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Social and spatial effects on genetic variation between foraging flocks in a wild bird population

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Abstract

Social interactions are rarely random. In some instances, animals exhibit homophily or heterophily, the tendency to interact with similar or dissimilar conspecifics, respectively. Genetic homophily and heterophily influence the evolutionary dynamics of populations, because they potentially affect sexual and social selection. Here, we investigate the link between social interactions and allele frequencies in foraging flocks of great tits (*Parus major*) over three consecutive years. We constructed co-occurrence networks which explicitly described the splitting and merging of 85,602 flocks through time (fission–fusion dynamics), at 60 feeding sites. Of the 1,711 birds in those flocks, we genotyped 962 individuals at 4,701 autosomal single nucleotide polymorphisms (SNPs). By combining genomewide genotyping with repeated field observations of the same individuals, we were able to investigate links between social structure and allele frequencies at a much finer scale than was previously possible. We explicitly accounted for potential spatial effects underlying genetic structure at the population level. We modelled social structure and spatial configuration of great tit fission–fusion dynamics with eigenvector maps. Variance partitioning revealed that allele frequencies were strongly affected by group fidelity (explaining 27%–45% of variance) as individuals tended to maintain associations with the same conspecifics. These conspecifics were genetically more dissimilar than expected, shown by genomewide heterophily for pure social (i.e., space-independent) grouping preferences. Genomewide homophily was linked to spatial configuration, indicating spatial segregation of genotypes. We did not find evidence for homophily or heterophily for putative socially relevant candidate genes or any other SNP markers. Together, these results demonstrate the importance of distinguishing social and spatial processes in determining population structure.

KEYWORDS

eigenvector maps, *Parus major*, population genetics, single nucleotide polymorphisms, social networks

1 | INTRODUCTION

In many animal species, individuals interact repeatedly with particular individuals while avoiding or ignoring others (Croft, James, & Krause, 2008; Krause, Croft, & James, 2007; Krause, James, Franks, & Croft, 2014; Krause & Ruxton, 2002). Repeated interactions can be with the same individuals (e.g., social interactions in breeding pairs or stable groups) and with counterparts of a particular pheno- or genotype. Preference to interact with similar counterparts (i.e., homophily) is common, can evolve under a wide variety of conditions (Fu, Nowak, Christakis, & Fowler, 2012) and can be reinforced by assortative social learning (the preference to learn from specific individuals; Katsnelson, Lotem, & Feldman, 2014). Homophily has been found for various phenotypic traits such as age and sex in bottlenose dolphins (*Tursiops* spp.; Lusseau & Newman, 2004), sex in Grevy's zebra (*Equus grevyi*; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007), body size in guppies (*Poecilia reticulata*; Croft et al., 2005) and personality in great tits (Aplin et al., 2013) and chimpanzees (*Pan troglodytes*; Massen & Koski, 2014). Genotypic homophily has been reported in humans (Christakis & Fowler, 2014; Fowler, Settle, & Christakis, 2011).

On the other hand, the tendency to interact with dissimilar individuals (i.e., heterophily) is not very often observed outside the context of reproduction, in which the two sexes interact to produce and raise offspring. However, heterophily can evolve under particular conditions (Fu et al., 2012). Heterophily has been found for sex in foraging great tits (Farine et al., 2015), which may be linked to future mate choice. Genotypic heterophily has also been reported, but it was only apparent in particular regions of the genome. For instance, disassortative mating with respect to genes of the major histocompatibility complex (MHC) has been reported for many animal species, but meta-analyses showed that overall support is present but weak (Kamiya, O'Dwyer, Westerdahl, Senior, & Nakagawa, 2014; Winternitz et al., 2013). In humans, social interactions are more common between individuals who differ in genomic regions associated with the immune system. This might be adaptive if interacting with individuals which are resistant to different pathogens, rather than similar pathogens, reduces infection risk (Christakis & Fowler, 2014).

Genetic homophily and heterophily can have profound effects on the evolutionary dynamics of populations. For example, if mates are selected locally, any type of preference for particular genotypes (either homophily or heterophily) will result in a nonrandom pool of potential mates. Genetic homophily might therefore result in inbreeding or local adaptation. Individual fitness can be affected by homophily and heterophily, because fitness does not only depend on an individual's own phenotype, but is also affected by the phenotypes it is interacting with. For instance, the outcome of competition for food depends on the competitiveness of others. In this context, selection is shaped by the so-called social environment. These additional selection forces, called social selection (West-Eberhard, 1983), can accelerate or counteract natural selection (Wolf, Brodie, & Moore, 1999). To understand nonrandom social associations or social selection, it is critical to disentangle social processes (i.e., sexual and social selection) from spatial processes (e.g., the phenotype-dependent response to local variation in ecological conditions, or those arising from limited dispersal), because spatial process could otherwise be misinterpreted as social processes. For our purpose, we define spatial processes as all processes that affect the location and movement of individuals and are spatially stable over the time period of our study. Social processes are all processes that affect the spatial location and movement of individuals and depend on the movements or spatial locations of others.

In this study, we test for a relationship between social interactions outside breeding seasons and genetic variation in the great tit, a seasonally breeding passerine. Between breeding seasons, individuals join foraging flocks consisting of about 2–50 individuals (Ekman, 1989). Individuals are more likely to join the same foraging flock when they are born in close spatial proximity and when they are siblings (Grabowska-Zhang, Hinde, Garroway, & Sheldon, 2016); however, the consequences for the spatial distribution of genetic diversity remain unknown. The foraging flocks show fission–fusion dynamics (Farine et al., 2015), the process of changing flock composition and sizes over time, due to single or multiple individuals joining or leaving these flocks (Krause & Ruxton, 2002). The movement of individuals between flocks potentially homogenizes the genetic structure, but such homogenization might be prevented by either homophily or heterophily at a broader spatial scale. We tested whether allele frequencies in foraging flocks were affected by the tendency to be associated with preferred flock members in general (which we call group fidelity from this point onwards) and genome-wide homophily or heterophily specifically. We partitioned social and spatial effects to investigate whether allele frequencies resulted from the spatial distribution of animals or whether there were additional social forces driving preference for group fidelity, and whether preference was due to homophily or heterophily. We also tested whether homophily or heterophily was present for three categories of candidate genes which are likely to affect social interactions (See Table S2). We tested candidate genes for personality, because phenotypic homophily for personality has been found in our population (Aplin et al., 2013), circadian timing because we expect individuals to flock with others with similar circadian rhythms, and novelty seeking, because we expect individuals with similar exploratory tendencies to flock. Lastly, we tested a panel of markers across the genome to determine whether heterophily or homophily was present for single loci. As shown by Christakis and Fowler (2014) regions of the genome may differ, with some specific regions showing heterophily while most of the others show homophily. An overview of our research questions and hypotheses can be found in Table 1.

