Social ecology of a woodland songbird community: from individual movements to the emergence of population social structure

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ABSTRACT

Social structure can have profound evolutionary and ecological implications for animal populations. Structure can arise and be maintained via social preferences or be indirectly shaped by habitat structure. Quantifying the drivers of social structure is important to understand how social networks can shape evolutionary landscapes. Here, we study a large community of wild birds fitted with uniquely-coded passive integrated transponder (PIT) tags and recorded on a grid of automated feeders fitted with radio frequency identification (RFID) antennae. These data reveal that preferred movement pathways between sites that are consistent between years and not predicted by habitat features alone drive between-year consistent multi-level community structure in the social network. Our study highlights how ecological factors can shape social structure at the population scale, which has widespread implications for understanding eco-evolutionary dynamics.

INTRODUCTION

The social environment can fundamentally shape the life histories of animals. Who individuals associate with can determine the information they have access to [1, 2, 3], affect how well they can exploit resources [4, 5, 6], and impact their ability to successfully reproduce [7, 8, 9, 10]. Social structure can also influence population processes, such as the spread of information within [11, 12, 13] and between [14] species, and the spread of disease among individuals [15, 16]. Finally, individuals can experience selection arising from properties of their social groups [7, 8] or their communities [17]. Quantifying the factors that shape individuals' social environments is therefore a key step in determining the evolutionary drivers of sociality [18, 19] as the mechanisms that determine where, and with whom, individuals live their lives are what selection arising from population processes (e.g. disease burden or information use) can act upon.

Population social structure (the patterns of connections that emerges from interactions among individuals, often represented using social networks) is generally considered to arise from individuals making decisions about whom to associate with [20]. However, because spatial proximity is a key requirement for associations or interactions (i.e. connections) among animals [21], patterns of connections among individuals are bound to be shaped by a number of extrinsic factors, such as geometry and structure of the habitat that promote or restrict individual movements. At a local scale, habitat structure, such as understorey density, can channel individual movements, thus influencing the propensity for contact among individuals. At a broader scale, movement 'highways' can significantly reduce the social distance among individuals despite a large spatial separation, and therefore facilitate the flow of information or disease [22]. For example, sleepy lizards (*Tiliqua rugosa*) living in open habitats had fewer contacts with conspecifics than those living in more structured habitats [23]. Whilst habitat features can promote movements, the geometry of habitat (such as habitat fragmentation) can introduce barriers that constrain individual movements. Such barriers can result in a structure where the social distance between two individuals (i.e. their degrees of separation in a social network) on either side of this barrier could be much greater than their actual spatial distance. Habitat geometry and features can therefore impose structure in a social network that could easily be interpreted as arising socially. Given that local heterogeneity in gene flow can lead to rapid evolutionary differentiation [24], integrating knowledge about fine-scale environmental heterogeneity into studies of social structure could fundamentally alter our understanding of adaptation and the ability for animals to respond to selective pressures.

A major challenge in identifying extrinsic factors that drive population social structure is the need to have information about the movement of individuals in space, the patterns of social connections among the majority of individuals in a population, and information about the habitat in which they live. Recent technological advances have eased the logistical constraints of sampling many individuals moving across large areas [25, 26, 27]. In particular, passive integrated transponder (PIT) tags are cheap electromagnetic tags that can be fitted to many individuals at once [28], thus overcoming the challenges associated with studying entire animal communities. Because PIT tags do not rely on battery power to emit a signal, but instead are detected by affecting the magnetic field in radio frequency identification (RFID) antennas, they provide the unprecedented ability to track individuals across years and life stages. Further, advances in the analytical tools, such as social network analysis [29] and community detection algorithms [30], are facilitating greater insight into patterns of social structure. However, although technological advances have underpinned a boom in the study of animals' social networks [31], much less effort has focused on identifying key mechanisms that form communities and shape social structure at the scale of populations.

In this paper, we investigate the patterns of individual movement and the resulting community structure in a large contiguous mixed population comprising 5 species of wild songbird over 4 winters [Farine et al *in prep.*]. We first quantify movements across the landscape across all four years to determine if individuals move evenly through space, or if there are consistent movement corridors. We determine whether preferred movement pathways are maintained across generations, and whether they are associated with understorey habitat density and the geometry of the woodland. Second, we use patterns of connections among individuals to construct social networks, and use these social networks to determine at what scales population social structure is most consistent across years. Doing so helps us to elucidate the relative importance of different potential drivers (both social and habitat) that underpin population social structure.

RESULTS

Quantifying individual movements

To determine whether individuals moved freely through Wytham Woods, or if movement patterns are shaped by features of the habitat, we first quantified the daily movement rates between different feeding stations. Our population consisted of a total of 5163 unique PIT-tagged individuals (see Methods), of which 3051 were great tits (*Parus major*), 3960 were blue tits (*Cyanistes caeruleus*), 403 were marsh tits (*Poecile palustris*), 232 were coal tits (*Periparus ater*), and 110 were nuthatches (*Sitta europaea*). We detected the presence and group membership of birds using a grid of 65 bird feeders filled with unhusked sunflower seed, and studied the population over 4 winters.

We first created a movement network combining the data across all years (Figure 1, see methods). We found that the majority of movements (n=83071) occurred between feeding stations where more birds were present. However, not all birds followed the same patterns. First, we found that birds in their first winter made many more moves than adult birds: first year birds accounted for 61% of all movements despite making up only made up 38% of the population on average. Further, their movement networks included many more long-distance movements than those of adults (Figure 1), resulting in a significantly higher average movement distance (Figure S1). Second, we found that although great and blue tits exhibited similar movement patterns, marsh tit movements were typically much more localized (Figures S2, S3). Thus, age and species both affected the distribution of overall movements. These patterns suggest that many social processes, such as disease spread or information transmission (both within and between species) will be linked to demographic processes.

