

Analysing plant–pollinator interactions with spatial movement networks

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Abstract. 1. Pollinators, such as bees, face the complex challenge of efficiently exploiting patchily distributed floral resources across large landscapes.

2. In the present study we consider the utility of spatial network statistics to analyse the foraging patterns of bees moving between feeding sites at various spatial and temporal scales.

3. We explain how spatial movement networks can be derived theoretically and experimentally to describe bee foraging decisions.

4. We illustrate this approach by analysing six datasets of bumblebees and honeybees foraging in arrays of artificial flowers, and showing how network metrics change as foragers gain experience with the spatial distribution of feeding sites.

5. We compare network analyses with more conventional statistics used to characterise bee foraging movements and discuss the implications of our novel statistical and modelling approach for pollination ecology.

Key words. Bumblebees, foraging, honeybees, movement ecology, pollination, route optimisation, spatial networks.

Introduction

Bees play a key role in the reproduction of wild and cultured plants. Over recent years, their widespread declines have raised considerable concern for food security and the sustainability of our ecosystems (Goulson *et al.*, 2015; Klein *et al.*, 2017). Central to understanding the impact of pollinator loss on plant reproduction is the foraging behaviour of bees (Thomson, 1986; Waser, 1986). Most bees are central-place foragers, meaning that they collect food (nectar and pollen) to provision their brood in a single nest (Michener, 2000). By exploiting plants and developing foraging routes to visit them, individual bees may bias pollen flow and fashion the genetic structure of plant populations, therefore calling for more research of bee spatial strategies at the individual and collective levels (Ohashi & Thomson, 2009; Burkle & Alarcón, 2011; Mayer *et al.*, 2011).

Historically, bees were assumed to use simple movement rules that would yield maximal energy gains to exploit patchily

distributed resources, such as moving between nearest unvisited flowers (Ohashi *et al.*, 2007), making short trips after encountering highly rewarding flowers (Chittka *et al.*, 1997) or keeping constant heading directions between visiting flowers (Pyke & Cartar, 1992). While these rules of thumb may hold true when bees forage at small spatial scales (within an inflorescence or a flower patch), mounting evidence shows that this is not the case at larger spatial scales, when bees move between distant locations (flower patches or plants). In these conditions, foragers of many bee species tend to develop stable foraging routes that they follow for several hours or days (e.g. Euglossine bees: Janzen 1971; bumblebees: Heinrich, 1976; honeybees: Buatois & Lihoreau, 2016). These routes are sometimes called traplines in analogy to the fixed circuits that trappers follow when examining a number of traps distributed widely in space (Thomson *et al.* 1997). Route formation is based on the acquisition of spatial memories encoding the location of the different food resources, the colony nest site, and other prominent environmental features (e.g. visual landmarks) (Collett *et al.*, 2013). With training, bumblebees and honeybees can learn to find the shortest path to visit a few artificial flowers (equivalent to natural flower patches) once and return to the

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nest (*Bombus impatiens*: (Cresson; Apidae) Ohashi *et al.*, 2007; *Bombus terrestris*: (Linnaeus; Apidae) Lihoreau *et al.*, 2012a; *Apis mellifera*: (Linnaeus, Apidae) Buatois & Lihoreau, 2016), an optimisation behaviour analogous to solving the Travelling Salesman Problem in graph theory (Cook, 2012). This mathematical problem is notoriously difficult (if not impossible) to solve for large graphs, because the number of possible paths increases factorially with the number of nodes in the graph (e.g. 6 paths for 3 nodes, >3 million paths for 10 nodes), and finding efficient solutions often requires complex algorithms and systematic approaches (Polyakovskiy *et al.*, 2014; Dorigo & Gambardella, 2016).

While there is evidence that bees exhibit routing behaviour in nature (Janzen, 1971; Heinrich, 1976), to what extent these observations in simplified experimental conditions can be extrapolated to the field, where individuals may interact to exploit numerous highly variable resources scattered across large landscapes, is an open question.

Field data on such multi-destination routes among flower patches are even more complex and challenging to analyse, and conventional behavioural metrics do not suffice to capture detailed information about routing behaviour under field conditions (Thomson *et al.*, 1997; Makino & Sakai, 2004, 2005; Makino, 2013; Lihoreau *et al.*, 2016). We argue that network statistics derived from graph theory hold considerable promise to characterise these complex movement patterns at the individual and collective levels and to identify the decision rules underpinning spatial strategies. In developing routes between flowers, foragers form movement networks embedded in space (Barthélemy, 2011), where 'nodes' are feeding locations (flower patches or plants), and 'edges' are flight paths between them (see examples in Fig. 1a–e) (Thomson *et al.*, 1997; Lihoreau *et al.*, 2016). These spatial movement networks are directed, meaning that individuals move from one particular location to another (movement vectors). Networks are also weighted so that the thickness of edges is proportional to the frequency of movements between nodes. Because most bee species are central-place foragers, their spatial movement networks also include the nest site, a specific node at which every flower visitation sequence starts and ends. Therefore, in principle, an optimal movement network for a bee connects all flowers and the nest using the shortest possible path (optimal network in Fig. 1e). Discrete temporal network analysis can then be performed depending on the time intervals with which a visitation matrix is built. For instance, matrices may be developed by considering flower visits made in a single foraging bout (dynamic network) or by cumulating the flower visits of several foraging bouts (static network). A major advantage of network statistics is that they allow for analyses of very large spatial datasets and the derivation of new empirically testable hypotheses (e.g. Perna & Latty, 2014; Jacoby & Freeman, 2016). Several analytical packages (e.g. *igraph*, *sna*, *tnet* packages in R, graph-tool in Python, UCINET) and both local metrics (e.g. measures describing the level of importance of a node in a network) and global metrics (e.g. measures describing the general level of connectivity of the entire network) can be readily calculated to characterise space use by pollinators from an individual-based point of view to measure,

compare and predict their behaviour across different temporal scales.

In a recent field survey, Dupont *et al.* (2014) applied an individual-based plant–pollinator network analysis to flower visitation data of different bumblebee species. The study showed significant modularity in space use by bees based on plant characteristics so that foragers tended to visit patches of aggregated plants with numerous flowers and use taller plants to move from one module to another (Dupont *et al.*, 2014). Although the analytical approach developed in this study is very appealing, field surveys only provide partial information about the foraging experience of individual bees, the location of their nest relative to different plant patches, and the temporal dynamics of their foraging patterns. All these parameters are critical in determining bee foraging behaviour (Chittka & Thomson, 2001). Experimental advances on model bee species, such as bumblebees and honeybees, using artificial flowers delivering controlled rates of food resources combined with automated movement tracking, now allow for collecting high-resolution spatial and temporal data on bee foraging patterns in complex, yet controlled, environments [e.g. motion detection cameras on flowers: Lihoreau *et al.*, 2016; Radio Frequency Identification (RFID): Ohashi *et al.*, 2010; harmonic radars: Lihoreau *et al.*, 2012b; QR tags: Crall *et al.*, 2015; 3D video tracking: Ings & Chittka, 2008]. Extensive recordings of individual-based data using these semi-field approaches provide an interesting opportunity to start examining the cognitive processes underpinning the foraging patterns of bees and how they change across time in ecologically relevant conditions.