We explicitly modelled the fission–fusion dynamics of foraging flocks as well as their spatial configuration with techniques which have recently been developed for spatial analysis. We deployed Asymmetric Eigenvector Maps (AEMs; Blanchet, Legendre, Maranger, Monti, & Pepin, 2011) and distance-based Moran's Eigenvector Maps (db-MEMs; Dray, Legendre, & Peres-Neto, 2006) to model

TABLE 1 Overview of the questions and hypotheses addressed in this study. The unit of interest is the variance which our models try to explain with the social and spatial components. For the social and spatial components, we note whether the observed proportion of the variance should be equal (O = E), larger (O > E) or smaller (O < E) than expected by chance. The randomized unit is the unit which was randomized in the randomization protocol

Question	Unit of interest	Hypotheses	Social component	Spatial component	Randomized unit
Is the genetic structure at the population level affected by nonrandom movements of individuals?	Total variance in allele frequencies of flocks for all SNPs	H_0: No, random movements	O = E	O = E	Identities of individuals leaving a gathering event (Figure 3a)
		H_1: Yes, group fidelity	O > E	O = E	
		H_2: Yes, spatially restricted movements	O = E	O > E	
Is the genetic structure at the population level affected by clustering of genetically similar or dissimilar individuals?	Total variance in allele frequencies of flocks for all SNPs	H_0: No, no preference	O = E	O = E	Identities of all individuals within a year (Figure 3b)
		H_1: Yes, genomewide homophily	O > E	O = E	
		H_2: Yes, genomewide heterophily	O < E	O = E	
		H_3: Yes, spatial clustering of genetically similar (or related) individuals	O = E	O > E	
		H_4: Yes, spatial clustering of genetically dissimilar individuals	O = E	O < E	
Is the distribution of particular candidate genes in the population differentially affected by social structure?	Total variance in allele frequencies of flocks for SNPs associated with the candidate genes	H_0: No, not different	O = E	*N.A.*	Identities of all SNPs associated with candidate genes
		H_1: Yes, homophily for candidate genes	O > E	*N.A.*	
		H_2: Yes, heterophily for candidate genes	O < E	*N.A.*	
Is the distribution of particular single loci in the population differentially affected by social structure?	Total variance in allele frequencies of flocks for single SNPs	H_0: No, not different	O = E	*N.A.*	Identities of single SNPs
		H_1: Yes, homophily for particular single loci	O > E	*N.A.*	
		H_2: Yes, heterophily for particular single loci	O < E	*N.A.*	

fission–fusion dynamics of the foraging flocks and their spatial configuration, respectively. Both methods decompose network structures into uncorrelated components (eigenvectors), which can be used to describe network patterns. AEMs decompose directed networks which we used to model changes of foraging flocks over time (i.e., fission–fusion dynamics). Db-MEMs decompose undirected networks which we used to model the spatial configuration of those flocks. A major advantage of using eigenvector maps to describe spatial patterns and fission–fusion dynamics is that eigenvectors are orthogonal, and therefore, they can be used as predictors in regression or redundancy analyses. By simultaneously introducing AEMs and db-MEMs into the same model, we can partition variance into social and spatial processes and estimate their relative contributions to the variance observed in the dependent variables. We partitioned the variance in allele frequencies of 4,701 autosomal SNPs between foraging flocks to AEMs and db-MEMs. This enables us to quantify the relative importance of pure social processes such as preference or avoidance of certain conspecifics, and the distribution of individuals in space in driving allele frequencies across social groups (Figure 1). Simulations to assess this methodology can be found in the supplementary materials. To our knowledge, this is the first study to disentangle social and spatial processes in the genetic structure of animal groups and the first study in nonhuman animals to investigate whole genome heterophily and homophily.

2 | MATERIALS AND METHODS

2.1 | Study system

This study was conducted in the great tit population of Wytham Woods, a 385 ha mixed deciduous woodland near Oxford, UK (51°46′N, 1°20′W; Figure 2), over 3 years. In this population, 250–450 great tit pairs breed annually. Breeding pairs occupy exclusive territories, but when their offspring fledge, these territories break down. After fledging, offspring roam around with their parents and those families typically break apart after a few weeks (Naef-Daenzer, Widmer, & Nuber, 2001), while the parents often stay together Culina, Hinde, & Sheldon, 2015, Firth, Voelkl, Farine, & Sheldon,

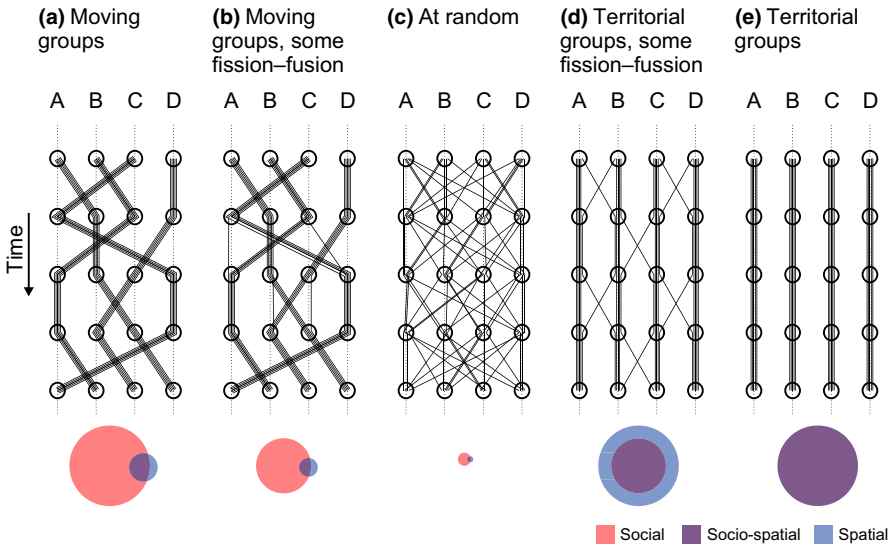


FIGURE 1 Schematic presentation of exemplar fission–fusion networks and associated Venn diagrams, showing the relative contributions of social and spatial structure to allele frequency variation between flocks given various degrees of group and site fidelity by individuals. A, B, C and D represent different spatial locations. The open circles represent observations of foraging flocks at those locations, and the continuous lines between the open circles are movements of individuals from one observation to another. The Venn diagrams below the fission–fusion networks represent the relative contributions of social structure (in red) and space (in blue) and are all similarly scaled. In (a), individuals move completely at random, not restricted by group or site. In (b), individuals are perfectly site and group faithful. In (c), flocks are site faithful, but some individuals change flocks. In (d), individuals stay continuously with the same flock, but those flocks are largely unconstrained in space. (e) is similar to (d), but there are some occasions in which individuals change groups [Colour figure can be viewed at wileyonlinelibrary.com]