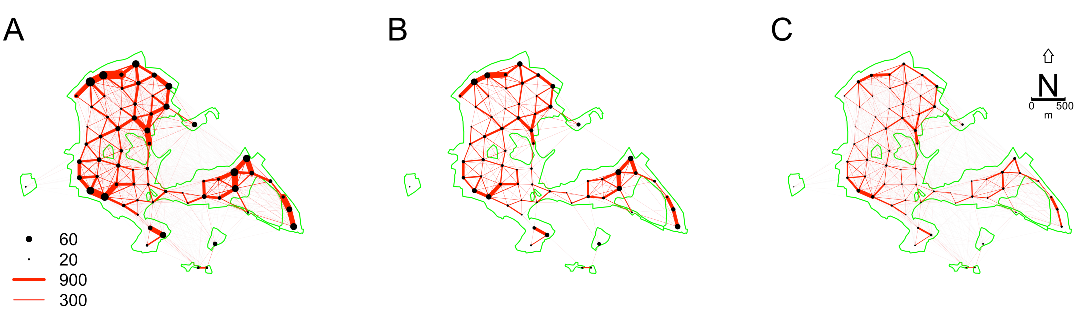

Figure 1: Total movements of (A) all birds, (B) adults, and (C) juveniles from all species over 4 winters of data. The thickness of each line represents the number of observations of a bird moving between the two feeding stations (black points) in the

same day. The size of the points represents the average number of individuals observed at each feeding station. The green outline represents the outline of Wytham Woods and four small external woodplots.

Testing the predictors of movement propensity

Habitat structure is likely to shape movement patterns by birds during the winter in several ways. First, for arboreal species, individuals are more likely to move through the forest than over open group, and thus the distance between foraging patches needs to be calculated through the forest and thus the presence of open areas is likely to have some impact on the spatial patterns of movements. Second, within the forest, the understory structure of the habitat could create preferred areas of movement by providing shelter from predators. Finally, additional factors such as local traditions could maintain consistent movement pathways, when generations mix and where social learning occurs. We compared the patterns of movement observed across years, and relate these to spatial distance and habitat features. To avoid the potential confounding effect of population density in our statistical analyses, we re-defined edges in the movement network as the probability that an individual detected at either site moves between them on a given day (see methods). Edge weights ranged from 0 representing no movement between adjacent sites to 0.83 representing that each individual detected had an 83% chance of moving between the two sites on a given day (Figure S4). For each pair of sites, we also estimated the density of understorey vegetation between them using data collected at 100m intervals throughout Wytham Woods [32] (see methods). Because Wytham Woods is unevenly shaped, we also calculated distance between feeding sites as *forest distance*, which is the shortest line without leaving boundaries of the forest. To enable direct comparison between each predictor variable, we scaled each predictor to zero mean and unit variance.

Weighted multiple regression quadratic assignment procedure (MRQAP) [33] revealed that the movements by birds between feeding stations were significantly more similar from year to year than expected by chance, even when accounting for forest distance and habitat structure (see Table 1, Figure 2). In all years, birds were significantly more likely to move between 'close' feeding stations than distant ones, and were also more likely to move between feeders that were separated by higher understory habitat density. However, the propensity to move between feeders observed in previous years was consistently the strongest predictor of future movements. The coefficient values for movements predicted by the previous year are typically an order of magnitude larger than those of other predictor variables, suggesting that some undetected factors are driving patterns of movements by birds across this woodland. Because for many feeding stations the distance and forest distance are very similar (see Figure 2), we also tested whether birds were less likely to move between feeding sites that were separated non-forest by calculating the difference between forest distance and Euclidian distance. We found that birds moved less between feeders with a larger difference in distance (i.e. the path through the forest was much longer than the straight-line path), suggesting that birds are avoiding crossing open fields (Table 2).

Table 1: Results of multiple regression quadratic assignment procedure used to test whether previously observed patterns of movement (probability of moving between sites per capita), distance between sites (distance through the forest), and habitat density (percentage cover) between sites explain the observed patterns of movement. Bold values represent significant coefficients, * represents significance at $P < 0.01$, ** represents significance at $P < 0.001$. All variables are scaled to 0 mean and unit variance to enable comparison between effect sizes.

Year	Previous Year	Forest Distance	Habitat Density
2013	**0.903****	**-0.028***	-0.010
2014	**0.877****	**-0.060****	-0.010
2015	**0.787****	**-0.091****	-0.019

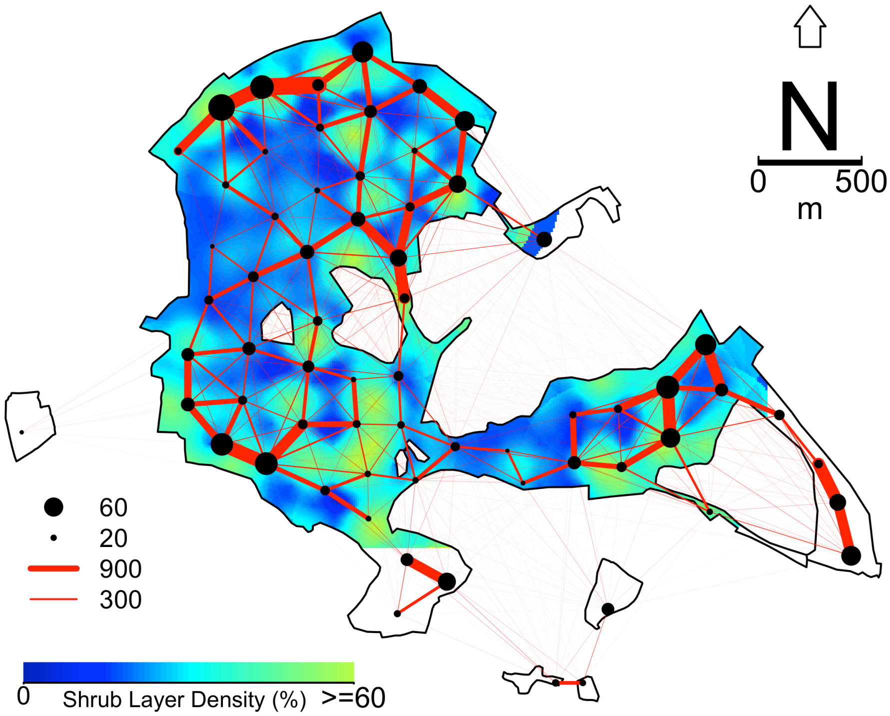

Figure 2: Total movement of all birds (from Figure 1A) overlaid on the shrub layer density (0.5m to 2.5m above ground). Areas with a white background have no habitat data available.