In the present study, we describe how spatial network statistics can be used to analyse the foraging patterns of bees, both at local and global levels. We illustrate the potential of this approach for comparative analyses by statistically comparing spatial optimisation in the movement patterns of bees across spatial scales, the number of flowers and flower configurations using standard network metrics. Our analysis is based on published movement datasets of bumblebees and honeybees of known age, foraging experience and colony origin, foraging in arrays of artificial flowers in the lab and in the field. To validate our approach, we compare our results with analyses of more conventional behavioural metrics used in previous studies, such as the number of re-visits to flowers and overall travel efficiency (distance/number of flowers visited).

Material and Methods

Experimental data

Six datasets of bee flower visitation sequences were analysed. Three datasets were obtained on the bumblebee *Bombus terrestris* (experiment 1: Lihoreau *et al.*, 2012a; experiment 2: Lihoreau *et al.*, 2011; experiment 3: Lihoreau *et al.*, 2012b). The three other datasets were obtained on the honeybee *Apis mellifera* (experiments 4–6: Buatois & Lihoreau, 2016).

All the datasets were generated according to the same general methodology and are thus comparable. In all experiments, bees were individually marked (coloured number tags or paint dots on the thorax) and maintained in colony nest boxes (bumblebees) or hives (honeybees) equipped with a transparent, colourless,

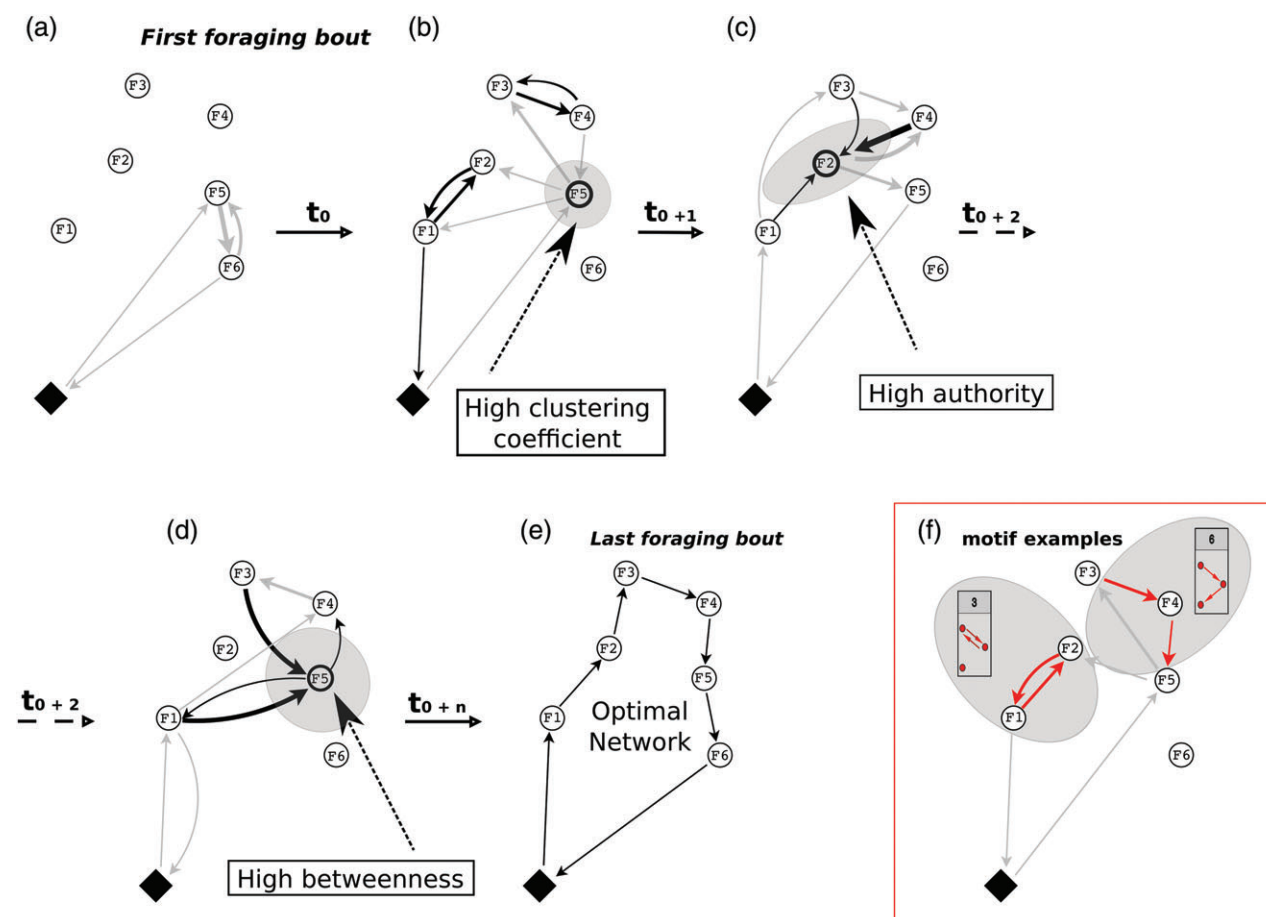


Fig. 1. Examples of local and global metrics calculated on a bee spatial movement network. Nodes of the network (white circles) represent flowers (F1–F6) and the colony nest (black square). Edge directions indicate individual movements between flowers and the nest. Edge thickness is proportional to the frequency of bee movements from one flower to another (i.e. edge weights). In this hypothetical network, from (a) to (e), the forager tends to increase the number of visited flowers with experience (t_0 , $t_0 + 1$, $t_0 + 2$, $t_0 + n$) while reducing both the number of revisits to flowers and the time needed to visit all (i.e. network optimisation). Examples of local network measures are shown (black arrows): (i) High clustering coefficient calculates the degree to which neighbours of a given node are themselves highly connected; (ii) Authority score indicates the existence of highly visited nodes; (iii) High betweenness centrality value counts the number of shortest paths that pass through a focal node. (f) Hypothetical network illustrating two common network motifs (red arrows) in bee movement data (motifs 3 and 6, see Fig. 3). [Colour figure can be viewed at wileyonlinelibrary.com].

entrance tube. The tube was fitted with a series of shutters to control all departure and arrival of foragers at the colony. Workers collected sucrose solution (40% w/w) on artificial flowers outside the colony. Flowers consisted of a blue plastic landing platform (diameter = 60 mm) with a yellow feeding spot in the middle. Bees were initially pre-trained on a flower from which they could collect *ad libitum* sucrose solution. Each individual was tested alone. A regular forager that made at least five foraging bouts (foraging trips starting and ending at the nest colony box) in 1 h was selected. The crop capacity of this forager was estimated by averaging the total volume of sucrose solution collected from a training flower over another three foraging bouts. The forager was then tested with all test flowers placed in a specific spatial arrangement (see experimental arrays in Fig. 2). During the test, each flower provided the same amount of sucrose solution, chosen so that the bee had to visit all flowers to fill its nectar crop to capacity before returning to the colony nest

box (e.g. 1/5th of the crop capacity available in each flower in an array of five flowers). Flowers were refilled by the experimenter at the end of each foraging bout, meaning that any revisit to a flower within the same foraging bout was not rewarding. Bees were tested for 22–80 consecutive foraging bouts in the same array of flowers. All flower visits (when a bee landed on a flower) were recorded and used to reconstruct the complete foraging history of each bee.

