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The influence of space on the structure (e.g. modularity) of complex ecological networks remains largely unknown. Here, we sampled an individual-based plant–pollinator network by following the movements and flower visits of marked bumblebee individuals within a population of thistle plants for which the identities and spatial locations of stems were mapped in a 50×50 m study plot. The plant–pollinator network was dominated by parasitic male bumblebees and had a significantly modular structure, with four identified modules being clearly separated in space. This indicated that individual flower visitors opted for the fine-scale division of resources, even within a local site. However, spatial mapping of network modules and movements of bumblebee individuals also showed an overlap in the dense center of the plant patch. Model selection based on Akaike information criterion with traits as predictor variables revealed that thistle stems with high numbers of flower heads and many close neighbours were particularly important for connecting individuals within the modules. In contrast, tall plants and those near the patch center were crucial for connecting the different modules to each other. This demonstrated that individual-based plant–pollinator networks are influenced by both the spatial structure of plant populations and individual-specific plant traits. Additionally, bumblebee individuals with long observation times were important for both the connectivity between and within modules. The latter suggests that bumblebee individuals will still show locally restricted movements within sub-patches of plant populations even if they are observed over a prolonged time period. Our individual-based and animal-centered approach of sampling ecological networks opens up new avenues for incorporating foraging behaviour and intra-specific trait variation into analyses of plant–animal interactions across space.

Ecological networks describe the structure of interactions among multiple species or individuals. These interactions can be trophic, antagonistic or mutualistic, forming food webs, host–parasitoid webs or mutualistic networks (Ings et al. 2009). The study of ecological networks has developed rapidly in the past decade and several structural (i.e. topological) features such as modularity have been revealed (Bascompte and Jordano 2007, Olesen et al. 2007). A modular network consists of weakly inter-linked subsets (modules), e.g. species interact more with species within their own module than with species in other modules (Pimm 1979, Paine 1980, Lewinsohn et al. 2006, Olesen et al. 2007). Modularity as well as other structural features of ecological networks show temporal dynamics and can change over time (Olesen et al. 2008, Dupont et al. 2009, Dupont and Olesen 2012). Moreover, network structure might not only vary across time but also across space, e.g. along a humidity gradient (Devoto et al. 2005), altitude (Ramos-Jiliberto et al. 2010), or latitude (Trøjelsgaard and Olesen 2013). However, to date ecological network analyses are often non-spatial, i.e. they do not explicitly incorporate space into the analytical framework (Dale and Fortin 2010, Kissling et al. 2012).

Quantification of spatial structure in network topology could help to understand many basic and applied questions in ecology and evolution (Carstensen et al. 2011, Hagen et al. 2012, Montoya et al. 2012, Dáttilo et al. 2013). For instance, in island biogeography the presence–absence of bird species on islands has been analysed with a network approach to identify the role of individual islands for source–sink dynamics of avifaunas within archipelagos (Carstensen et al. 2011). At the landscape level, many habitats are permeable for species and their interactions (Hagen et al. 2012) and ecological networks from different habitats are therefore connected across habitat borders, with important implications for the restoration of ecosystem services (Montoya et al. 2012). At the population level, a spatial network approach can reveal that pollen flow in a plant population is non-randomly structured because groups of mother trees and donor trees are located in spatially well-defined modules (Fortuna et al. 2008). At the local scale, an ecological network might also be spatially structured due to

the small-scale movement and dispersal behaviour of animal species and individuals (Viswanathan et al. 1999). However, to our knowledge only few studies have attempted to incorporate such small-scale movements of animals into the analysis of ecological networks.

Recently, ecological networks have been used not only to analyze interactions among species, but also interactions among individuals (Araujo et al. 2008, Dupont et al. 2011, Gómez et al. 2011, Gómez and Perfectti 2012, Tur et al. 2014). Studies of individual-based plant–pollinator networks have revealed that conspecific individuals vary widely in number of interaction partners (Dupont et al. 2011, Gómez et al. 2011) or niche breath (Araujo et al. 2008, Tur et al. 2014), and hence in their topological role within the network. In species-level networks, topological roles of species have been shown to be important for network coherence and stability (Olesen et al. 2007, Goméz et al. 2012, Pocock et al. 2012). However, such network studies have not explicitly addressed the spatial constraints on network structure, despite the fact that local space use of consumers and the spatial distribution of resources are likely to affect interactions. The few existing studies of plant–pollinator networks at the level of individuals indicate that the spatial position of plants within the population (Gómez et al. 2011, Gómez and Perfectti 2012), or local neighbourhood, plant height and number of flower heads (Dupont et al. 2011), are important determinants of the topological role of a plant individual within a population. Hence, not only plant traits important for the attraction of pollinators (Klinkhamer et al. 1989, Klinkhamer and van der Veen-van Wijk 1999, Weber and Kolb 2013), but also the physical position of the plant individual might influence their topological role within networks. Additionally, inter- and intraspecific variation in morphological and/or behavioural traits of pollinators (e.g. body size or sociality) could potentially influence the structure of individual-based plant–pollinator networks.