Table 2: Results of multiple regression quadratic assignment procedure used to test whether birds moved less between feeding sites separated by open space. For each pair of sites, we calculated the difference between the forest distance and the Euclidian distance. Bold values represent significant coefficients, * represents significance at P < 0.01, ** represents significance at P < 0.001. All variables are scaled to 0 mean and unit variance to enable comparison between effect sizes.

Year	Previous Year	Relative Distance
2013	**0.919****	-0.001
2014	**0.906****	**-0.019***
2015	**0.828****	**-0.029***

Quantifying community structure

Population-level social structure can have significant implications for population processes. For example, high levels of clustering can reduce the spread of disease within populations [34]. Thus far, we have shown that both social and habitat features are likely to contribute to where animals move. Here we investigate how these patterns contribute to the emergent structure of the population. From the detections of individuals at feeding stations, we inferred flock membership and social network structure (see methods) using well established approaches developed for this population [7, 12, 13, 14, 29, 35, 36, 37, 38]. We then inferred communities in the social networks using the edge betweenness community detection algorithm in the R package *igraph* [39], and explored the between-year stability of individual co-membership to the same community (see Methods).

To investigate population social structure at different scales, we cut the social network into *k* communities, where ranged from 2 to 65 (the latter representing the total number of locations with a feeding station). If communities are structured exclusively by extrinsic fctors, we expected a drop in the stability of co-membership by individuals as we created more fine-scale communities. For example, if a population is spread across three isolated patches of woodland, then we expect that birds will always occur within the same three communities (one for each woodland) each year. By contrast, if communities are structured socially, then we expected smaller communities (local cliques) to be more stable. For example, for a territorial pair-living species living in a lattice-like uniform environment, an algorithm will be able to isolate each pair when identifying k=N/2 communities, whereas the communities detected for smaller k values will be essentially random. When applied to our social network data, we uncovered two scales that maximized the propensity for pairs of individuals that were observed in the same community to be re-observed in the same community in the following year. When social networks were partitioned into 2 or 3 communities (Figure 3), individuals observed in the same community in one year and observed again in the following year re-occurred in the same community approximately 90% of the time. These communities largely represent the geometry of Wytham Woods, with two core habitats (north-west and the east), and a small wood to the south that is only attached by a narrow neck of vegetation representing a third community.

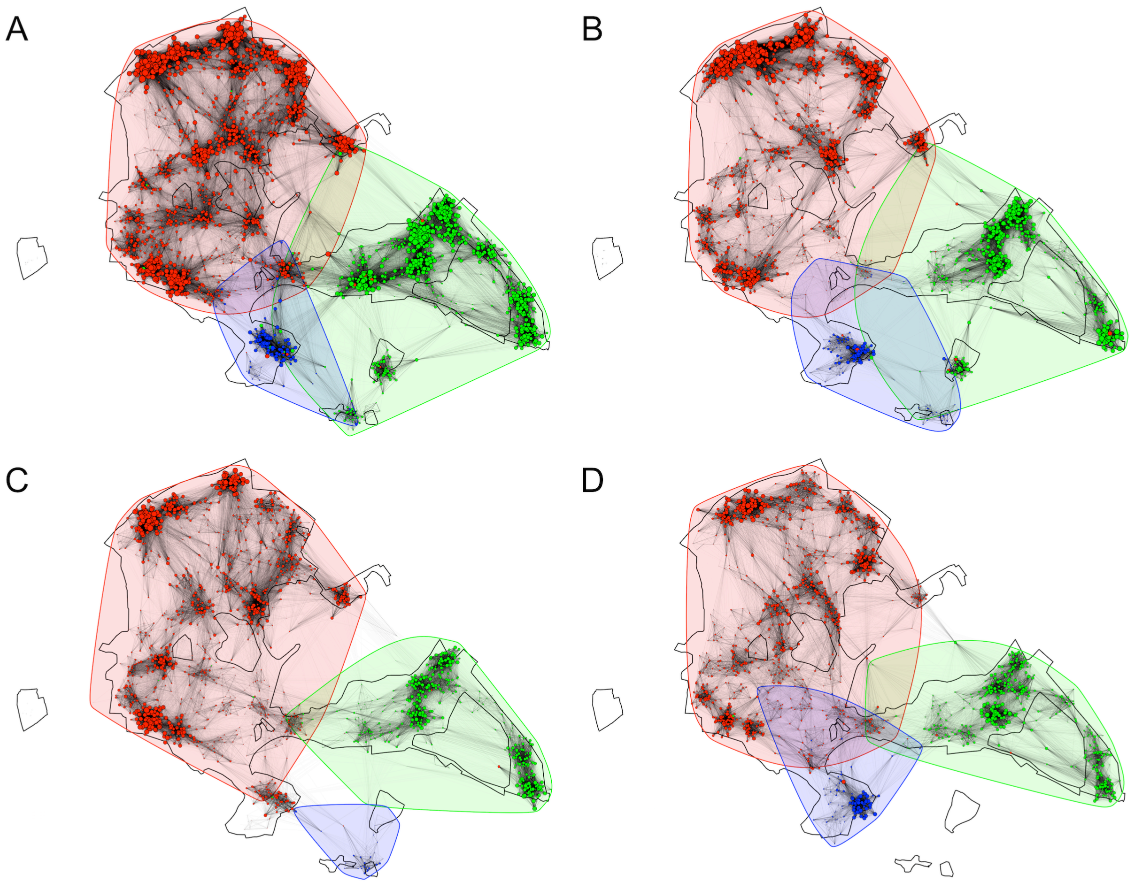

Figure 3: The probability that two birds observed in the same community in one year remain in the same community in the following year, given that both are observed. The probability is calculated with the social network partitioned into the same specified number of communities (2 to 65) in all years.