Experiments were conducted in six different arrays, varying in their spatial scale, their number of flowers, and the spatial configuration of flowers. Experiments 1, 2, and 4 (Fig. 2a,b,d) were completed in flight rooms at small spatial scales and with controlled illumination (Lihoreau *et al.*, 2011, 2012a; Buatois & Lihoreau, 2016). Experiments 3, 5, and 6 (Fig. 2c,d,e) were completed in outdoor open fields at a small spatial scale for experiment 5 and large spatial scales for experiments 3 and 6 (Lihoreau *et al.*, 2012b; Buatois & Lihoreau, 2016). Details

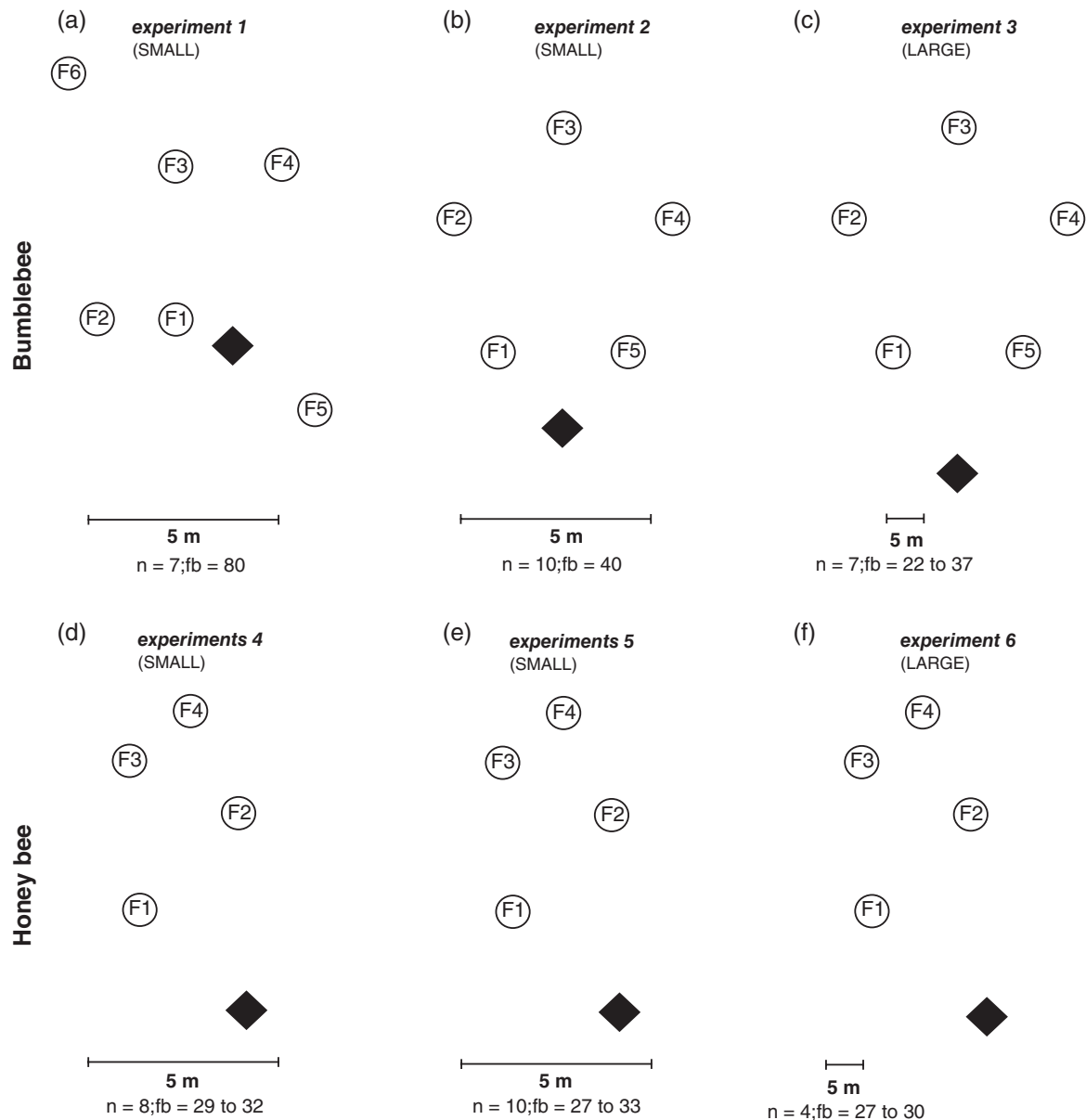


Fig. 2. Spatial arrangements of the artificial flowers (F1–F6) and the colony nest (black square) in the six experiments under investigation (scale is in meters). Number of bees (n) and foraging bouts (fb) are shown for each experiment. (a) Experiment 1: bumblebees in the lab (Lihoreau *et al.*, 2012a). (b) Experiment 2: bumblebees in the lab (Lihoreau *et al.*, 2011). (c) Experiment 3: bumblebees in the field (Lihoreau *et al.*, 2012b). (d) Experiment 4: honeybees in the lab (Buatois & Lihoreau, 2016). (e) Experiment 5: honeybees in the field (Buatois & Lihoreau, 2016). (f) Experiment 6: honeybees in the field (Buatois & Lihoreau, 2016). Spatial scales are provided for each array (i.e. SMALL or LARGE).

about the spatial arrangement of flowers, the number of bees tested, and the numbers of foraging bouts per bee are given in Fig. 2.

Network analyses

We built spatial networks of bee foraging movements in which flowers were nodes and movements were edges (Fig. 1). Edges weight corresponded to the frequency of movement between

flowers. To describe foraging movements and compare them across experimental conditions and species, we calculated three local network metrics describing the role of each flower in the bee movement network and one global network metric to infer on the efficiency of the network structure.

Local network measures. At a local level, the ‘weighted clustering coefficient’ was calculated, which assesses the degree to which nodes tend to cluster together (Barrat *et al.*, 2004). Here

a high clustering value indicates that neighbouring flowers of a given flower are themselves highly connected, i.e. frequently re-visited (Fig. 1b).

We used the 'Kleinberg's authority score' (Kleinberg, 1999) to measure the relative importance of a node in a network (Fig. 1c). Given A , an individual movement matrix across flowers, the Kleinberg's authority score is defined as the principal eigenvector of the inverted matrix $t(A)^*A$. This metric assigns large values to flowers that are most often used while accounting for the number of visits to adjacent flowers (i.e. flowers connected by at least one edge). Therefore, a high Kleinberg's authority score indicates that a specific flower is more often visited than all its neighbour flowers. This may be the case, for instance, at the early stages of a route development when bees often return to a reference flower from which they explore and attempt to locate new flowers (Ohashi *et al.*, 2007; Lihoreau *et al.*, 2010, 2016).

We calculated the 'weighted betweenness centrality'. This metric reflects the importance of a node as an intermediary of the network, based on the number of shortest paths connecting all pairs of nodes that pass through the focal node (Opsahl *et al.*, 2009). In a bee movement network, a high weighted betweenness centrality characterises a flower that is acting as a bridge among multiple other flowers (Fig. 1d).