2015). The offspring assimilate into the population, but dispersal is spatially restricted, meaning that individuals interact more with others born in close proximity and also slightly more with siblings (Grabowska-Zhang et al., 2016). As part of a long-term monitoring project, all nestlings and most breeding birds are ringed for individual identification and breeding performance has been recorded systematically since the early 1960s (e.g., Lack, 1964). Over winter, birds are caught by mist netting at the feeding stations at regular intervals to ring immigrating birds. Up to 90% of the birds in the population are estimated to be ringed and tagged (Aplin et al., 2013).

2.2 | Identifying foraging flocks

Since 2007, we have equipped birds with PIT tags (passive integrated transponder tags) encased in plastic rings, which are used for automated radio frequency identification (RFID). Additional catching with mist nests was undertaken during the winter to mark part of the immigrating birds. Between September 2007 and March 2010, that is, the nonbreeding seasons of 2007–2008, 2008–2009 and 2009–2010, we concurrently placed 20 feeding stations in the woodland equipped with RFID readers (Francis Instruments, Cambridge, UK) to register the identity and time and date of PIT-tagged birds visiting those feeding stations (see supplementary video in Farine, Aplin, Garroway, Mann, & Sheldon, 2014). The feeding stations were rotated over 60 approximately equally spaced locations every 3 days (Figure 2). We used Gaussian mixture models (GMMs) to assign records (detections on the feeder) of individuals into flocks (bursts or "waves" of activity on the feeders). The Gaussian mixture models identify instances of individuals visiting the same feeding station close in time, which are defined as "gathering events" (Psorakis, Roberts, Rezek, & Sheldon, 2012). Those gathering events serve as snapshots of the composition of foraging flocks and have been demonstrated to outperform other flock-detection methods (Psorakis et al., 2015). We used the movements of individuals between gathering events to quantify fission–fusion dynamics across the three winters see Fig. S2 for more details on the movements between different feeding stations.

2.3 | Genotypes and minor allele frequencies

We collected blood samples for genotyping from breeding birds from 2001 onwards. These individuals were genotyped on a SNP chip with 9,193 markers. This SNP chip was developed based on transcriptome sequencing of great tits from Wytham Woods and genomic sequencing of great tits from populations in the Netherlands (Santure, Gratten, Mossman, Sheldon, & Slate, 2011; van Bers et al., 2010, 2012). Of those 9,193 markers, 7,032 passed quality control (using the criteria genotype call rates >95%, minor allele frequency >0.05 and Hardy–Weinberg equilibrium $p > .001$, calculated using PLINK v1.06; Purcell et al., 2007). A total of 4,878 markers were incorporated into a linkage map for our population (van Oers et al., 2014), and we focussed subsequent analysis on this subset of markers. Owing to sex-biased dispersal, with females dispersing longer distances than males (Verhulst, Perrins, & Riddington, 1997), gene flow differs between markers on the autosomes and the sex chromosomes. Therefore, we only used the 4,701 SNPs which were

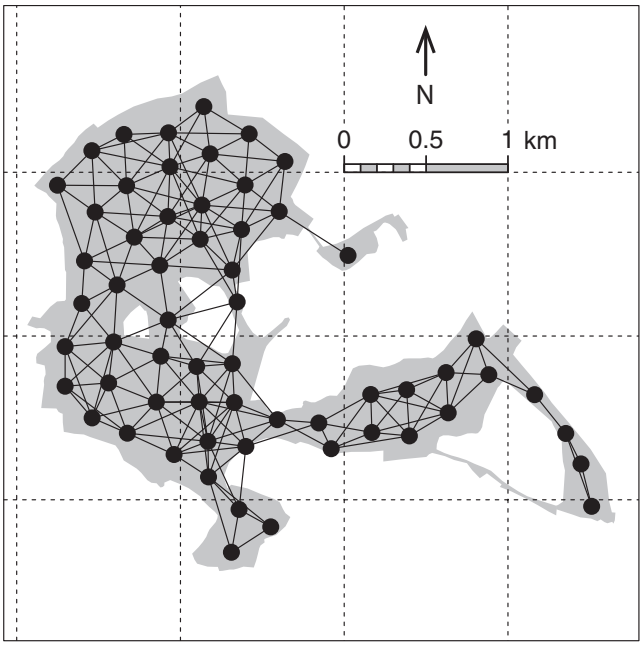


FIGURE 2 The outline (in grey) of Wytham Woods, Oxfordshire, United Kingdom. Black dots represent the 60 locations at which 20 feeding stations rotated about in this study. Lines connecting the dots identify feeding stations which are considered neighbouring sites (i.e., sites that are less than 498.7 m apart; the longest edge of the minimum-spanning tree). Dashed lines are a 1 by 1 km grid

located on the autosomes. The markers were used to genotype 2,652 great tits, primarily focussing on adults with life history and morphological data (van Bers et al., 2012); of these, 962 were recorded at the feeding stations in 2007 (N = 757), 2008 (N = 727) and 2009 (N = 743). A total of 339 genotyped individuals were recorded in two winter seasons and 88 in all three winter seasons.

2.4 | Modelling fission–fusion dynamics

To model fission–fusion dynamics, we used Asymmetric Eigenvector Maps (AEMs; Blanchet, Legendre, & Borcard, 2008). AEMs belong to a family of statistical methods which are based on calculating eigenvectors for adjacency or incidence matrices (Legendre & Legendre, 2012). These matrices describe graphs (i.e., networks) of spatial structure in which nodes represent the spatial locations and edges a measure of distance between them. Adjacency matrices are node-by-node matrices in which x_{ij} is the spatial distance between nodes i and j. Incidence matrices are node-by-edge matrices in which x_{ij} is one when node i is connected by edge j to another node and zero if not. These spatial configuration matrices can, however, be replaced by other adjacency or incidence matrices. In our case, we used matrices that describe the fission–fusion dynamic of birds moving between flocks. The nodes in these networks were the gathering events (i.e., flocks), and the edges were movements of birds between them. AEMs have been developed to model directional spatial processes, for example, the distribution and abundance of a species in riverine systems (Blanchet et al., 2011). The social structure in our population is also directional, because individuals can only move from one gathering event to another where the latter is later in time.

