1000 m radius circle using CORINE land cover data (European Environment Agency, 2013) and ARCGIS software (ESRI, 2008). We compared the two land-use types (arable vs. grassland) and the eight crop and/or management types in the function of semi-natural area ratio and Shannon habitat diversity in the 1000 m radius circle around the focal fields. We found that arable fields and

grasslands (t -test; $t = 0.37$, $df = 146.901$, p -value = 0.711) and the seven crop and/or habitat types (Anova; $df = 6$, $F = 1.99$, $p = 0.070$) did not differ in the sense of habitat diversity. The percentage of semi-natural habitats was higher around grasslands (that is a semi-natural habitat itself; $t = -5.79$, $df = 147.252$, $p < 0.001$). Here especially pastures were surrounded by higher percentage of semi-natural habitats compared to the arable fields (Anova; $df = 6$, $F = 4.24$, $p < 0.001$; Tukey-test: pasture – Cereal: 0.007; Appendix A).

We sampled flower-visiting bees by transect walk method along two parallel 100 m long transects (1.5 m width either side) per field, at least 30 m from the edge and 50 m from each other, over 20 min per transect once per month in May, June, July in 10–12 days' periods on dry and warm days with minimal wind, and 20 °C minimum temperature, between 9 AM and 6 PM. All bee specimens and plant species that were visited by the bees were identified at species level.

Based on plant-visitation field data from 38 arable field and 38 grassland communities, we created a, total" interaction network of 256 species: 123 plant (Appendix B) and 133 wild bee species (Appendix C). For clarity, we omitted samples that were impossible to taxonomically specify (e.g. individuals identified only at genus level) – These represented only 3.65% of individuals in the samples. The interaction network is a weighted (by frequency of visits), undirected (effects spreading in both bottom-up and top-down direction) and unsigned (all interactions are mutually positive) graph.

We note here that this pooled, total" network represents the plant-pollinator community at a larger-scale, with lower spatial resolution (at the landscape level). We have also studied 16 subnetworks of this, total" network, describing particular locations (habitat types). We note that these communities (and the networks) are not perfectly independent of each other (e.g. pastures are subsets of grasslands), they must be considered as various appropriately defined subsets. Based on land use, we constructed separate networks for grasslands (G) and arable fields (A). According to habitat type and land management, we constructed separate networks such as shrubby grassland (SHG), cereal field (CEF), hay meadow (HAM), cornfield (COF), pasture (PAS), stubble (STU), alfalfa (ALF) and fallow (FAL). Moreover, based on existing temporal data series, for the grassland (G) and the arable field (A) networks, we could construct interaction networks for May (G5 and A5), June (G6 and A6) and July (G7 and A7), where numbers refer to months. The details of these communities and land use effects are studied and discussed in Kovács-Hostyánszki et al. (2016).

Most of the networks contained either isolated species or smaller (dwarf) components including only a few species. We focused on the giant component of the networks, presenting also the pollinator species composition in the dwarf components (Appendix D). We note that the identity of components is perfectly consistent (a component with only species i and j and another component with only species j and k imply the existence of a third component with only species i and k). In the case of the total network, there was only a single dwarf component (of two species), and this component was deleted together with all the isolated nodes (species sampled in the field with no detected interaction partner).

For the total network, we have also calculated the relative abundance values (RA_i) of pollinators: this equals the number of individuals of species i per all identified individuals. The sum of RA_i values equals one. We plotted the RA_i values with and without the honeybee (APIMEL) in Appendix E: almost 35% of the pollinator individuals belonged to honeybee (a), so the plot without honeybee (b) could show the abundance rank of further, wild bee species.

3. Methods

Several methods have been used for studying mutualistic, bipartite networks in ecology (Benedek et al., 2007; Blüthgen et al., 2006; Podani et al., 2014). In this paper, we studied some global properties of the plant-pollinator networks, quantifying them by simple topological

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