Because the aim of the study was to characterise general trends of spatial optimisation by bees across time at the network level (route efficiency) and not at the node level (role played by individual flowers), for all the local metrics we calculated mean values over all flowers at each foraging bout. Betweenness scores were normalised according to an algorithm that weights the betweenness value for the number of flowers visited in the network (Freeman, 1979). Authority scores were scaled from 0 to 1. Clustering coefficients vary between 0 and 1 and need no normalisation. In these conditions, an optimal network (in which a bee would visit all flowers once and return to the nest by travelling the shortest distance to visit all flowers) and a suboptimal network (in which a bee would travel longer distances for visiting the same amount of flowers) would be characterised by the maximum average betweenness of 0.5, the maximum average authority score of 1, and the minimum average clustering coefficient of 0 (Fig. 1e).

Global network measures. At the global level, the triadic structures of the network were examined, i.e. motifs (Milo *et al.*, 2002), which represent triadic patterns of connection between nodes in a directed network. Network motifs can be representative of various biological processes such as information flow (Nandi *et al.*, 2014), resource exchange (Quevillon *et al.*, 2015) or disease spread (Waters & Fewell, 2012). In a bee movement network, the analyses of network motifs might help to identify behavioural rules underpinning trapline formation (Fig. 1f) while allowing for unbiased comparison across different datasets (Shizuka & McDonald, 2015). Whereas a detailed temporal network analysis of motifs might be used to better understand the mechanisms of network functionality (Kovanen *et al.*, 2011), here a discrete approach was used by counting all the 16 possible triadic motifs to connect three flowers (including the nest) observed at each foraging bout and thus

not strictly related to the exact temporal sequence of visits on flowers (Fig. 1f). For each experiment, the triadic motifs of the observed bee foraging networks at each foraging bout were compared with those of the theoretical optimal network connecting all flowers and the nest using the shortest possible path. As only two out of the 16 possible triadic motifs (Fig. 3a–f) can be observed in the optimal movement network (Fig. 1e), these global measures inform us about the overall efficiency of the routes developed by bees.

Statistical analyses

Local network measures. All analyses were conducted in the statistical environment R (i.e. version 3.2.3). For each foraging bout of each bee we extracted weighted clustering coefficient values, authority scores, and weighted betweenness centrality values of each flower, using the functions 'clustering_local_w' and 'betweenness_w' in the *tnet* package (Opsahl, 2009) and the function 'authority.scores' in the *igraph* package (Csardi & Nepusz, 2006). We ran three different regression models for weighted betweenness, authority, and weighted clustering coefficient values using the sequential number of foraging bouts, type of array (i.e. small or large spatial scale), species (i.e. bumblebee or honeybee), and all the interactions among these predictors as fixed effects. Individual identity nested in an experimental array was used as a random effect in all models. Model selection was carried out for the three different parameters ranking candidate models according to their Akaike Information Criterion (Akaike, 1985). Beta regression for the three averaged local network measures was used (clustering coefficient, weighted betweenness centrality, and authority scores) because their values were constrained between 0 and 1. A zero inflation method was applied using the Beta Inflated (BEINF) family function from the *gamlss* package (Rigby & Stasinopoulos, 2005). Model selection of the Beta regression mixed models is shown in the supplementary materials (Tables S1–S3). Because network metrics are correlated, a Bonferroni correction was applied by setting the alpha level of significance at 0.017 (Tylianakis *et al.*, 2007).

Global network measures. Motifs were calculated using the 'triad.census' function in the 'igraph' package (Csardi & Nepusz, 2006). Only two out of the 16 possible triadic motifs (motif 2 and 6: Fig. 3a–f) are representative of the optimal movement network (Fig. 1e). Depending on the number of flowers in the array, motif 1 (triadic structure where the three nodes – a, b, c – have no connection among them, i.e. the empty graph a, b, c) can also occur and is represented for a maximum of 7 times in a network with 7 flowers. Motif 2 (triadic structure with a single connection between the three nodes, i.e. $a > b, c$) and motif 6 (triadic structure where $a > b > c$ are all connected by two directed lines) of the optimal movement network can also occur at different frequencies depending on the network size (i.e. for 7 flowers: 21 and 7; for 6 flowers: 12, 6; for 5 flowers: 5, 5; as indicated by red horizontal lines in Fig. 3). We analysed the tendency of bees to modify their motifs frequency with time by applying a generalized linear mixed effect model for count