Here, we investigate how intra-specific variation in space use of individual flower-visitors affects the structure of a local plant–pollinator network. We use an animal-centered approach and map the movements of tagged bumblebee (*Bombus* spp., Apidae) individuals to investigate the flower visitation of a spatial network of thistle stems (*Cirsium palustre*, Asteraceae). We focus on structural patterns that emerge from local space use and resource partitioning of bumblebees rather than on gene flow among plant individuals. We apply modularity analysis as an analytical tool to identify modules of closely interacting bumblebee individuals and thistle stems and then test to what extent these modules have a spatial component. We expect that the role of individuals in the plant–pollinator network is related to the spatial position of plants and to intraspecific variation in traits of bumblebee individuals and plants. More specifically, we hypothesize that network modules and topological roles are related to 1) plant attractiveness and reward size (e.g. height and number of flower heads), 2) spatial plant population structure, and 3) localized space use of bumblebee individuals. We show that topological features of individual-based networks have a spatial component which is related to movement of pollinators and the spatial location and traits of plants.

Material and methods

Study site

The study site was a humid forest meadow at Moesgaard Have, Denmark (56°04′50″N, 10°13′52″E). It was bounded on three sides by mixed deciduous forest dominated by *Fagus sylvatica* (Fagaceae) and on one side by a cultivated field. During the study period, the thistle *Cirsium palustre* (Asteraceae) was the most abundant flowering plant. It attracted a variety of pollinators, including bumblebees, syrphid flies and butterflies. Field work was conducted from 18–24 July 2012. The thistle population was at peak flowering during the first days of observation. Towards the end of the period, flowering of the thistles had passed the peak (i.e. several flower heads were withering).

Plant data

We marked all spatially distinct flowering stems of *Cirsium palustre* (hereafter 'thistle') within an area of 50×50 m bounded on two sides by a forest. We focused on thistle stems because they are spatially discrete units that can be used as individual entities ('nodes') in a network. We acknowledge that different stems may be connected by underground rhizomes, and hence belong to the same genetic individual. Nevertheless, we refer below to thistle stems as 'individuals' although they might be genetically similar. A few thistle stems occurred outside the 50×50 m patch, but these were not included in the study. The maximum height of flowering stems (hereafter 'height') was measured with a folding meter stick. Additionally, for each stem the number of receptive flower heads was counted approximately every second day and the mean number of flower heads was calculated. The spatial location of all flowering stems were mapped using a triangulation method combined with measurements from plants to fix-points within the patch. This included measuring distances from any given stem to all the nearest neighbours and recording the distances to two fix-points. Using these distance measurements together with the position of trees from a geo-referenced orthophoto (with 16 cm resolution), we were able to digitize the position of all thistle stems using the 'Distance–Distance' tool in ArcGIS 10.

For each thistle stem, we calculated several variables describing their spatial position to the center of the patch as well as to their neighbouring conspecifics. To determine the distance to the center of the patch, we first identified the patch center in ArcGIS 10 using all plant locations and the 'Mean Center' tool in the 'Spatial Statistics' toolbox. This defined the center of the patch as the average x- and y-coordinates from all plant locations. The distance of each thistle stem to the mean center was then determined using the 'Point Distance' tool in the 'Analysis' toolbox. To determine the number of neighbouring stems for each focal stem we used a 1 m, 2 m and 5 m radius and counted the number of conspecifics. Numbers of neighbours were calculated in R x64 ver. 2.15.2 using the dnearneigh() and card() functions in the package 'spdep'.

Bumblebee data

A total of 71 bumblebee individuals were caught at the study site and immediately marked. Ten individuals were marked on 18 July, 38 individuals on 20 July, 20 individuals on 23 July, and three individuals on 24 July 2012. Marking was done between 9:30–13:30 with small number tags. These were glued onto the thorax, taking care not to impair the mobility of the bumblebees. As a measure of body size, we measured body length (including the head) with a digital caliper. Marked bumblebees were released in the plot immediately after marking and allowed to forage on the plants. Nearly all bumblebee individuals found in the plot were marked, although a few non-marked individuals arrived after the marking period. Bumblebee individuals were identified in the field to species and caste.

To measure flower visitation and movement of bumblebee individuals, three to five observers walked around in the patch until encountering a marked bumblebee. This marked bumblebee was then followed as long as possible, registering the sequence of thistle stems visited and the total time of the observation period. We observed bumblebee individuals on the 20, 23 and 24 of July 2012 between 9:15–16:30, amounting to a total 16.6 h of direct tracking of individual bumblebees. This encompassed the main diurnal activity period of the bumblebees in the meadow. The weather was sunny or overcast, no rain, with light to moderate wind and temperatures of 23–27°C. We collected 12 marked bumblebee individuals on 20 July and 16 marked individuals on 24 July (total of 28 specimens). These were weighed in the lab and sent to a taxonomic expert for verification of caste and species identification (see Acknowledgments).