Specifying the algorithm to detect 4 communities significantly decreased the probability of individuals being re-observed in the same community (no overlap in the 95% confidence intervals in Figure 4), suggesting that there is no stable 4th community. Partitioning the network further by specifying the algorithm to detect more than 4 communities then increased probability that two individuals occurring in the same community in one year and both observed in the following year again re-occurred in the same community. Thus, the patterns of social organization at both the population scale (2-3 communities) and at a local scale (>50 communities) were extremely stable year-to-year. This result suggest that multiple levels of community structure exist in this population. Partitioning the network into larger number of communities did not result in one community per feeding station, instead several large communities were maintained and many small ones were created (Figure 5). Finally, we found no evidence that the composition of species in communities changed based on how many communities were created (Figure S5). Thus, the partitioning of the network into more (smaller) communities did not segregate individuals into species-specific clusters, and so stable community structure at a local scale was not explained by simple species-level processes.

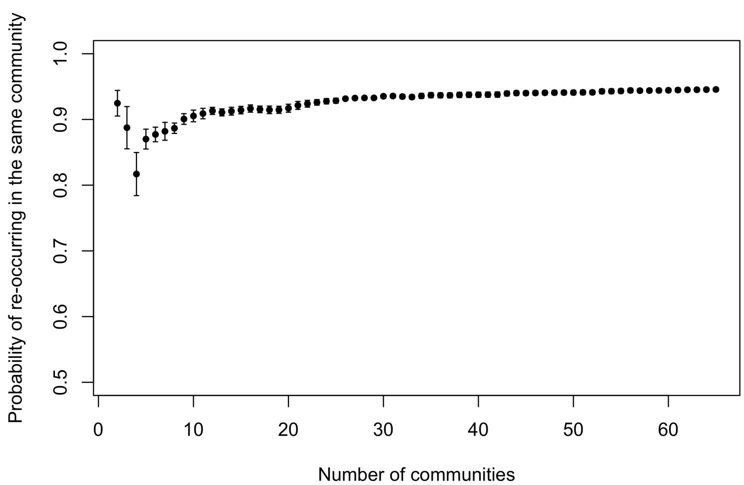

Figure 4: The social network for each year of the study partitioned into 3 communities. Each point represents one individual, and its colour represents the community it is assigned into. The size of each point represents its weighted degree (larger points have more and/or stronger connections to other individuals). Points are drawn at the average location that the individual was observed, with a small amount of jittering added to reduce the overlap between individuals observed in the same location.

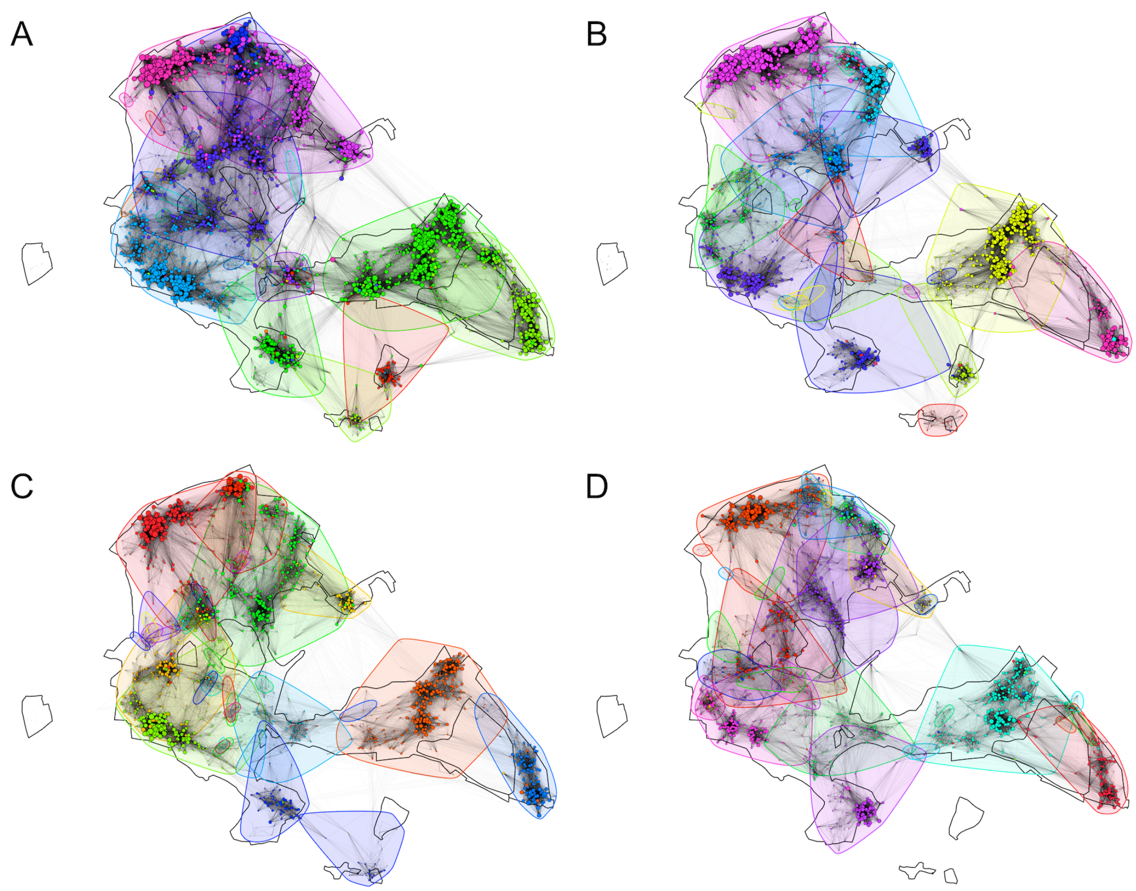

Figure 5: The social network for each year of the study partitioned into 65 communities. Each point represents one individual, and its colour represents the community it is assigned into. The size of each point represents its weighted degree (larger points have more and/or stronger connections to other individuals). Points are drawn at the average location that the individual was observed, with a small amount of jittering added to reduce the overlap between individuals observed in the same location.

Linking movement patterns to community structure

What drives the consistent patterns of community structure in the social network of this population? Understanding how communities emerge in the social networks is important for determining which behaviours (i.e. mechanisms) group-living could act on as agents of selection. Uncovering the processes that drive community structure becomes notably more complex when studying species where individuals form fission-fusion groups, as no single individual is likely to be responsible for the global patterns of connection. Instead social structure arises from the interactions among all individuals taken together. One plausible mechanism that is likely to underpin some aspects of community structure is the patterns of movements. Individuals living at two locations with frequent movements of individuals between them will be more likely to be connected in the social network, and therefore more likely to be in the same community and share similar social environments.