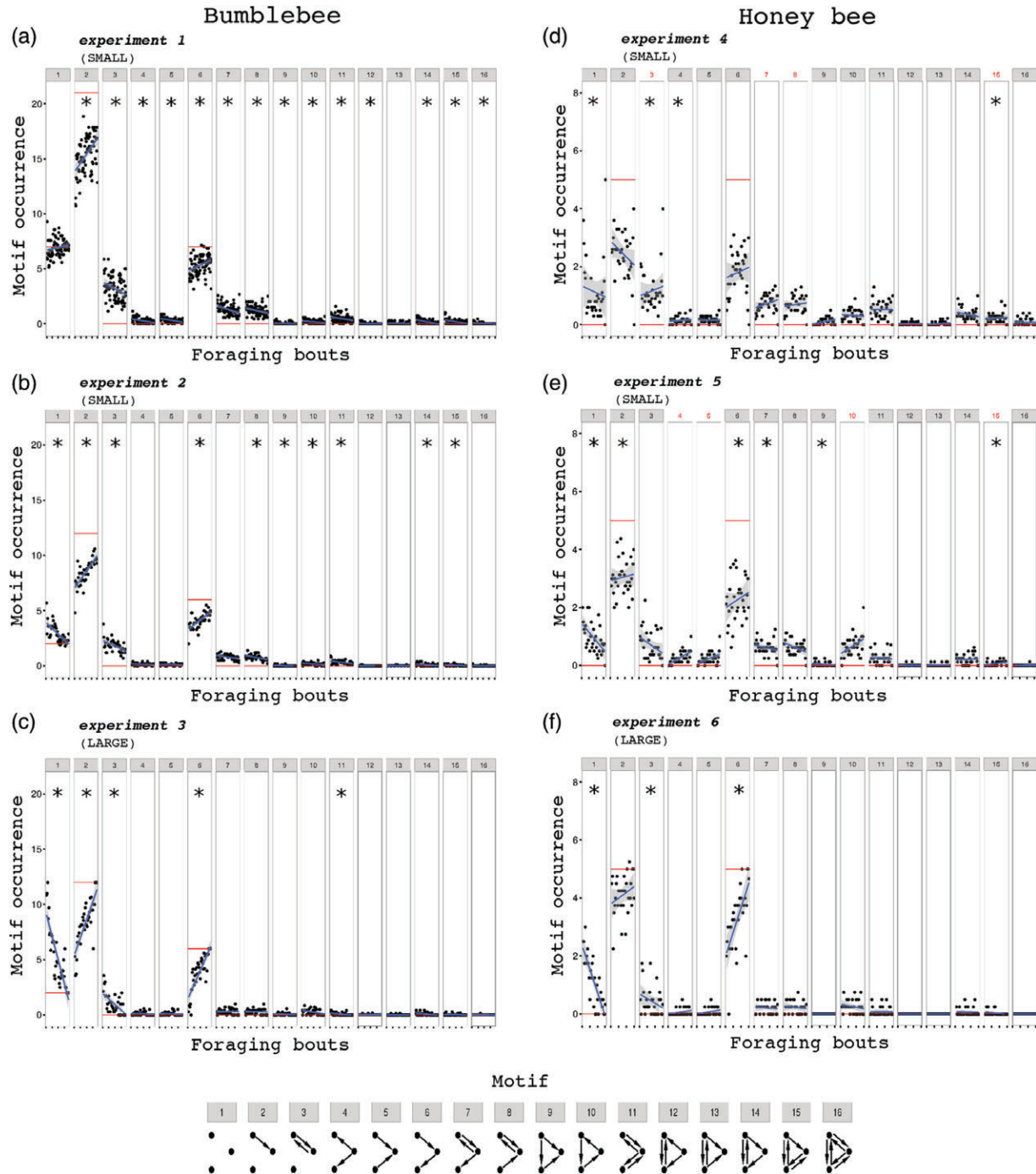


Fig. 3. Distribution of all possible network triadic motifs across foraging bouts. For each motif, the x-axis represents the temporally ordered foraging bouts. Red horizontal lines indicate the frequency of each motif expected in the optimal network. Best fitted lines obtained from generalised linear models using foraging bouts as predictor and frequency of motif as response variable are shown for each motif along with their standard errors (blue line and shaded grey area). Significant effects of time on the frequency of each motif are highlighted with asterisks. GLMM estimates, Z-values and P-values for each motif in each experiment are available in Tables S4–S9. The relationship going in the opposite direction of the optimal network is numbered in red. Alpha level is set at 0.05. Spatial scales are provided for each graph (i.e. SMALL: a,b,d,e; or LARGE: c,f, see also Fig. 2). [Colour figure can be viewed at wileyonlinelibrary.com].

data (i.e. GLMM with Zero Inflated Poisson distribution error) using the observed frequency for each motif and for each dataset as response variable, the number of foraging bouts as predictor, and individual identity as random effect.

Other measures. To illustrate the benefits of using the network approach relative to more conventional analyses, we also calculated non-network measures used in previous studies for assessing the ability of bees to develop efficient routes (Lihoreau *et al.*, 2011; Lihoreau *et al.*, 2012a, 2012b; Buatois & Lihoreau, 2016). For each foraging bout of each bee, we calculated the number of revisits to flowers, and the distance travelled (assuming straight lines between flowers) divided by the number of flowers visited. Both measures of route efficiency are expected to decrease with increasing network efficiency and reach a minimum in an optimal movement network. A GLMM was applied for count data to study the impact of experience (foraging bout) on the number of revisits to flowers and a linear mixed effect model (LMM) for the travelled distance divided by the number of flowers visited. Both models were run for each experiment using individual identity as a random effect.

Results

Local network measures

The average weighted betweenness centrality increased as bees accumulated foraging experience in the six experiments [$\text{estimate}_{\text{bout}} = 0.066$, standard error (SE) = 0.004, $t = 17.11$, $P < 0.001$], indicating that individuals tended to visit all flowers at a similar frequency by the end of training (Fig. 4). This tendency was stronger in large spatial scale arrays ($\text{estimate}_{\text{small_array}} = -0.067$, SE = 0.005, $t = -13.55$, $P < 0.001$). Interestingly, in small spatial scale arrays bumblebees showed higher average weighted betweenness centrality ($\text{estimate}_{\text{honeybees}} = -1.172$, SE = 0.164, $t = -7.15$, $P < 0.001$) and a tendency to develop optimal networks faster ($\text{estimate}_{\text{honeybees}} = -0.020$, SE = 0.008, $t = -2.533$, $P = 0.011$) than honeybees (Fig. 4).

The average Kleinberg's authority scores also increased as bees accumulated experience in the six experiments ($\text{estimate}_{\text{bout}} = 0.083$, SE = 0.03, $t = 2.781$, $P = 0.004$), meaning that all flowers became equally important in the network. For both bee species, the average authority scores were lower in small spatial scale arrays than in large spatial scale arrays ($\text{estimate}_{\text{small_arrays}} = -0.446$, SE = 0.103, $t = -4.334$, $P < 0.001$). However, honeybees had larger average authority scores than bumblebees in the small spatial scale arrays ($\text{estimate}_{\text{small_arrays_honeybees}} = 0.582$, SE = 0.111, $t = 5.229$, $P < 0.001$) meaning that honeybees tended to use all possible connections between flowers equally whereas bumblebees only used a few.

The average clustering coefficient tended to decrease with time, as bees accumulated foraging experience (Fig. 6). Specifically, bumblebees showed a significant decrease in average clustering coefficient while honeybees maintained stable values throughout the experiments ($\text{estimate}_{\text{bout_honeybees}} = 0.018$,

SE = 0.004, $t = 4.185$, $P < 0.001$). Honeybees showed a completely different trend at small spatial scales, by increasing their average clustering coefficient scores with experience ($\text{estimate}_{\text{honeybees_small_arrays}} = 0.407$, SE = 0.148, $t = 2.752$, $P = 0.006$). This again illustrates the much-reduced route optimisation efficiency of honeybees in comparison to bumblebees at small spatial scales (Fig. 6).

Overall, these changes in all three local network measures were more pronounced at larger spatial scales, where flowers were distant from each other and the colony nest, both for bumblebees and honeybees (Figs 4–6).

Global network measures

While bees initially used the 16 possible motifs to link flowers, they gradually reduced the number of motifs to only use two of them by the end of training (motifs 2 and 6), a behaviour that is characteristic of route optimisation (Fig. 3). This tendency was less pronounced for honeybees at small spatial scales (Fig. 3d and e). Analyses of the frequency usage of each motif confirmed that honeybees at small spatial scales often presented opposite tendencies than honeybees at large spatial scales or bumblebees at all spatial scales (Fig. 3d: motifs 3, 7, 8 and 15; Fig. 3e: motifs 4, 5, 10 and 15) (for detailed motifs analysis see Tables S4–S9).

Other measures

Conventional statistics for bee movement analyses showed trends towards a general increase in movement efficiency with experience. In all experiments, bees decreased the number of revisits to flowers as they accumulated foraging bouts (Table S10). Bees also tended to decrease their travelled distance divided by the number of visited flowers, except in the case of honeybees foraging in small spatial scale arrays (Table S10).

Discussion

Network analyses are increasingly used in behavioural and ecological research, providing a whole new range of metrics to describe and model interactions between individuals and their environment (Croft *et al.*, 2008; Jeanson, 2012; Pinter-Wollman *et al.*, 2013). In pollination ecology, this approach has proved particularly powerful to describe interactions between plant and pollinator species, for instance using undirected bipartite networks based on field surveys of pollinator abundance (e.g. Fontaine *et al.*, 2006; Bascompte & Jordano, 2007; Campbell *et al.*, 2011; Burkle *et al.*, 2013; Coux *et al.*, 2016). Here we show how spatial network analyses can be developed to study the movement patterns of individual bees exploiting multiple feeding locations at various spatial and temporal scales in simplified experimental conditions. We argue that this approach holds considerable promise to analyse pollinator movements in more complex and ecologically realistic experimental designs and to generate new empirically testable hypotheses for pollination ecology research.