Modularity analysis

We used the method of functional cartography by simulated annealing to test for modularity and to identify modules (for further details see Guimerà and Amaral 2005a, b, Olesen et al. 2007). The method is a stochastic optimisation technique, which combines multivariate optimization and statistical mechanics to maximize a measure of modularity M of the network (Kirkpatrick et al. 1983). To apply this method, we constructed an individual-based plant–pollinator matrix where the columns represent plants (thistle stems) and the rows the bumblebee individuals. The matrix represents a two-mode network where the cell entries denote if a bumblebee individual visited a particular thistle stem (presence = 1) or not (absence = 0). We only included bumblebee individuals that visited flowers and only thistle stems whose flower heads had been visited by a bumblebee. Using this matrix, we calculated modularity M using the method developed by Guimerà and Amaral (2005b):

$$M = \sum_{s=1}^{N_M} \left(\frac{I_s}{I} - \left(\frac{k_s}{2I} \right)^2 \right), M \in \left[0; \left(1 - \frac{1}{N_M} \right) \right]$$

where N_M is the number of modules in the network, I is the number of links in the network, I_s is the number of links between all individuals in module s ("within-module links"), and k_s is the number of all links of individuals in module s. Thus, M describes the degree to which a network consists of sub-groups (modules), each consisting of tightly interacting nodes (Olesen et al. 2007). Modularity M is high when many links are found inside modules and few links between modules. We assessed the significance level of M with a t-test by comparing its value to the mean and standard deviation of 100 randomizations ($M_{rand} \pm$ SD) where the same degree (connectivity) distribution was kept as in the original network. Note that the number of modules N_M is not defined a priori, as it is a result of the optimization process. N_M represents the optimal number of partitions when M is maximized for the network.

Based on the assignment of individuals to modules, we calculated two parameters, the within-module degree z and the among-module connectivity c (Guimerà and Amaral 2005a, b, Olesen et al. 2007). These define the topological role of the thistle stems and bumblebee individuals within the network, with z measuring how well-connected an individual is to other individuals in its own module and c how connected an individual is to other modules. The z_i is the standardized number of links of an individual i to other individuals in the same module,

$$z_i = \frac{k_{is} - \bar{k}_s}{SD_{ks}}$$

where k_{is} is number of links of individual i to other individuals in the same module s_i, while $\bar{k}_s$ and SD_{ks} are average and standard deviation of within-module links for all individuals in s_i. The among-module connectivity c_i is calculated as:

$$c_i = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{is}}{k_i} \right)^2, c \in [0;1[$$

where k_i is the number of links of individual i. If all links of i are within its own module, then $c = 0$. If links are distributed evenly among modules, then c is close to 1.

We used the program NETCARTO (Guimerà and Amaral 2005a, b) to calculate the number of modules, to sort individuals into different modules, and to test the significance level of M. This program gave consistent results in several different runs. We further use the terminology from Olesen et al. (2007) and classify nodes with $z \leq 2.5$ and $c \leq 0.62$ as 'peripherals', with $z \leq 2.5$ and $c > 0.62$ as 'connectors', with $z > 2.5$ and $c \leq 0.62$ as 'module hubs', and with $z > 2.5$ and $c > 0.62$ as 'network hubs'.

Spatial structure of modules

We used kernel densities created in ArcGIS 10 to map the spatial aggregation of thistle stems within each module. The kernel density function calculates the density of stems in the neighbourhood around the focal stem and creates a smoothed surface resembling density curves. Kernel densities will be spatially structured if thistle stems within each module show spatial clumping. The kernel densities were made with a cell size of 8.0×10^{-3} (low values create smooth surfaces) and a search radius of 2 m (the neighbourhood search area for each focal thistle stem).

Furthermore, we also used the flight paths of individual bumblebees to illustrate the effect of individual movements

on modularity. We approximated the spatial movements of bumblebee individuals within each module by mapping the straight lines between subsequently visited thistle stems. This was done in ArcGIS 10 using the 'Make Tracking Layer' tool in the 'Tracking Analyst' toolbox.

Influence of traits on the topological role of individuals in the network

We used generalized linear models (GLM), model averaging and multi-model inference based on the bias-corrected Akaike information criterion (AICc) (Johnson and Omland 2004) to assess the effect of plant and bumblebee traits on the topological role of individuals within the network. To characterize topological role, we used within-module degree (z-value) and among-module connectivity (c-value) of thistle stems and bumblebee individuals as response variables in our GLMs. For the z-value, we run all GLMs with a Gaussian error distribution because the frequency distribution of z-values and model residuals approximated a normal distribution. For the c-values, the frequency distribution indicated a bimodal pattern due to a strong excess of zeros ('ultra-peripheral nodes'; Guimerà and Amaral 2005b), as typical for pollination networks (Olesen et al. 2007). Hence, we performed our analyses with all c-values >0 and used GLMs with Gaussian error distribution to model the effects of traits on among-module connectivity c.