We investigate whether the regular movements of individuals between particular feeding stations are responsible for global community structure (see Methods). We found that when we partitioned the network into few communities, the individuals at feeding stations connected by many movements occurring were very likely to be allocated to the same community (Figure 6). This supports our hypothesis that the extrinsic habitat features shape the broad patterning of the community (i.e. the presence of 2-3 distinct clusters of individuals, see Figure 3). However, at more local scale, we found that the assortativity coefficient decreased (Figure 6). Thus, as the social network is partitioned into more communities, movements between sites explained less of the community structure, despite the fact that individuals become more likely to re-occur in the same communities across years (see Figure 4).

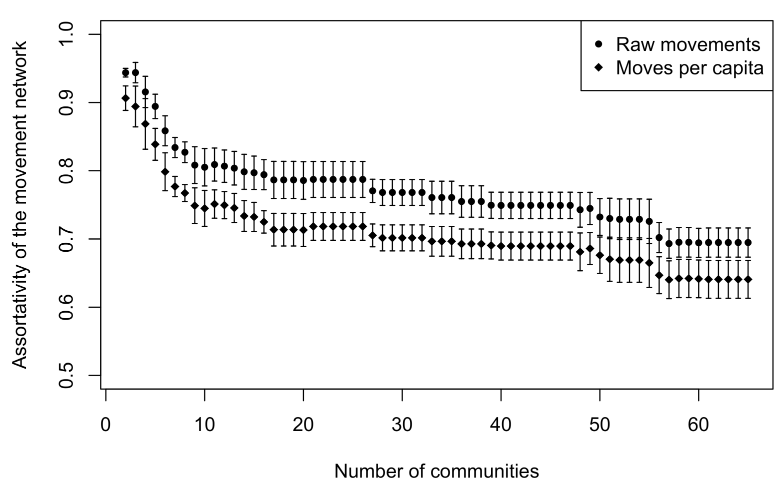

Figure 6: The correlation of movements between feeding stations and community structure decreases with increasing numbers of communities. Each feeding station is allocated to the community in which the majority of individuals are members and used as a trait value to calculate assortment using the raw movement networks (Figure 1A) and the per capita movement network (Figure S2A). High values represent stronger connections between feeding stations in the same community.

DISCUSSION

Our study revealed two levels of social structure in a large community of wild birds containing several thousands of individuals from five species. At a broad scale, the social network contained two to three communities that were easily predicted by the regular movement paths used by birds. The movement of birds through the woodland were repeatable each year, but the similarity in movements across years was only partly by the geometry of the study area and fine-scale variation in habitat structure. Our results suggest that some other processes, potentially social processes such as local traditions [12, 40], may also be involved. If that is the case, then broad-scale social structure could be, in part, the result of a socially-transmitted inter-generational effect. At a more local scale, we found highly stable social structure, with local clusters of individuals from all five species re-associating each year to maintain consistent communities. Our study highlights how multiple factors shape the social ecology in a population of wild birds.

The link between extrinsic habitat factors and community structure in animal populations has been investigated before. For example, community and sub-community structure in Galapagos sealions *Zalophus wollebaeki* are largely driven by the structure of male territories [41]. However, territorial behaviours are unlikely to play a major role in structuring the winter population of birds in Wytham Woods because the majority of individuals were great tits and blue tits, which are both non-territorial during the winter. In non-territorial wintering golden-crowned sparrows

(*Zonotrichia atricapilla*), social network communities were also found to be more structured than expected given the spatial overlap in the home-range of birds [42]. The surprising aspect from that study is that golden-crowned sparrows maintain a stable community structure in their wintering range despite having migrated a long distance from their breeding areas. The phenomenon observed in both tits and sparrows suggests that winter sociality is likely to play an important role that goes beyond simple group size effects, and thus could have carry-over effects into breeding performance in the following spring (e.g. [7]).

A potentially important feature that we extracted in our study was differential movement patterns between classes of individuals. We found that juveniles typically made more long-distance movements than adults. This pattern, which is likely to arise from juvenile dispersal behaviour, has a number of implications for social processes. To overcome strong seasonal changes in the environment, juvenile tits rely on learning from adults [43]. As they move through the landscape, juveniles copy the adults in their local environment, and a recent study demonstrated that tits exhibit a strong conformist (copy the local majority) social learning strategy [12]. However, stability in local community structure means that local traditions (behaviours that differ among different social groups in a population) can easily become entrenched [12]. Juveniles could therefore play an important role in facilitating transfer of new information into social groups. At the same time, juveniles are likely to come into contact with a greater number of individuals, and thus could play an important role in spreading diseases or pathogens across communities (as suggested in humans [44]).

By investigating the stability of community structure at different scales, we found evidence that tits in Wytham Woods live in a multi-level community structure. Multi-level community structure occurs when animals form small groups, or clusters, of individuals with whom they associate most strongly, and a larger groups composed of individuals with whom they associate loosely or indirectly. There is increasing interest in multi-level community structure as it can have major implications for how social processes occur [45, 46, 47, 48]. Multiple factors can shape the movement (or not) of individuals among social units. These factors can be broadly split into two categories: social factors (such as relatedness [49, 50, 51], cultural similarity [52], or species identity [45]) and habitat factors (features of the environment that modulate how individuals move, and thus whom they encounter). Although recent studies have begun teasing apart social versus habitat factors that determine the patterns of contact among individuals with different phenotypic characteristics [37], little is known what drives the emergence of global population-level structure. Cantor et al [52] recently used simulations to suggest that multi-level communities can emerge when individual segregate into clans formed around similar cultural behaviours. In our study, we found evidence that both habitat and social factors contribute to multi-level community structure. The general geometry of Wytham Woods introduced a repeatable set of large-scale communities (Figure 3). Environmental features (notably habitat density) that promote or hinder movement by individuals (Figure 2) can shape whom individuals encounter. Together, these features are likely to play a major role in how the population is broadly structured. In addition, by studying birds that form mixed-species communities, our study highlights that complex interaction patterns, such as associations among kin or cooperation, are not pre-requisites for multi-level structure to emerge. Instead, social mechanisms, such as social preference[37] and phenotypic drivers[35], determine who individuals affiliate with, while the woodland geometry and habitat density determine who individuals can come into contact with.