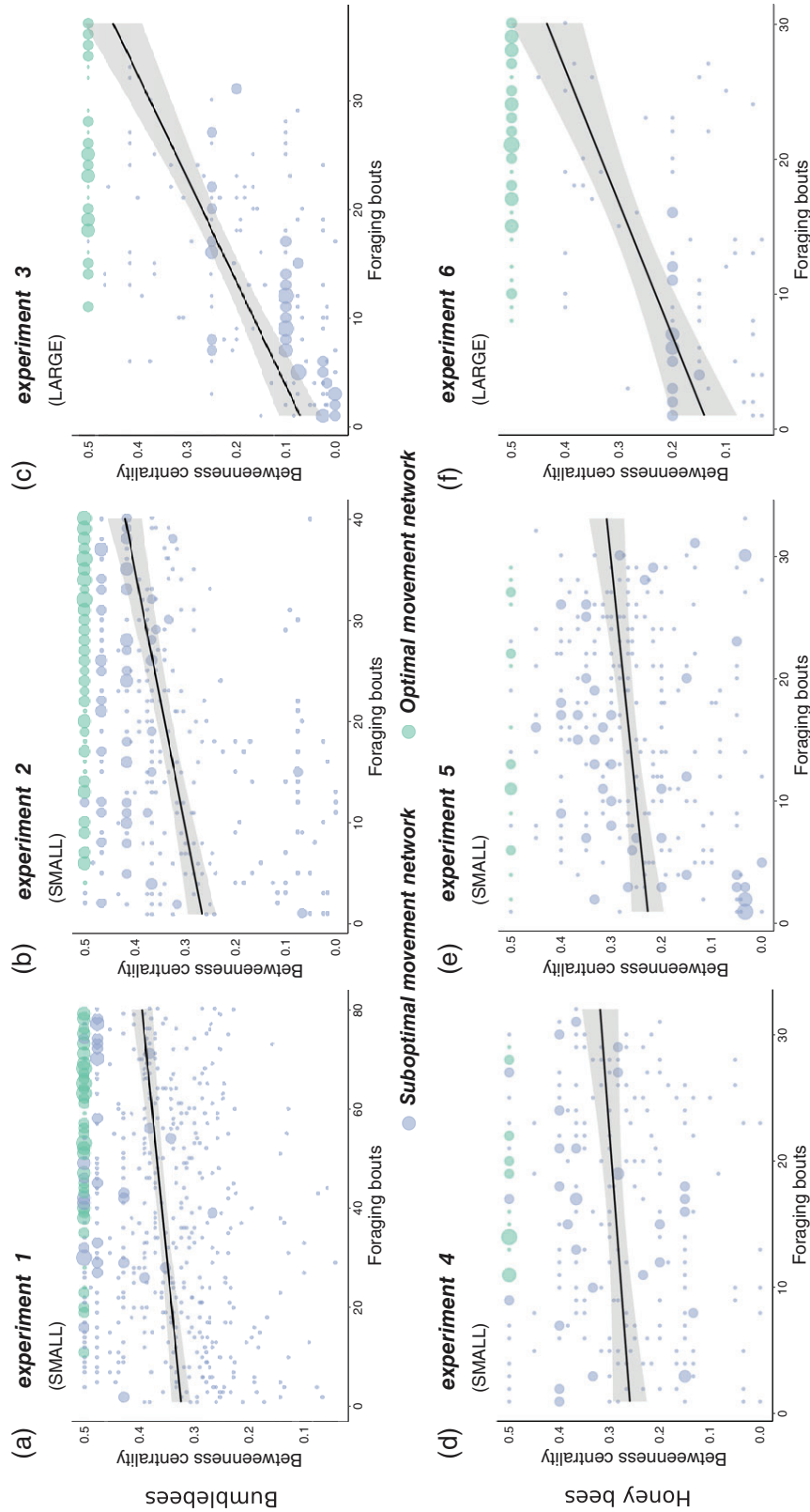


Fig. 4. Average weighted betweenness centrality values for each individual bee at each foraging bout. Black lines and grey shaded areas represent, respectively, the best fitted lines and their standard errors obtained from zeroinflated mixed effect models built using foraging bouts as fixed effect and individual identity as random (see details in the methods). Spatial scales are provided for each graph (i.e. SMALL: a,b,d,e; or LARGE: c,f; see also Fig. 2). [Colour figure can be viewed at wileyonlinelibrary.com].