In the plant GLMs, we used distance to the patch centre, plant height, number of flowers, and the number of conspecifics in a radius of 1 m, 2 m and 5 m as predictor variables. For the bee models, we used body length (as a measure of body size) and nest builder/parasitic (categorical variable representing sociality) as predictor variables. In addition, we included the total minutes a bee was observed as a predictor variable to indicate observer effort. All predictor and response variables were scaled before the analysis (standardized to mean = 0 and SD = 1) to facilitate the comparison of coefficients (Schielzeth 2010). We then fitted all possible models nested within each full model and ranked them on the basis of AICc weights (w_i; Burnham and Anderson 2002, Johnson and Omland 2004). We averaged the parameters of the 95% confidence set of models (cumulated sum of $w_i \leq 0.95$), weighted by w_i, and considered confidence intervals excluding zero to indicate significant effects on the response variables (z- and c-values, of either thistle stems or bumblebee individuals). This model averaging approach allows to assess the effects of traits on the topological role of thistles and bumblebees while accounting for model selection uncertainty (Burnham and Anderson 2002). It provides robust estimates of model parameters and avoids model selection bias (Johnson and Omland 2004).

Results

Plant and bumblebee data

Of the 244 flowering stems of *Cirsium palustre* in the patch, 202 plants were included in the network analysis. Of these plants, trait data were available for a subset of 193 plants (96%). Visited plants had an average height of 116.4 ± 19.3 cm (n = 193, range: 50–161 cm) and had an average of 2.78 ± 1.74 receptive flower heads/day (n = 193, range: 0.33–14 receptive flower heads/day). Number of flower heads per thistle stem was not strongly correlated with plant height (Spearman rank: $r = 0.30$, $p < 0.05$). Thistle stems excluded from the network (non-visited plants) were significantly smaller (t-test: $t = 3.65$, DF = 231, $p < 0.05$), had fewer flower heads (t-test: $t = 3.79$, $p < 0.05$, DF = 240), and were located more towards the periphery of the patch than stems included in the network (visited plants).

The marked bumblebee individuals represented eight different species, including both parasitic (*Bombus bohemicus, B. campestris, B. sylvestris, B. norvegicus*) and nest building species (*B. hypnorum, B. pascuorum, B. lucorum* and *B. pratorum*). All species of bumblebees were observed foraging on the thistle flower heads, and none of them were cheaters (i.e. nectar robbers). Out of 71 marked individuals, 51 bumblebee individuals were observed on at least one marked thistle stem, and 40 of these were males. The majority of males (35) were parasitic bumblebees, and of 24 taxonomically verified specimens, the majority belonged to *B. bohemicus* (11) and *B. sylvestris* (8). In the following, we only consider male bumblebee individuals (n = 40) because sample sizes for workers were too small. The 40 males were tracked during 186 observation periods with a total of 859 minutes (mean ± SD: 4.62 ± 6.18; range: 0.02–41 minutes/period). During a single observation period, bumblebees visited 1–72 thistle stems (on average 9.3 ± 10.7 plants per observation period, n = 186). For the subset of 28 bumblebee individuals for which body mass data were available, body length strongly correlated with body mass (Spearman rank: $r = 0.69$, $p < 0.05$). Hence, field-based measures of body length were a good estimate of bumblebee body mass.

Modularity and space

The interaction matrix for the network analysis consisted of 40 bumblebee individuals, 202 thistle stems, and 949 links between bumblebees and plants. The network was significantly modular ($M = 0.379$, $M_{rand} = 0.294$, SD = 0.004, $t = 21.25$, $p < 0.05$). The NETCARTO program identified four modules in addition to a satellite consisting of one bumblebee individual and one thistle stem (Table 1). The four modules ranged in size from 42 to 72 nodes and 127 to 426 links (Table 1). Interestingly, these four modules were spatially segregated (Fig. 1A), although modules tended to

Table 1. Key characteristics of modules identified in an individual-based thistle-bumblebee network.

Module	Color in Fig. 1	No. of nodes	No. of bees	No. of plants	No. of links	Within module links	Between module links
1	pink	61	10	51	334	143	191
2	green	42	4	38	127	60	67
3	blue	72	13	59	392	221	171
4	red	2	1	1	1	1	0
5	yellow	64	13	51	426	211	215