We first constructed fission–fusion networks for each year. Edges connected two gathering events (i.e., the nodes) when at least one bird moved between those gathering events, without having been present at any other gathering event in the meantime. We also only used gathering events with at least two genotyped individuals present. Next, we transformed the fission–fusion networks into incidence matrices for each year. For every node (i.e., gathering event), we gave edges (i.e., movements of birds) a value of 1 when the edge was part of the path connecting the node to the origin and a zero when it did not (Legendre & Legendre, 2012). See Figure 3 for an example fission–fusion network with corresponding incidence matrix. The origin is a fictitious gathering event in which all individuals were present before any other gathering event. The origin and edges connecting directly to the origin were removed before further analyses. More information on the construction of the incidence matrices can be found in Blanchet et al. (2008), Borcard, Gillet, and Legendre (2011) and Legendre and Legendre (2012).

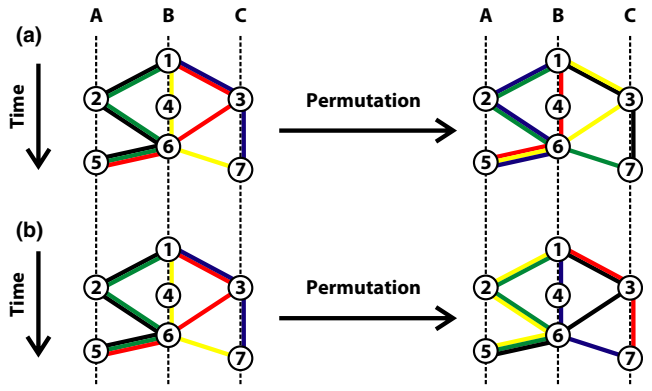
Next, we performed partial singular value decomposition of the matrices to estimate the first 500 eigenvectors with the R-package "IRLBA," which makes use of the implicitly restarted Lanczos bidiagonalization algorithm (Baglama & Reichel, 2012). We used this method to estimate a subset of eigenvectors rather than the singular value decomposition method present in the base package of "R," which calculates all eigenvectors, because our incidence matrices were too large for calculating all eigenvectors. We kept the 500 estimated eigenvectors for further analysis; those axes described broadscale social patterns.

2.5 | Modelling spatial configuration

We modelled space with distance-based Moran's Eigenvector Maps (db-MEMs; Dray et al., 2006), based on a distance matrix which we computed from the spatial coordinates of the feeding stations. From the distance matrix, we built a neighbour network which linked all feeding stations within the minimum distance which was necessary to keep the network fully connected (498.7 m, i.e., the longest edge of the minimum-spanning tree; Figure 2). For all feeding stations which were not neighbouring (more than 498.7 m apart), we replaced the distance in the distance matrix by four times the threshold value (4 × 498.7 = 1,998.4 m) as suggested by Borcard and Legendre (2002). Next, we performed a principal coordinate analysis on the truncated distance matrix, resulting in 20 db-MEMs (Fig. S1). We used those db-MEMs to describe spatial patterns. The db-MEM analyses were performed with the R-package "PCNM" (Legendre, Borcard, Blanchet, & Dray, 2013).

2.6 | Variance partitioning

For all gathering events, we calculated the allele frequencies across all 4,701 mapped autosomal SNPs (all SNPs were biallelic) among all



	a	b	c	d	e	f	g	h	i
1	1	1	1	.	.	.	.	.	.
2	1	.	.	1	.	.	.	.	.
3	.	1	.	.	1	1	.	.	.
4	.	.	1	.	.	.	1	.	.
5	.	.	.	1	1	.	1	1	.
6	.	.	.	.	.	.	.	1	.
7	.	.	.	.	.	1	.	.	1

FIGURE 3 A graphical representation of the randomizations used for testing (a) group fidelity and (b) homophily and heterophily. The numbered circles represent gathering events at three different feeding stations (A, B and C). The coloured lines are the movements of individuals between gathering events (every colour represents a different individual). To test for group fidelity, we randomly shuffled movements of individuals. For example, from gathering event 1, the movement of the red individual is replaced by the black individual and the movement of the blue individual by the yellow individual. From gathering event 3, which now consists of individuals black and yellow, the black individual follows the original path of the blue individual and the yellow individual replaced the movement of the red individual. Individuals follow a path which was physically possible for individuals to follow, but was not necessarily done by any of the individuals (e.g., the red path after the randomization [gathering events 1,4,6 and 5]). To test for homophily and heterophily, we randomly shuffled all identities of individuals. For example, the black individual replaced the red individual and the red individual replaced the blue individual. Individuals only followed paths which were completely followed by others. (c) The incidence matrix of the networks drawn in (a) and (b). Rows are nodes (i.e., gathering events) and columns are edges (i.e., movements). For example, the one in row 1 and column a indicates that node 1 is connected to another node by edge a. This other node is 2, because row 2 also has a 1 in column a [Colour figure can be viewed at wileyonlinelibrary.com]

individuals present at the gathering events. We used variance partitioning to estimate the fractions of variation in allele frequencies between gathering events explained by social (modelled with fission–fusion dynamics) and spatial (based on the distance between logging sites) structure. In variance partitioning, redundancy analysis is used to estimate the fractions of variation in a set of multivariate response variables explained by two or more sets of explanatory variables as well as the fractions in which they overlap (Peres-Neto, Legendre, Dray, & Borcard, 2006). This collinear fraction, which we call here the fraction explained by socio-spatial structure, is not simply a fraction for which we are uncertain whether it resulted from spatial or social structure, but is the product of the inherent role space plays in social interactions. The fraction explained by social structure minus the collinear fraction will be called pure social structure and the fraction explained by spatial structure minus the collinear fraction will be called pure spatial structure. Because foraging flocks also move between feeding stations, we were able to separate the effects of pure social structure from socio-spatial and pure spatial structure. Variance partitioning was performed with the R-package "VEGAN" (Oksanen et al., 2013).