The presence of multi-level community structure can have implications for evolutionary dynamics of populations. First, restricted movement can reduce gene flow and lead to divergence in the evolutionary trajectories of sub-parts of each population. Garant et al. [24] demonstrated that differential dispersal reinforces local variation in selection for nestling body mass. In their study, they found that trends in genotypic variance for body mass in nestlings were very different in the eastern sectors of Wytham Woods and the northern sectors. These two areas represent the two largest population-level communities we found in our study. Second, individuals in the same community will have more similar social environments than individuals occurring in different communities. Thus, any social effects arising via the social environment, such as indirect genetic effects [53], could accelerate patterns of divergence within single populations. Finally, the social environment itself can act as an agent of selection [18, 54], and therefore processes that shape social structure are likely to impact the overall strength and direction of selection experienced by populations.

Together the findings from our study highlight how stable social structure can be maintained in populations as a consequence of both social affiliations and features of the habitat that individuals live in. The combination of strong clustering together with some random movements in networks can facilitate the spread of disease or information through the network [34]. This prediction is supported by evidence from the rapid spread of a recent disease [55] and of novel traditions [12] in this population. At the same time, consistent population social structure can lead to phenotypic and genotypic divergence [24], with potential implications for how animals can adapt to changing environmental conditions. Integrating information about animal social structure with data on both pulse and long-term selective events could yield novel insights into the evolution of social behaviour. However, as our study highlights, determining the capacity for populations to respond to selective pressures will require an understanding of a range of different drivers shaping their social structure.

DATA COLLECTION METHODS

Study location, study species, and population dynamics

The study was undertaken in Wytham Woods, Oxfordshire, UK (51° 46’ N, 01° 20’ W), a 385ha area of broadleaf deciduous woodland surrounded by open farmland. Pairs of birds hold territories during the breeding season (April – June), but form loose fission-fusion groups during the winter, flocking with unrelated individuals that forage for ephemeral food sources. Flocks often contain multiple species [38], and our study also includes data on the five most common flocking species: blue tits, marsh tits, coal tits, and nuthatches. Tits are generally short-lived—great tits have a mean life span of 1.9 years. This short generation time results in high annual population turn-over and inter-annual variation in population sizes. Very good breeding conditions lead to large population sizes, whereas poor breeding conditions result in fewer juveniles and a much reduced population size.

Understorey habitat density

We used data from Kirby et al. [32] to quantify the habitat structure between each feeding site. In that study, the authors recorded, among other measures, the shrub cover density (0.5m to 2.5m above ground) along the diagonal of 164 different 10m x 10m quadrats equally spaced throughout Wytham Woods. Here we use data from the 2012 census, which falls roughly in the middle of our study period. To extrapolate from the 164 sites, we generated a surface plot where we extrapolated the data to a 10 x 10m grid of points. The resulting figure accurately captures variation in habitat density based on our knowledge of the study site. To calculate habitat density between each pair of feeding sites, we calculated the mean habitat density along a 20m-wide transect connecting the two sites.

PIT-tagging birds

All birds in the study were caught in either a nest box (as parents and as chicks) or a mist-net (approximately half the population are birds that immigrate). Each bird was fitted with uniquely numbered British Trust for Ornithology metal leg ring, and a uniquely-coded passive integrated transponder (PIT) tag (IB Technologies, UK) that was fully enclosed in a molded plastic ring fitted to the other leg. Each PIT tag contains a unique code that can be recorded by antennae (see next section), and these were then matched to the bird's ring number. We ceased fitting PIT tags to coal tits from October 2012 as the tags were aggravating pox lesions on birds legs during a naturally-occurring epidemic. For each bird that was caught and tagged, we recorded the age and sex (where possible following [56]).

Data collection

We placed 65 automated feeding stations in a evenly-spaced grid covering the entirety of Wytham Woods and small isolated patches of woodland nearby. Commercial bird feeders (Jacoby Jayne, UK) were fitted with a radio frequency identification (RFID) antenna on each of the lower two access holes and other access holes were blocked. The antennae recorded the unique PIT tag code, time and date for each visit by a marked bird. For the duration of the study, the feeding stations were scheduled to open and begin logging at 6am on Saturday mornings, and shut after dusk on Sunday evening. Feeders were in place December to February in the winter 2011-12 (13 weeks), from December to early March of winters 2012-13 and 2013-14 (14 weeks each), and for January and February in the winter of 2014-15 (8 weeks). This data collection resulted in 49 unique weekends and 98 complete data logging days over the 4 winters. In latter years, 6 feeders covering two external sites were replaced for a separate experiment, and thus the data were not included in these analyses.

Inferring flocks and flock membership

The data logged from the PIT tag detections produces bursts of detections in the temporal data stream. These vary in length depending on the size of the flocks present which increases during the course of the day, [57]. We used a recently-developed statistical method called Gaussian Mixture Models [58] to extract the start and end times for each distinct flock. This machine-learning method statistically fits Gaussian curves of varying sizes to each burst in the data and allocates each record to the distribution, or 'gathering event', into which it falls. Gaussian Mixture Models provide a more robust estimation of the social network structure than alternative methods [59].

Constructing movement networks

From the logging data, we recorded every case of movement by a bird from one feeding station to another within the same day (a total of 83071 movements over 4 winters), and used these to create movement networks that quantify the connectedness between each pair of feeding stations in the study. We used daily sequential detections to maximize our chances of correctly inferring direct movement pathway (e.g. moving between locations A and D via locations B and C) and minimizing our chances of incorrectly inferring movement pathways (e.g. estimating only a direct movement between A and D). Because the number of movements are inherently linked to number of individuals present at a specific pair of feeders, we also created a network describing the rate of movement between feeders, where the rate was defined as the probability that an individual at one focal feeder would be observed moving to the other focal feeder within a day.