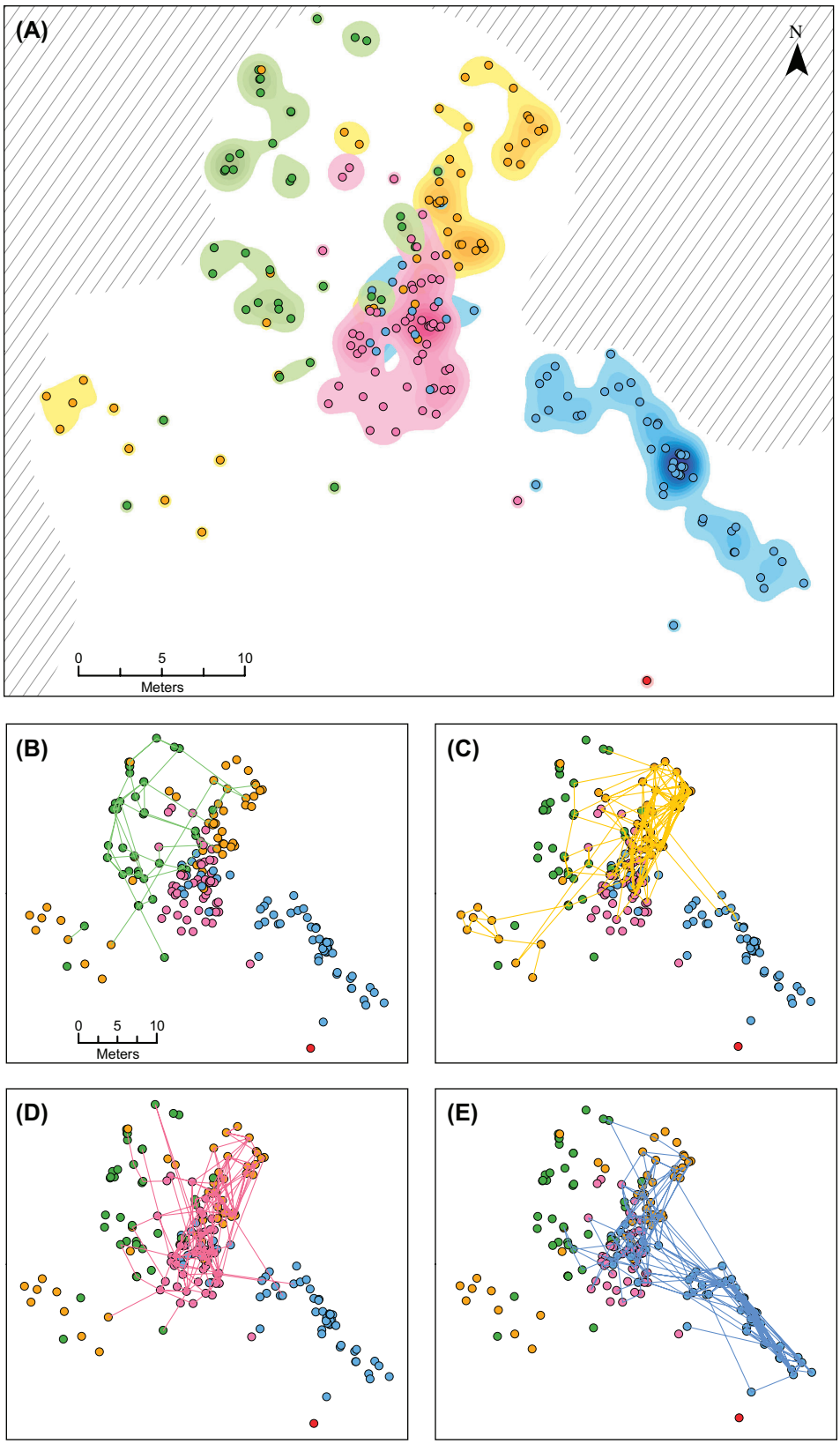

Figure 1. Spatial structure of an individual plant–pollinator network. (A) Kernel densities of thistle stems within the four modules of the network. The four modules are illustrated with different colours (shading of kernel densities uses the same intervals for all modules). Shaded area of the map denotes forest, while non-shaded area is meadow. (B–E) Flight paths of bumblebee individuals within the four modules. The flight paths were approximated by straight lines between thistles that were subsequently visited by bumblebee individuals. Flight paths were not shown on the map if a bumblebee was only observed on one plant (singleton). These singletons are, however, included in the modularity analysis.

overlap in the dense core (center) of the plant patch. Different species of bumblebees did not segregate among modules, and most modules comprised several different species of bumblebees.

Mapping of flight paths of bumblebee individuals within each module showed that the kernel densities of thistle stems (Fig. 1A) matched the movement behaviours of individual bumblebees (Fig. 1B–E). Within three of the four modules, individual bumblebee flight paths overlapped in the center of the patch (Fig. 1C–E). One module was only marginally attached in space to the other modules (Fig. 1B).

Topological roles of nodes

The topological role of thistle stems and bumblebee individuals within the network was quantified by the within-module degree z and the among-module connectivity c. All thistle stems had rather low z-values (within-module degree), but varied widely in c-values (among-module connectivity) (Fig. 2). A total of 32 thistle stems had particularly high c-values (>0.62; referred to as 'connectors') (Fig. 2). In contrast to plants, bumblebees showed pronounced variation in both z- and c-values (Fig. 2). Twelve bumblebee individuals had particularly high z-values (>2.5; referred to as 'hubs') and 11 of those had relatively low c-values (<0.62; referred to as 'module hubs'). These were individuals which were well-connected to other individuals within their own modules (Fig. 2), and hence were particularly important for defining the spatial modules (Fig. 1B–E).