2.7 | Group fidelity

To test whether individuals interacted repeatedly with the same flock members, we tested for group fidelity. We define social behaviour as different from gregarious behaviour in the sense that individuals act socially when they show a preference to interact with particular individuals (either specific individuals or specific phenotypes, compared to a preference to interact with any conspecific in the case of gregariousness). We used randomization tests to test for group fidelity. We produced null reference distributions by shuffling all individuals within each year, at every gathering event in order of time. Individuals would therefore not only follow the path of a random individual through space and time, but can switch paths at every gathering event given that there were other individuals present which took a different path from this particular gathering event (Figure 3a). Genes would therefore follow a path through space and time that could have been the path of an individual, if this individual was not socially or spatially restricted. However, unrealistic movements (e.g., too large distances in too little time or through unfavourable habitats) were excluded, because only movements which were actually made by an individual were included (i.e., no new edges were created in the fission–fusion network, only the identities were swapped). To test for group fidelity, we recalculated the minor allele frequencies for all SNPs in every gathering event. We repeated the variance partitioning for the randomized data sets and compared the relative and absolute variance in minor allele frequencies of the observed data sets to the values from the randomized data sets. We performed 999 randomizations, included the observed data and calculated two-sided *p*-values. All *p*-values reported in the results are *p*-values for all 3 years combined with the Fisher's combined probability test.

2.8 | Genomewide homophily and heterophily

To test whether individuals tended to associate with genetically similar or dissimilar individuals, we performed additional randomization tests. We randomized the data in such a way that it would produce null reference distributions under which individuals did not express homophily or heterophily. At every iteration, we shuffled the identities of the individuals within each year while keeping the movement patterns of individuals the same (Figure 3b). Genes would therefore follow the path of a random individual through space and time and appear at the gathering events this random individual was present.

To test for homophily, we recalculated the minor allele frequencies for all SNPs in every gathering event. We performed variance partitioning on the minor allele frequencies, with the hypothesis that if similar individuals flock together, the proportion of variance in minor allele frequencies attributed to social structure is larger than expected. To test for heterophily, we used the same randomization test, however, with the hypothesis that if genetically dissimilar individuals flock together, the observed gathering events will show less variance in minor allele frequency than the randomized data. We performed 999 randomizations, included the observed data and calculated two-sided *p*-values.

2.9 | Candidate SNPs

Of the selected SNPs for this study, 93 are known to be linked with 45 candidate genes for ecologically relevant traits (van Bers et al., 2012). These SNPs were selected mainly based on the zebra finch (*Taeniopygia guttata*) and chicken (*Gallus gallus*) genomes, but also from association studies in great tit, human, house mouse (*Mus musculus*), blue tit (*Cyanistes caeruleus*) and starling (*Sturnus vulgaris*). We selected three gene categories that might potentially affect social behaviour, namely candidate genes associated with "personality," "circadian timing" and "novelty seeking," which have 10, 6 and 13 SNPs associated with them respectively. We calculated the variation in allele frequency for those particular SNPs explained by pure social structure, socio-spatial structure and pure spatial structure. To test whether those SNPs were significantly more or less affected by social, socio-spatial or spatial structure than a random set of SNPs, we performed a randomization test. We randomly selected the same number of SNPs 999 times, calculated the fractions of variance in allele frequencies explained by social, socio-spatial and spatial structure and used those as null reference distributions.

2.10 | Single SNP homophily and heterophily

To test for the presence of homophily or heterophily for particular SNPs (which are not linked to candidate genes, but may be linked to other, uncharacterized, genes determining population structure), we repeated the variance partitioning for all SNPs separately and repeated the randomization tests for homophily and heterophily for all SNPs across the genome. We only focused on the variance explained by pure social structure. To reduce computation time, we used dynamic stopping rules for the randomization tests. For every SNP, we performed at least 99 randomizations. After 99 randomizations, we either stopped producing iterations when the reference distribution had at least 10 randomized values higher and 10 values lower than the observed value (i.e., sequential sampling; Besag & Clifford, 1991), or after 9,999 iterations, whichever was satisfied first. For all SNPs with 9,999 iterations, we estimated its *p*-value by modelling the tail on the reference distribution with the generalized Pareto distribution as described in Knijnenburg, Wessels, Reinders, and Shmulevich (2009) and using the Anderson–Darling goodness-of-fit test of the R-package "ADGOFTEST" (Gil Bellosta, 2011).

2.11 | Loci under selection

To detect loci under selection, the leading eigenvectors of the SNP genotype matrix can be used, because those eigenvectors can be interpreted as F_{ST} metrics for each SNP (Weir, 1996). High values of F_{ST} can indicate both population stratification and selection; however, by controlling for the background population structure, one can focus on selection (Chen, Lee, Zhu, Benyamin, & Robinson, 2016). We used the EigenGWAS method (Chen et al., 2016) to find loci under selection by first calculating the 10 leading eigenvectors on the SNP matrix for all individuals combined (using the EigenGWAS function in the R-package "SOMMER"; Covarrubias-Pazaran, 2016). Next, we calculated the genomic inflation factor (λ_{GC}) to control for background population structure by taking the ratio between the median observed chi-square value (calculated with the "estlambda" function in the R-package "GENABEL"; Aulchenko, Ripke, Isaacs, & van Duijn, 2007) and the median of the chi-square distribution (i.e., 0.455). We selected loci that were significant after controlling for the genomic inflation factor and Bonferroni correction for the eigenvectors with 4 or more significant SNPs. To test whether those loci were differentially affected by the social, socio-spatial or spatial structure than random we performed the same randomization tests as we did for the candidate SNPs.

3 | RESULTS

In 2007, 2008 and 2009, we detected 757, 727 and 743 marked birds visiting the feeding stations, respectively. Those birds participated in 39 740, 36 493 and 9 531 gathering events, which consisted of 1–37, 1–22 and 1–20 birds with medians of 3, 2 and 3, respectively. Of those individuals, 551 (73%), 485 (67%) and 341 (49%) were genotyped. The genotyped birds participated in 27 968 (70%), 22 319 (61%) and 4 573 (48%) gathering events with two or more participants being genotyped, which consisted of 2–32, 2–18 and 2–15 genotyped birds, respectively, all with medians of 3. On average, there were 0.060 pairs of first-degree relatives (parent–offspring or sibling pairs) present in gathering events with two or more participants.

3.1 | Variance partitioning

Across years, pure social structure explained 52.7%–62.3% (range of variance across years) of the variation in allele frequencies between gathering events. A further 10.3%–18.0% was explained by socio-spatial structure, and 1.2%–1.8% was explained by pure spatial structure (Figure 4). The fractions of variance explained were fairly similar between the 3 years.