Constructing social networks

We defined edges in the social network using the simple ratio index: $E_{AB} = \frac{x}{x+y_{AB}+y_A+y_B}$, where E_{AB} is the edge weight between individuals A and B, x is the number of times they were detected in the same flock, y_{AB} is the number of occasions they were both detected at the same time but not in the same flock, y_A is the number of detections of A where B was not seen, and y_B is the number of detections of B where A was not seen. The networks for each year were constructed using R package *asnipe* [60].

Linking movements to community structure

For each year's social network, we first split the network by specifying k = 2 to 65 communities (see main text). For each value of k, we allocated individuals to their most common feeder, and for each of the feeding stations, select the community that the majority of individuals present were members of. This enabled us to create a community label for each feeding station (and for each value of k), and link these to the network formed by the movement of individuals (Figure 1). To test whether the movement network shaped the community structure in the network for a given value of k, we quantified the assortativity coefficient of the network using communities as discrete trait values [61, 62]. Assortativity is the measure of how well connected alike nodes are compared to how well connected dislike nodes are, ranging from 1 (all edges connect nodes with the same traits) to -1 (all edges connect nodes with different traits).

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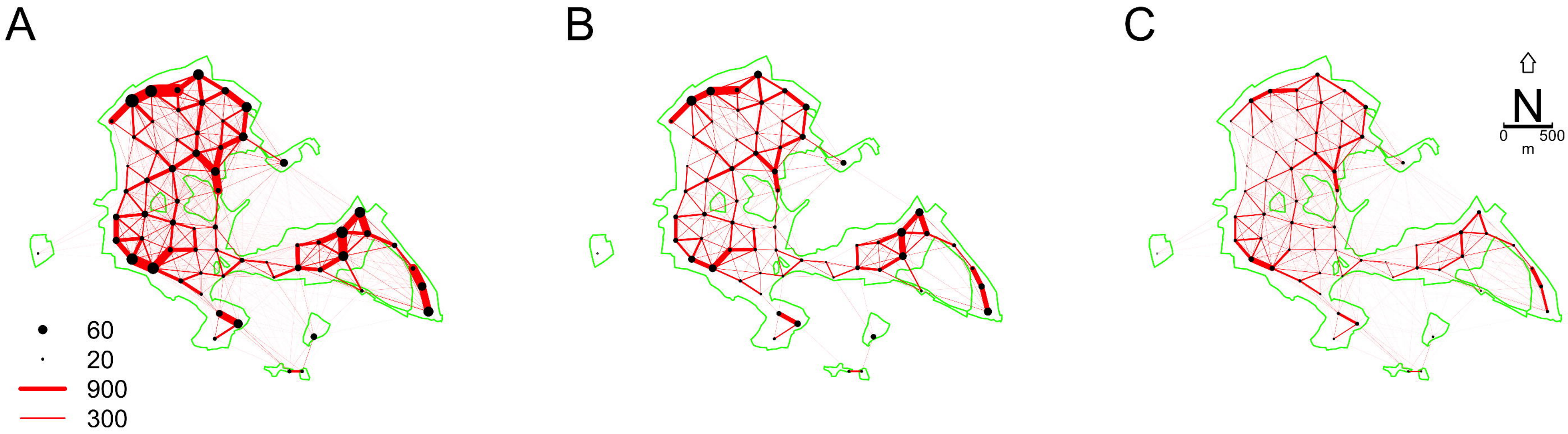
A
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C
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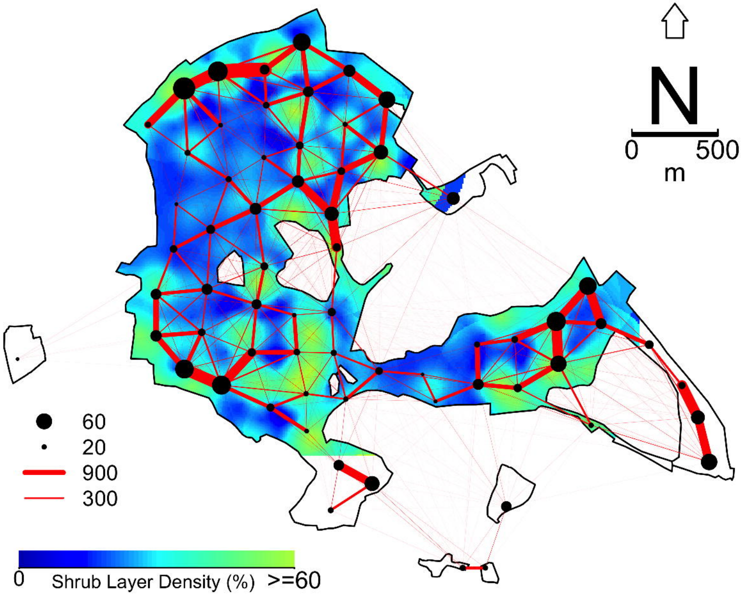
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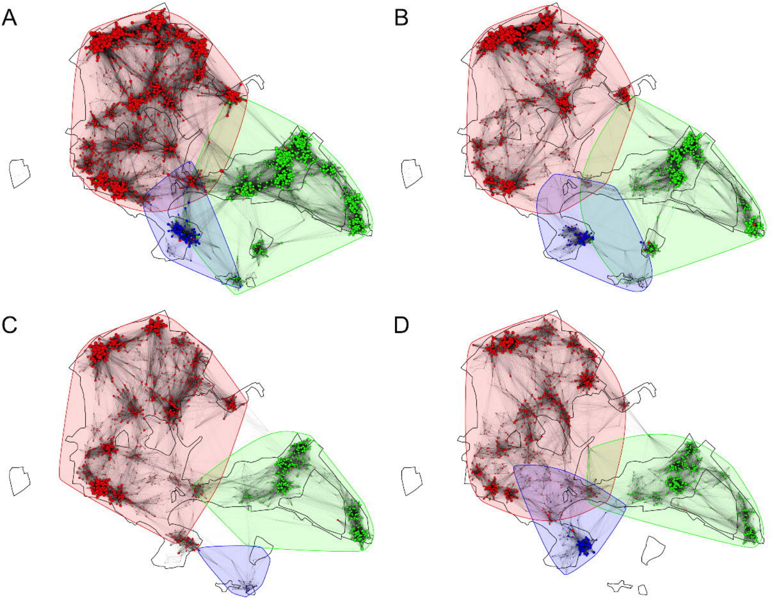
Shrub Layer Density (%)
>=60