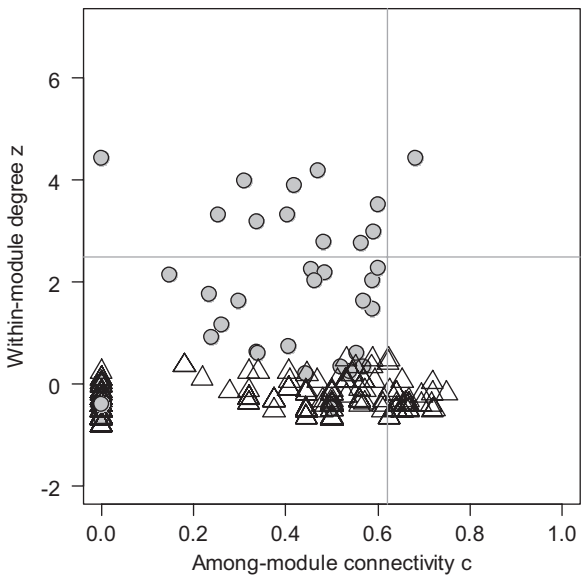

Figure 2. Topological roles of thistles (triangles) and bumblebees (dots) in an individual plant–pollinator network. The within-module degree z measures how well-connected an individual is to other individuals in the same module, whereas the among-module connectivity c measures how connected an individual is to other modules. The straight lines ($z=2.5$; $c=0.62$) delineate the roles of nodes in pollination networks as suggested by Olesen et al. (2007). Individuals with high z-values (>2.5) interact with many individuals within their own module and therefore play an important role in defining their own module. Individuals with high c-values (>0.62) interact with many individuals outside their own modules, and thus connect different modules of the whole network.

The hub individuals belonged to four different species: *B. bohemicus, B. sylvestris, B. campestris* and *B. hypnorum.*

Influence of traits on the topological role of nodes in the network

Model averaging and multi-model inference for plants showed that within-module degree z was mainly related to the number of flowers per thistle stem and the number of conspecifics in the 1 m neighbourhood (Fig. 3A). This suggested that thistle stems with many flowers and many neighbours in their immediate surroundings were particularly important for defining network modules. Other spatial and ecological traits did not have a significant effect on the z-values of thistle plants (Fig. 3A). In contrast to z-values, among-module connectivity c was mainly determined by distance to the patch center (negative effect) and the height of thistle stems (Fig. 3B). In other words, tall plants and those near the patch center tended to be the ones connecting different modules. The number of thistle conspecifics in the neighbourhood and the number of flowers per individual did not have a significant effect on the among-module connectivity c (Fig. 3B).

Similar multi-model inference for the bumblebee individuals in the network showed that within-module degree z was strongly related to observer effort, i.e. how long an individual bumblebee had been observed (Fig. 3C). Hence, individual bumblebees that were observed for long time periods were important for connecting to other individuals within their own modules. A similar, but weaker, effect of observation time was also evident for among-module connectivity c of bumblebees (Fig. 3D). This suggested that bumblebees observed for long time periods also tended to connect different modules. Specific traits such as body size and sociality (nest builder/parasitic) did not have a significant effect on neither z- nor c-values. However, only five (13%) of the male bumblebee individuals belonged to nest building species, and this could at least partly explain why sociality had no effect on the topological roles of bumblebees in the network. Species identity did not appear to explain the topological role of bumblebees.

Discussion

We sampled an individual-based plant–pollinator network by following the movements of marked bumblebee individuals between mapped flowering stems within a 50×50 m study plot of a thistle population. This network was modular and consisted of four modules that were spatially separated due to locally restricted movements of bumblebee individuals among thistles. Stems with many flowers and many close neighbours defined connectivity within modules whereas tall plants and those near the patch center connected different modules. Bumblebee individuals that were observed for long time periods tended to be the hubs of the network, and their movements were spatially constrained within modules. These results demonstrate how spatial and ecological features of individuals, in addition to sampling effort, can determine the structure of ecological networks via a fine-scale division of resources among flower visitors.