3.2 | Group fidelity

When testing for group fidelity, we found that the variance explained by pure social structure and by socio-spatial structure

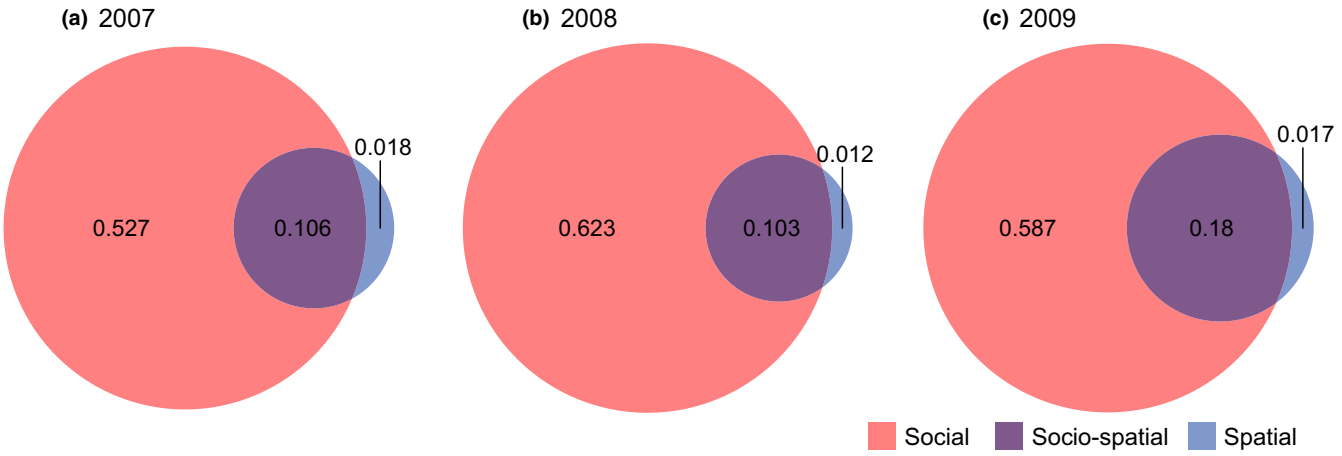


FIGURE 4 Venn diagrams showing the proportion of variation in all 4 701 allele frequencies between gathering events explained by social structure (in red) and space (in blue) for (a) 2007, (b) 2008 and (c) 2009 (39,740, 36,493 and 9,531 gathering events respectively). Circles are scaled within years, but not between years [Colour figure can be viewed at wileyonlinelibrary.com]

were 2.0–4.6 ($p < .001$) and 1.5–3.7 ($p < .001$) times higher than expected by chance. The effect of spatial structure on group fidelity varied between years and was between 1.12 times lower and 1.34 times higher than expected by chance (Figure 5a; Table S3). Group fidelity therefore explained a substantial part of the variation we found in allele frequencies. This was not only the result of individuals sharing the same spatial vicinity, but also of individuals specifically interacting with preferred group members.

3.3 | Genomewide homophily and heterophily

When we performed the randomizations to test for genomewide homophily and heterophily, the variance explained by social structure alone was 1.01–1.02 times lower than the null prediction ($p < .001$). Socio-spatial and spatial structure explained 1.05–1.15 ($p < .001$) and 1.08–1.18 ($p < .001$) times more variation than expected (Figure 5b; Table S4). Social structure explained 1%–2% less variation than expected by chance; indicating that allele diversity was slightly higher than expected as a result of social processes. Hence, individuals tended to associate with genetically dissimilar conspecifics given their local pool of potential associates. Spatial and socio-spatial structure explained 5%–18% more variation than expected by chance, indicating that genotypes were not randomly distributed in space, but rather clustered.

3.4 | Candidate SNPs

Variation in SNPs associated with personality was not explained by pure social structure ($p = .130$) or pure spatial structure ($p = .075$), but marginally by socio-spatial structure ($p = .049$; Figure 5c; Table S5). Variation in SNPs associated with circadian timing was not explained by pure social structure ($p = .161$), socio-spatial structure ($p = .137$) or pure spatial structure ($p = .187$; Figure 5d; Table S6). Variation in SNPs associated with novelty seeking was not explained by pure spatial structure ($p = .204$), but marginally and inconsistently by pure social structure ($p = .010$) and socio-spatial structure ($p = .018$; Figure 5e; Table S7). Particularly, the inconsistent patterns between years and marginal p-values, despite large sample sizes, weaken any of the support for effects of the social and spatial structure on variance in SNPs associated with candidate genes we found.

3.5 | Single SNP homophily and heterophily

None of the single SNPs explained significantly more or less variance than expected in both homophily (Figure 6a) and heterophily (Figure 6b) after Bonferroni correction and correction for the false discovery rate (Benjamini & Hochberg, 1995).

3.6 | Loci under selection

After controlling for the genomic inflation factor and Bonferroni correction, the principal eigenvector did not show any loci under selection but for the 2nd to the 10th eigenvectors, we found 16, 7, 5, 5, 4, 1, 2, 2, and 2 loci, respectively (Fig. S10). Those loci were not concentrated in particular parts of the genome, but spread seemingly random. We tested whether the loci found for 2nd to the 6th eigenvectors were nonrandomly distributed in the social and spatial structure, but this was not the case (Fig. S11).

4 | DISCUSSION

In this study, we explored the relative importance of social interactions and space for structuring allele frequencies in foraging flocks. We found that individuals tend to nonrandomly associate with the same flock mates during winter and those flock mates tended to be genetically more diverse than expected by chance. We showed that