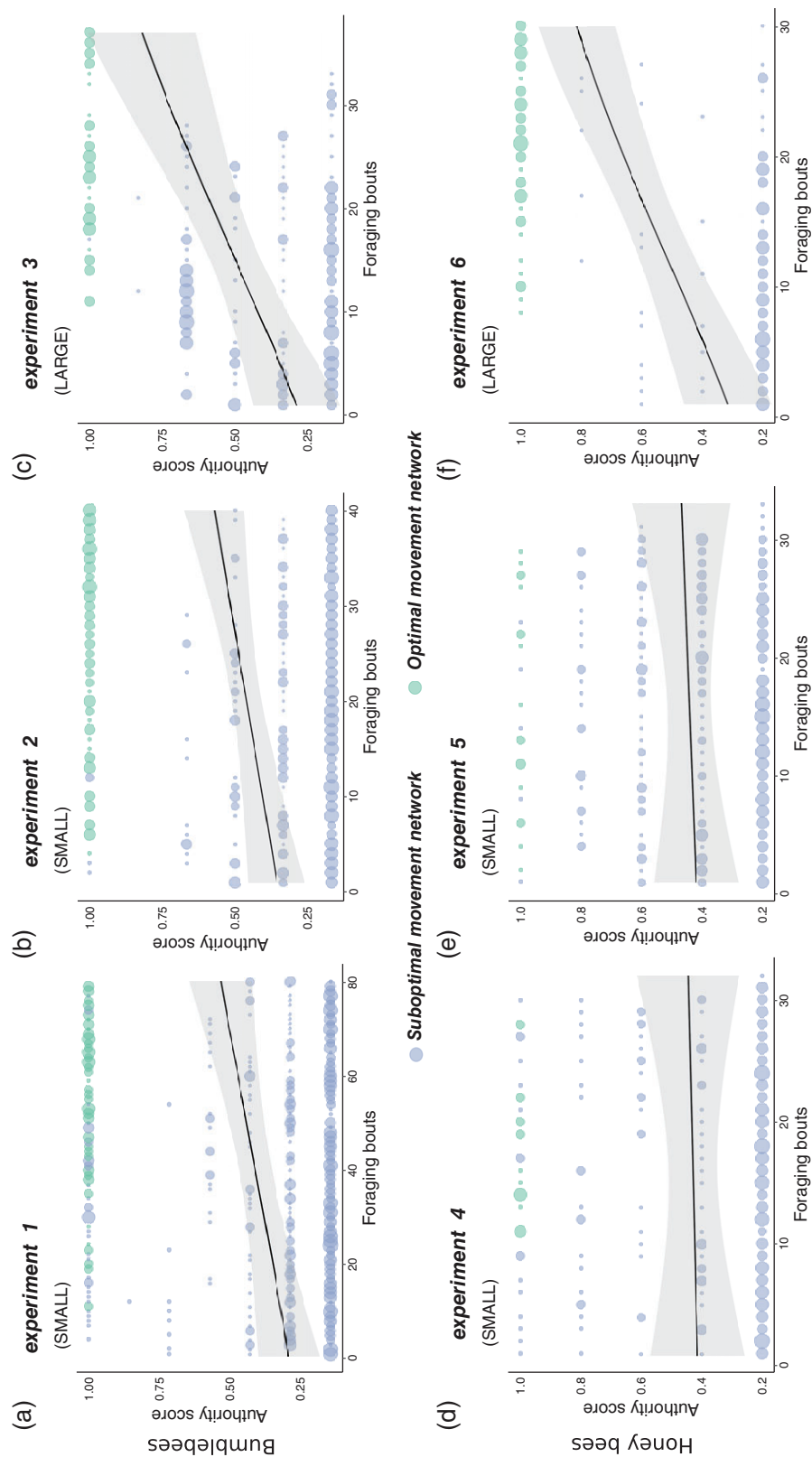


Fig. 5. Average authority score values for each individual bee at each foraging bout. Black lines and grey shaded areas represent, respectively, the best fitted lines and their standard errors obtained from zeroinflated mixed effect models built using foraging bouts as fixed effect and individual identity as random (see details in the methods). Spatial scales are provided for each graph (i.e. SMALL; a,b,d,e; or LARGE; c,f; see also Fig. 2). [Colour figure can be viewed at wileyonlinelibrary.com].

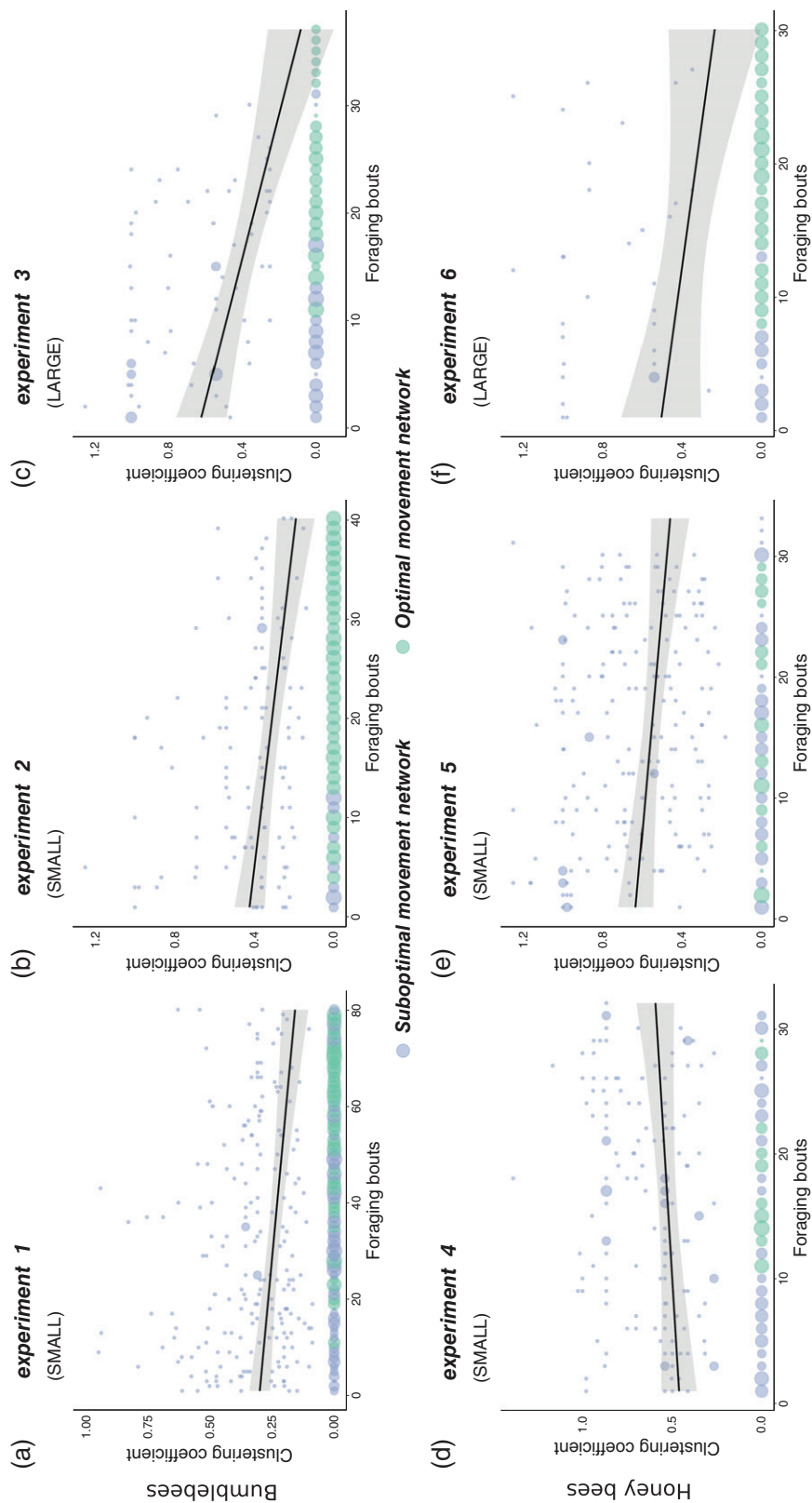


Fig. 6. Average clustering coefficient values for each individual bee at each foraging bout. Black lines and grey shaded areas represent, respectively, the best fitted lines and their standard errors obtained from zeroinflated mixed effect models built using foraging bouts as fixed effect and individual identity as random (see details in the methods). Spatial scales are provided for each graph (i.e. SMALL or LARGE; see also Fig. 2). [Colour figure can be viewed at wileyonlinelibrary.com].

As illustrated above, bee movement patterns can be described in terms of local and global network metrics that predictably change as individuals accumulate foraging experience. For instance, in a simple situation where only one bee exploits a stable array of flowers refilled between each foraging bout, both average betweenness values and average authority scores increased with time. In contrast, the average clustering of flowers decreased with time as bees started to develop optimal or suboptimal stable movement networks. This tendency for optimisation of spatial movement networks was also reflected in the dynamics of motif usage, resulting in bees increasing their usage of the only two motifs representative of an optimal foraging route. Interestingly, and in accordance with previous studies (e.g. Saleh & Chittka, 2007; Lihoreau *et al.*, 2012a; Buatois & Lihoreau, 2016), we found that bumblebees and honeybees rarely use optimal spatial networks at small spatial scales, where the cost of using a longer (suboptimal) path may be negligible. In contrast, foragers bees always used optimal spatial networks at large spatial scales, suggesting that they use more complex optimisation movement rules in more costly conditions. These results were confirmed with more conventional statistical approaches (e.g. flower re-visits, travel efficiency), thereby validating our approach. Importantly, the global network approach, based on motif analyses, brought new insights into the spatial behaviour of bees. For instance, the foraging patterns of honeybees were characterised by frequent back and forth movements between flowers (Fig. 6d - i.e. motifs 7 & 8) and disproportionate usage of specific flowers or local hubs (Fig. 6d - i.e. motif 4).