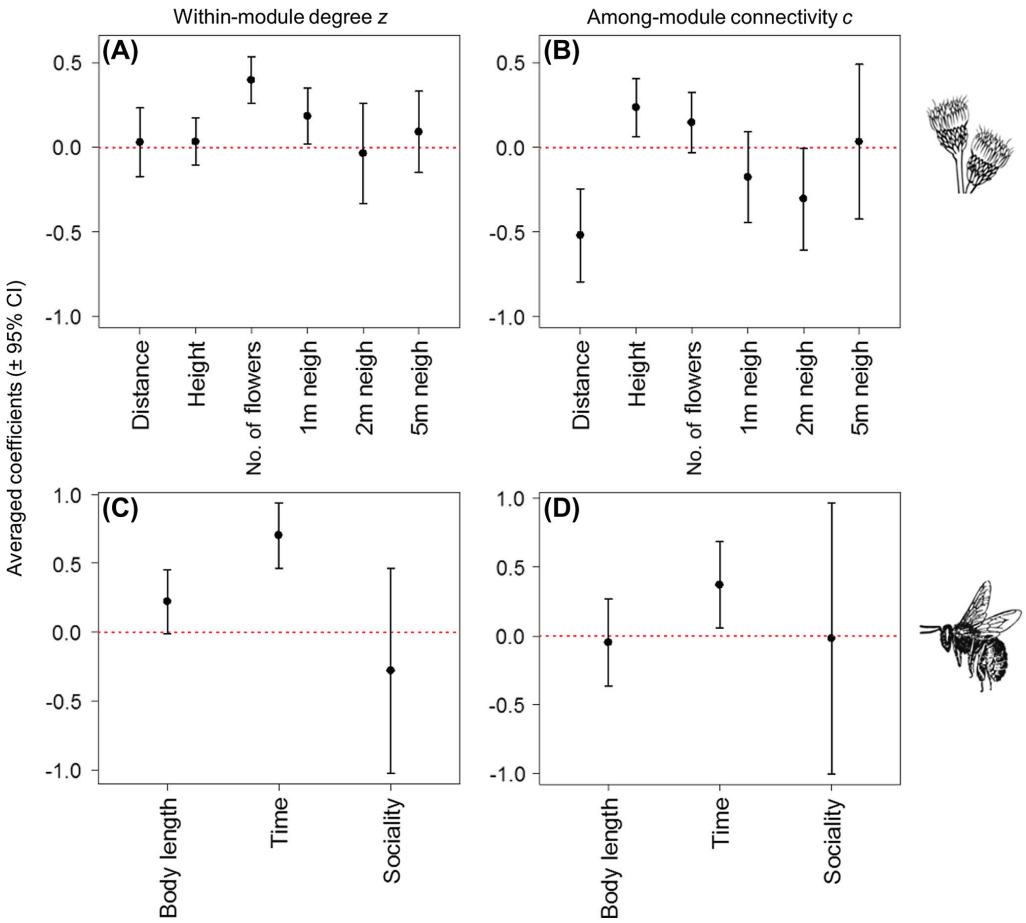

Figure 3. Average coefficients from multiple-predictor generalized linear models (GLMs) to explain the topological role (within-module degree *z* or among-module connectivity *c*) of thistles (A and B, upper row) or bumblebees (C and D, lower row) within an individual plant-pollinator network. Individual traits (thistles or bumblebees) and spatial characteristics (thistle only) were used as predictor variables in the GLMs. For thistles, distance to patch center ('distance'), stem height ('height'), number of flowers ('no. of flowers'), and number of conspecific neighbours in 1 m, 2 m and 5 m neighbourhoods ('1 m neigh', '2 m neigh', '5 m neigh') were included as predictors whereas body size ('body length'), total observation time in minutes ('time'), and nest builder/parasitic ('sociality') were used for bumblebees. Confidence intervals excluding zero indicated significant effects of spatial characteristics and ecological traits on network *z*- or *c*-values. The analyses for *c*-values include only *c*-values > 0 due to their binomial frequency distribution (compare Fig. 2). All predictor and response variables were scaled before the analysis (standardized to mean = 0 and SD = 1). See text for details about model selection and multi-model inference.

Movement behaviour and space use of bumblebees

Our results show that coexisting pollinators segregate their resource use in space, and that this fine scale movement behaviour of individual bumblebees results in a modular structure of the plant–pollinator individual network. Flight distances of foraging bumblebees have been suggested to reflect Levý flight behaviours which characterize optimized search efficiencies to randomly distributed flowers (Viswanathan et al. 1999). Although these random walks have been shown to fit observed foraging distances of bumblebees (Viswanathan et al. 1999), their existence remains controversial (Edwards et al. 2007). Our findings do not support Levý flights because such foraging behaviour would not result in locally restricted movements within sub-patches of a site (modules). Thus, other factors than optimal foraging among flowers may affect local space use of flower visitors within flower patches. For instance, in plants such as white clover *Trifolium repens* bumblebees can avoid visiting non-rewarding flowers because they can detect previously visited flowers (Heinrich 1979). Moreover, if resources are scarce, e.g. due to a high density of foraging bees, bumblebees tend to fly longer distances between flowers (Heinrich 1979, Viswanathan et al. 1999) and hence can adapt their foraging range (Makino and Sakai 2005). In addition to resource availability, predation risk (Llandres et al. 2012) or mate searching (Alford 1975, Benton 2006) could also influence the movement patterns of bumblebees. However, in our study bumblebees were only observed foraging. Most of the bumblebee species in our study are known to search for mates by scent-marking and patrolling a fixed route (Alford 1975, Benton 2006), but we could not observe such a behaviour. Disregarding mate searching behaviour, there could also be differences between workers and males because workers collect floral resources for the colony, while males collect nectar only for their own consumption. However, movement studies of *Bombus terricola* among plants of *Asclepias syriaca* do not support this idea as flight distances did not differ among foraging males and workers (Jennersten et al. 1991). Our data were not sufficient to test for differences in

movement behaviour between workers and males, and future studies are therefore needed to investigate if local space use and network structure differs among different castes.

Trait effects on ecological networks

At the level of interactions among species, trait constraints of both plant and animal partners are now increasingly recognized as forces that structure ecological networks (Stang et al. 2009, Olesen et al. 2010, Eklöf et al. 2013, Junker et al. 2013). In contrast to species-based networks, our results show how intra-specific trait variation among individuals can determine network structure. For instance, trait effects in thistles included phenotypic variation (e.g. plant height, number of flowers) as well as spatial characteristics (location within the population, number of neighbours). These results document that plants near the patch center are those that tend to connect different modules. Modules overlapped in the center of the patch where the tallest plants and the highest aggregation of plants were found (Fig. 1, 3). Another study of an individual-based pollination network documented that central plants (which are highly connected to other plants in the network via shared pollinators) can have a higher fitness than peripheral plants (which are less connected) (Gómez et al. 2011, Gómez and Perfectti 2012). Although we did not specifically measure fitness components, this could also apply to our study system. However, we acknowledge that the plant individuals in our study (i.e. thistle stems) are not genetically unique because *Cirsium palustre* is a clonal plant. In addition to the spatial location of stems, we show that other plant traits are also important for connecting different modules (e.g. plant height) or for defining connectivity within modules (e.g. number of flowers and number of close neighbours). Our results therefore support other field studies which demonstrate that plant height and number of flowers are important for attracting pollinators (Klinkhamer et al. 1989, Klinkhamer and van der Veen-van Wijk 1999, Weber and Kolb 2013). Other more subtle plant traits such as quantity and/or quality of the floral reward may also influence patterns of visitation (Heinrich 1979), and hence network structure. These questions would be interesting to address in the future.