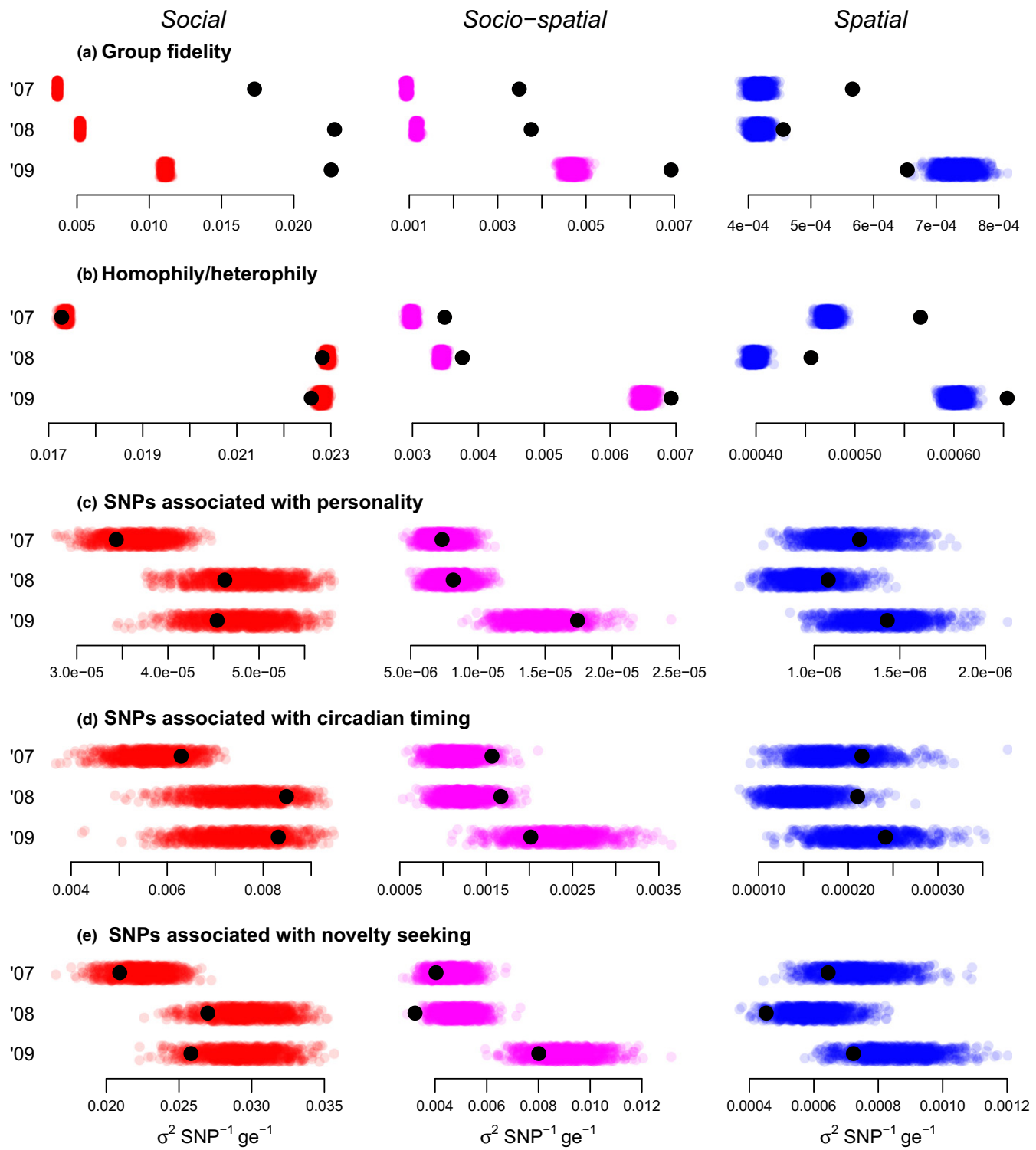


FIGURE 5 Results of the randomization test for (a) group fidelity (b) genomewide homophily and heterophily and the SNPs associated with (c) personality, (d) circadian timing and (e) novelty seeking expressed as the average amount of variance explained by one SNP at one gathering event. Black dots are the observed values, while coloured dots are the values of the null distributions. To ease comparison between all tests and years, the amount of variance in allele frequencies explained by each component was divided by the number of SNPs (to account for the variable number of SNPs involved in the different randomization tests) as well as the number of gathering events (ge) (to account for the difference in the number of gathering events between years) [Colour figure can be viewed at wileyonlinelibrary.com]

this was not exclusively due to individuals sharing spatial vicinities, but also due to some space-independent social preferences which promoted both group fidelity and genomewide heterophily. By contrast, we found that genomewide homophily primarily arose from limited spatial movements resulting in spatial variation in allele frequencies in the population. None of the alleles associated with

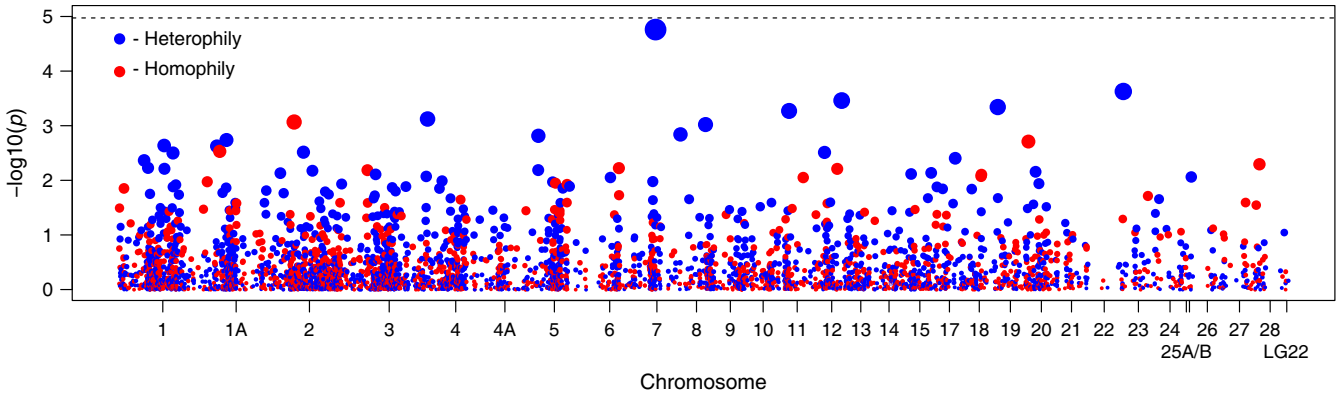


FIGURE 6 Manhattan plots of genome–social environment association studies for homophily and heterophily. SNPs explaining less variance than expected reveal heterophily and are blue. SNPs explaining more variance than expected reveal homophily and are red. Dashed line is the Bonferroni corrected significance level. Dot radius is linear to $-\log^{10}(p)$ [Colour figure can be viewed at wileyonlinelibrary.com]

candidate genes for personality, circadian timing and novelty seeking nor any other SNP markers were substantially affected by social structure.