The aim of this exploratory study was to introduce spatial network analyses for characterising bee movement patterns using relatively standard metrics. Further developments of this approach will provide a powerful, complementary, analytical tool to conventional behavioural metrics to inform researchers about spatial processes that are not captured by other measures. This approach should focus more on global measures of path optimality (e.g. network path length, geodesic distance 'Wasserman & Faust, 1994') to discriminate these different scenarios. For instance, network triads give new information about specific movement routines that may be repeated within a route, but that are hardly detectable with current measures of sequence repeatability (Thomson *et al.*, 1997; Ayers *et al.*, 2015). Ultimately, a major challenge for future studies will be to consider the high levels of heterogeneity among flower resources that bees may face in nature, taking into account variation in resource reward quantity and quality, signals, and competition among foragers in addition to spatial constraints of resource locations, to extend our approach to field conditions. Experimentally, bumblebees foraging in arrays of artificial flowers providing different nectar rewards face a trade-off between maximising their nectar intake rate and minimising travel distances when developing traplines (Lihoreau *et al.*, 2011). Analyses on non-averaged local metrics could be used to capture the effect of resource diversity in network formation and bring new insights into how bees integrate memories of multiple individual flowers in their spatial memory. The Kleinberg's authority score likely informs us about how bees use flowers as reference points relative to neighbouring flowers, perhaps to locate new flowers at the beginning of

route formation. The weighted clustering coefficient is a mean to determine the level of connections between sub-groups flowers, a measure that should greatly vary during the process of route optimisation. Other network measures, not used here, may also help understand how bees change their foraging area with experience or in the face of competition [e.g. modularity in Dupont *et al.* (2014)].

While some of the predictions tested here may seem rather intuitive, our analysis of bumblebee and honeybee movement patterns in relatively simple foraging conditions aims at illustrating how network statistics could serve future research in field and semi-field conditions. Motif network analyses offer the possibility to statistically compare networks to each other, either for the same individuals at different stages of route formation, or between different individuals, and between different species. Characterising the spatial foraging strategies of a wider range of pollinators, including wild and managed species is a key challenge of pollination ecology to identify and compare the real impact of these species on pollination services (Garibaldi *et al.*, 2013). For instance, our preliminary analysis suggests that at small spatial scales bumblebees display more efficient spatial movements than honeybees. Bumblebees tended to reach a frequency of each triadic structure that would lead to an optimal foraging network, whereas honeybees often showed the opposite behaviour. A possible explanation is the difference in social lifestyle between these two pollinator species. Honeybees, in contrast to bumblebees, have evolved a unique food recruitment system (the waggle dance) by which successful foragers communicate locational information about food resources to their nestmates upon their return to the hive (von Frisch, 1967; Dornhaus *et al.*, 2006). These insects may thus invest less in individual sampling and efficient route learning than species lacking the means to communicate foraging locations, such as bumblebees (Buatois & Lihoreau, 2016). Another possibility is the difference of typical foraging range between the two species. While bumblebees rarely cover more than 3 km to exploit floral resources (Osborne *et al.*, 2008), honeybees can travel more than 10 km within a single foraging trip (Pahl *et al.*, 2011), suggesting that they are better adapted to long flights and could start exhibiting optimisation movement patterns at larger spatial scales than bumblebees. Systematic comparisons of both species across a wider range of spatial scales will be needed to test these hypotheses.

Another key advantage of network analyses is that they allow for working on complete (raw) datasets and thus reduce the risks of arbitrarily discarding important information. In the case of pollinators, such approach may allow identification of specific movement patterns that occur at the early stage of route learning, for instance, exploration flights to locate flowers and store them in spatial memory, or exploitation flights to return to familiar locations (Woodgate *et al.*, 2016). Further development of pollinator movement networks may also include detailed dynamic temporal analyses of flower visitation sequences, which might reveal the differential effect of the individual experience on the probability to optimise the foraging route. Stochastic agent-based methods (Snijders *et al.*, 2010) recently applied to animal social networks (Boucherie *et al.*, 2016; Pasquaretta *et al.*, 2016), may also prove useful

to integrate rate of change of flower visitation sequences. New metrics could be developed to estimate network efficiency to account for the specificity of the structure of bee spatial movement based on individual experience. For instance, the direct integration of probability values based on the spatial distances between flowers will allow for a finer calculation of local network metrics which could be used to characterise the individual learning process and compare the likelihood to obtain an optimal foraging route depending on the early spatial experience of the bee. Explicit consideration of the nest as a specific node in the network, different from flowers, may also bring useful information about bee network dynamics and efficiency.

For all these reasons, we believe that pollinator movement networks constitute a highly promising conceptual framework for studying plant-pollinator systems from a mechanistic point of view in complement to more conventional behavioural measures. Ultimately, a comprehensive understanding of bee movement patterns between plants may provide new fundamental insights into pollination processes and the genetic structuralism of plant populations. The development of optimal routes by individual bees between particular plants can have important and predictable effects on plant reproduction and inbreeding (Ohashi & Thomson, 2009). Advances in DNA pollen analyses (see Clare *et al.*, 2013; and metabarcoding; Pornon *et al.*, 2016) now allow identification of flower species visited by individual bees during a given foraging trip. One can readily downscale the approach at an intraspecific level using pollen DNA and more variable genetic markers (e.g. microsatellite; Arif *et al.*, 2010) to identify individual plants visited by pollinators and infer patterns of pollen flow within a plant population that can then be verified by paternity analyses using plant progeny genotypes for these markers (Bernasconi, 2003). Coupling these approaches with existing models of bee movements (Lihoreau *et al.*, 2012b; Reynolds *et al.*, 2013; Becher *et al.*, 2016) will provide critical information about how the foraging strategies of bees directly influence pollen transfer and plant mating patterns across landscapes, and therefore a better assessment of consequences of bee declines on pollination.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12446

Table S1. Betweenness centrality model selection using the Generalised Akaike information criterion (GAIC). The three ranked best models with both FULL and NULL models are shown.

Table S2. Authority model selection using the Akaike information criterion (AIC). The three ranked best models with both FULL and NULL models are shown.

Table S3. Clustering coefficient model selection using the Generalised Akaike information criterion (GAIC). The three ranked best models with both FULL and NULL models are shown.

Table S4. Experiment 1 - GLMMs frequency of each network motifs and foraging bouts.

Table S5. Experiment 2 - GLMMs frequency of each network motifs and foraging bouts.

Table S6. Experiment 3 - GLMMs frequency of each network motifs and foraging bouts.

Table S7. Experiment 4 - GLMMs frequency of each network motifs and foraging bouts.

Table S8. Experiment 5 - GLMMs frequency of each network motifs and foraging bouts.

Table S9. Experiment 6 - GLMMs frequency of each network motifs and foraging bouts.

Table S10. Conventional statistics. Number of re-visits to flowers and travelled distance divided by the number of visited flowers for bumblebees (experiments 1, 2 and 3) and honeybees (experiments 4, 5 and 6) in large (experiments 3 and 6) and small (experiments 1, 2, 4 and 5) spatial scale arrays. Two types of statistical modelling approaches were used: a generalized linear mixed effect model for count data (GLMM) to study the impact of experience (foraging bout) on the number of revisits to flowers and a linear mixed effect model (LMM) for the travelled distance divided by the number of flowers visited. Both models were run for each experiment using individual identity as random effect. Both models were run for each experiment using individual identity as random effect. Estimates, their standard errors (SE), the appropriate statistics (z-value for GLMM or t-value for LMM) and *P*-values are shown.

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