For bumblebees, we found no or only a weak effect of sociality (nest builder versus parasitic) and body size on the topological role of individuals in the network. Only few bumblebee individuals belonged to nest building species and the effect of sociality on network structure therefore needs further investigation. We found observer time influencing both within-module degree z and among-module connectivity c. Hence, individuals observed for long time periods were not only important for connecting to different modules but also for connecting to other individuals within their own modules. The latter is particularly interesting because it suggest that bumblebee individuals will still show locally restricted movements even if they are observed over a prolonged time period.

Plant-centered versus animal-centered networks

We used an animal-centered approach, in which we followed tagged bumblebee individuals and their movements among flowering plants within a patch. This is different from most other plant–pollinator networks which are usually plant-centered, i.e. interactions of the network are observed as visits of pollinators to focal plants (Bosch et al. 2009). Our animal-centered approach resulted in an asymmetric network dominated by plant nodes (A/P ratio = 0.20), in contrast to plant-centered multi-species networks, which are typically dominated by animals and hence have a higher A/P ratio (A/P ratio average $\pm$ SD = 3.5 ± 2.5, n = 54; Trøjelsgaard and Olesen 2013). The sampling focus on pollinators rather than plants may in part explain why bumblebees, but not thistle stems, were hubs (with high z-values) and plants were connectors in our network. In plant-centered multi-species networks, plant and pollinators are typically hubs and connectors, respectively (Olesen et al. 2007, Dupont and Olesen 2009). Few other studies have investigated plant-pollinator networks from the animals' perspective, possibly due to the difficulties of following mobile organisms, and in defining the spatial delimitation of the network. Examples of other animal-centered approaches are networks from pollen load data of pollinators (Bosch et al. 2009, Olesen et al. 2010, Tur et al. 2014), which also add novel interactions to the network that are not observed with focal plant observations (Bosch et al. 2009, Olesen et al. 2010).

Integrating space into ecological network research

The integration of space into ecological networks at different spatial scales is now at the forefront of ecological research (Dale and Fortin 2010, Carstensen et al. 2011, Hagen et al. 2012, Kissling et al. 2012, Dáttilo et al. 2013). One possibility to integrate spatial structure into ecological networks is to give nodes (e.g. plants) a spatial location. In landscape ecology, networks can be constructed with habitat fragments (nodes) and the distances (links) among them, and together with the spatial coordinates of the nodes this allows analyzing them in a spatial context (Dale and Fortin 2010). Habitat fragments can also be connected via shared species which then allows spatial network analyses on the basis of species compositions (Carstensen et al. 2011). In our study, we recorded the spatial coordinates of thistle stems which enabled us to measure several characteristics of the plants that are related to space (e.g. plant density in the local neighbourhood, distance to patch center). Together with the recorded bumblebee movements we were able to demonstrate that modularity (usually considered a non-spatial network metric) can have a spatial component, driven by the fine-scale division of resources among flower visitors within sites. This small-scale partitioning of space among co-occurring bumblebees may also lead to spatial segregation of pollen transfer. Thus, gene flow of plants pollinated by the bumblebees can be more or less delimited within sub-patches, while less outcrossing occurs among sub-patches. Plants connecting several modules (the connectors, in our study system the stems that were located towards the center of the patch) will not only receive more visits, but will also have the highest outcrossing rate. In contrast, structurally peripheral plants will mostly receive pollen from other plants in their own module. This could be tested in more detail in the future.

Other spatial network analyses at a landscape scale have revealed that gene flow occurs in well-defined modules

formed by groups of trees and their shared pollinators (Fortuna et al. 2008). Spatial analyses of species-centered networks at the landscape scale have further demonstrated that groups of bats share the same roosting trees, leading to spatially segregated and well-defined network modules (Fortuna et al. 2009). However, to date only few studies have incorporated direct measurements of animal movements into the analysis of complex ecological networks (Jacoby et al. 2012, Fox and Bellwood in press). Here, we made a first step towards integrating animal movements and individual-based plant–pollinator networks, and we suggest that this approach has great potential to improve our understanding of animal space use at local and landscape scales.

Conclusions

Most previous studies of ecological networks have been species-based, but the analysis of individual-based and animal-centered networks provides ample opportunities to broaden our knowledge of plant–animal interactions. Extensions of networks to spatial ecology are currently limited, but linking space and network theory will allow answering a range of questions across taxa and ecosystems. The approach illustrated here allows incorporating movement behaviour and intra-specific trait variation into network research and thus opens up new avenues for merging foraging theory with network ecology.

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