A
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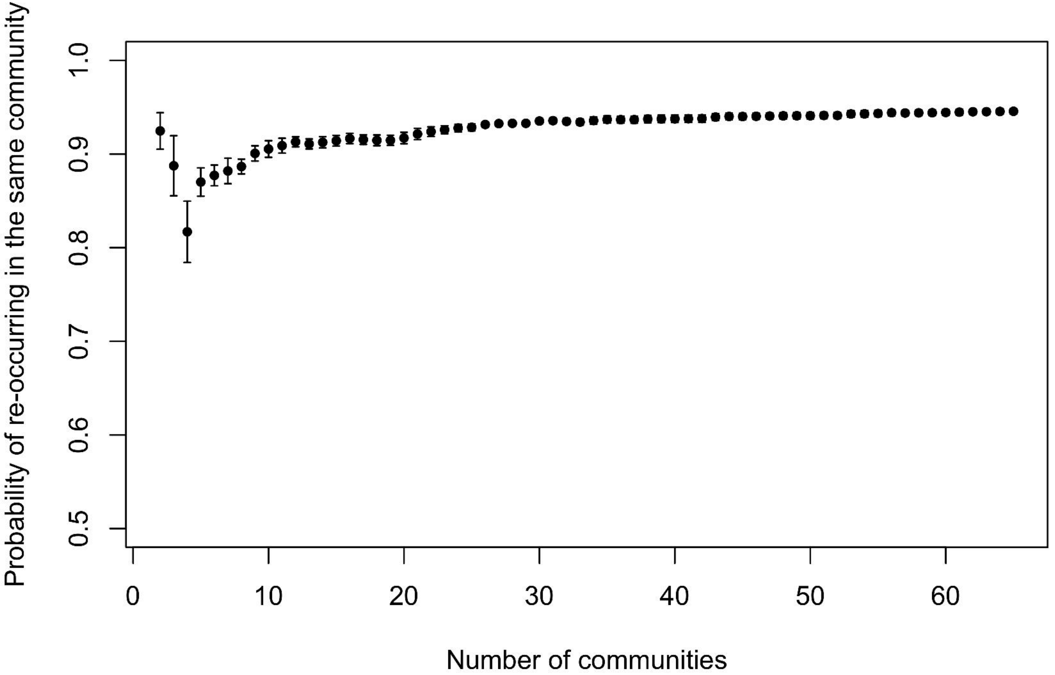
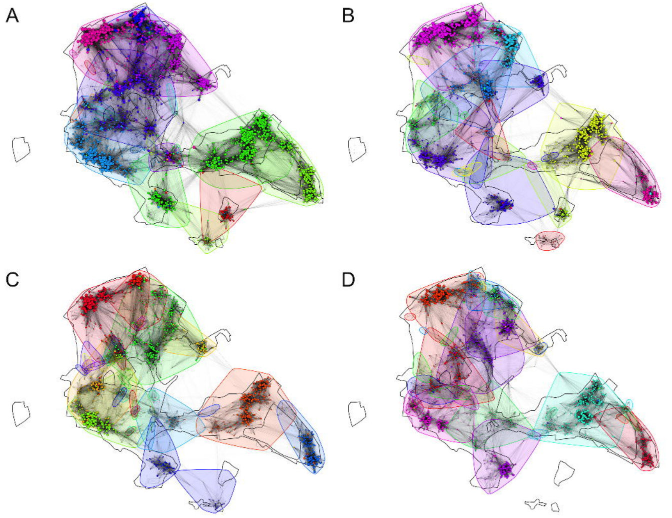
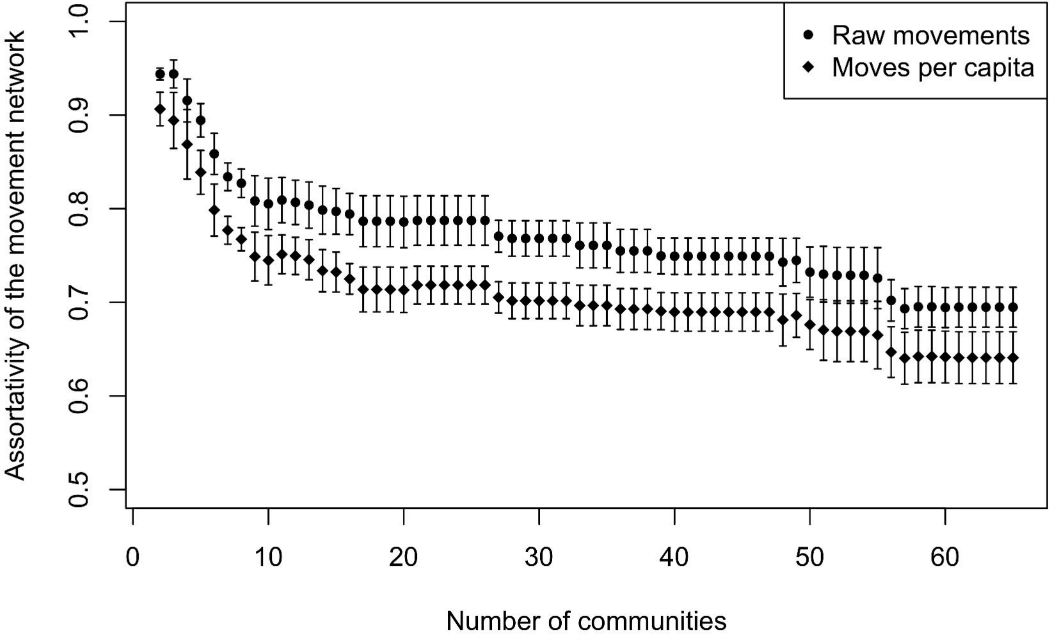


Probability of re-occurring in the same community
1.0
0.9
0.8
0.7
0.6
0.5
0
10
20
30
40
50
60
Number of communities


A
B
C
D



Raw movements
Moves per capita
Assortativity of the movement network
0.5
0.6
0.7
0.8
0.9
1.0
0
10
20
30
40
50
60
Number of communities