4.1 | Group fidelity

The great tits in our study population showed significant group fidelity. This means that individuals not only congregate passively, for example to dilute predation risk (Krause & Ruxton, 2002), confuse predators (Landeau & Terborgh, 1986), benefit from selfish herd effects (Hamilton, 1971) or improve the detectability of predators (Caraco, 1979) and food (Krebs, MacRoberts, & Cullen, 1972), but also showed a preference for repeated interactions with particular individuals. Although this was partly the result of spatial limitations on the movements of birds, for instance due to territoriality or site preference, as shown by the significant effect of the socio-spatial component of the model, there was also a substantial pure social component. Intraspecific mutualism is arguably the simplest explanation for this (Clutton-Brock, 2002). Individuals could for instance alternate between foraging and vigilance behaviour, which promotes the evolution of group fidelity. Great tits do produce more alarm calls in the presence of familiar individuals than in the presence of unfamiliar individuals, which is in line with intraspecific mutualism (Krams, Krama, & Igaune, 2006), and are also more likely to join known territorial neighbours when mobbing predators (Grabowska-Zhang, Sheldon, & Hinde, 2012). Alternatively, intraspecific mutualism could be the result of spatial hierarchy dominance. Individuals tend to be dominant in the area of their former breeding territories (Ekman, 1989). Further, a previous study on wintering social structure in this population has demonstrated that individuals' fitness is related to the relative time that they dispersed into the population relative to their social associates (Farine & Sheldon, 2015), suggesting that local population structure has evolutionary implications.

We can exclude kin selection as a cause of group fidelity, because kin selection would have resulted in pure social effects for homophily as well, which we did not find. Interestingly, another study in the same population found that the composition of gathering events was largely unstable within days and only marginally differed from random after more than ten minutes (Farine et al., 2015). The combination of this and our study suggests that, although there was a high turnover rate of individuals in flocks, individuals did regularly encounter particular individuals over winter. This has also been confirmed by state-dependent modelling of re-encounter rates in Aplin et al. (2013). Our study shows that this was not exclusively driven by the spatial configuration of individuals.

4.2 | Genomewide homophily and heterophily

Although the effect was rather small, genomewide heterophily was present as the result of pure social processes. This suggests that individuals tend to interact more with genetically dissimilar individuals. This genetic dissimilarity is probably present at many loci, albeit with weak effects on the individual loci, because we did not find any signals in the analyses for single SNPs. This finding seems at odds with conclusions of previous studies: for instance, great tits do not show preference to mate or associate with genetically distant individuals (Szulkin, Zelazowski, Nicholson, & Sheldon, 2009), and they tend to interact more with their siblings in their first nonbreeding season (Grabowska-Zhang et al., 2016). However, both those processes are not purely social and are more likely to be represented by the genomewide homophily we found for socio-spatial processes. Perhaps, parents and offspring—though they live in close proximity and therefore have a higher probability than random to encounter—display active avoidance. However, the underlying social processes resulting in genomewide heterophily remain unclear. While genomewide homophily was not the result of pure social processes, but rather socio-spatial and pure spatial processes, it does nonetheless affect the genetic structure of the population. This is in line with a previous study in our study population which showed that limited dispersal and natural selection due to environmental conditions resulted in fine scale spatial structure in genotypes (Garroway et al., 2013). The fact that we found genomewide homophily resulted from spatial and social–spatial processes suggests that it was not the result of individuals actively being homophilous (at least at the

genomewide level), but rather caused by exogenous processes such as limited dispersal.

4.3 | Candidate genes and single SNP homophily and heterophily

We did not find convincing evidence for social and spatial processes affecting the allele frequencies of candidate genes or single SNPs. However, we cannot conclude that social structure did not affect the distributions of particular social genotypes, because of the following reasons. First, even though we analysed a limited number of SNPs, the probability of detecting effects is low given our sample size. Thousands of individuals are needed to have sufficient power to reliably detect or refute correlations between phenotypes and SNPs (Wray et al., 2013). Second, we expect social traits to be complex, so will be affected by interactions between many genetic and environmental factors (Robinson, Grozinger, & Whitfield, 2005). Third, the Great tit genome turned out to have low linkage disequilibrium (Laine et al., 2016); therefore, the 4,701 SNP markers might not sufficiently cover the whole genome to pick up signals of particular genes. A denser SNP chip would improve the coverage over the genome. Finally, the spatial distribution of birds could arise from social processes occurring at a broader scale, such as when individuals make decisions about where to settle during dispersal.

4.4 | Evolutionary perspective

As shown in this study, allele frequencies in foraging flocks are affected by nonrandom social and spatial processes. Those processes have been recognized to drive spatial autocorrelation of pheno- and genotypes (Fortin & Dale, 2005; Sokal & Oden, 1978), but this is the first study to separate social from spatial processes. If the nonrandom distribution of genotypes between foraging flocks also translates into nonrandom mating, it will potentially affect the evolutionary dynamics of the population. Whether flock composition affects pair formation remains to be tested. It has been shown that mate choice is at least restricted in space (Szulkin et al., 2009) and is likely to be affect by social structure as well. As social interactions can affect the strength of selection (Wolf et al., 1999), we also investigated whether social and spatial structure affected the distribution of loci under selection. We did not find evidence for this, but this might have been caused by the low linkage disequilibrium between our SNPs.

4.5 | Temporal and spatial effects

Dealing with and describing the effects of temporal dynamics and spatial heterogeneity on social networks are a current challenge in the study of animal social networks (Blonder, Wey, Dornhaus, James, & Sih, 2012; Farine & Whitehead, 2015; Pinter-Wollman et al., 2014). Both aspects are important for investigating evolutionary consequences of social interactions, because one needs to either look at changes over time or compare networks (or parts of a network) in different environments. Suggested methods to deal with temporal dynamics are either using discrete methods in which different networks for different time periods are produced (time-aggregated networks) or continuous methods in which the temporal aspects of the data are maintained (time-ordered networks; Blonder et al., 2012; Pinter-Wollman et al., 2014), as in our analyses. The analytical tools for continuous networks are less well developed than the discrete networks (Blonder et al., 2012; Pinter-Wollman et al., 2014). Taking space into account is limited to using spatially restricted randomization techniques and calculating network properties for the observed and randomized networks (Pinter-Wollman et al., 2014). The method presented here can be used for continuous analysis of temporal network data, but its most important virtue lies in the combination of temporal and spatial effects. The current upscaling of social network analysis (Krause et al., 2014) will result in the increase of the relative importance of dealing with spatial effects, for which we presented here an attractive method. This method has previously been used for analysing spatial data together with univariate covariates (e.g., Lasky et al., 2012), but here we extend the use to social network data, which is multivariate. One must, however, note that the method we used here focuses on network properties and not so much on particular individuals or dyads, which would be an interesting area for future research.

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DATA ACCESSIBILITY

Input files and Eigenvector maps (db_MEMs and AEMs) are available from Dryad (https://doi.org/10.5061/dryad.7n731).

AUTHOR CONTRIBUTIONS

R.R., C.J.G., J.S. and B.C.S. designed this study. The phenotypic data and blood sampling were organized by B.C.S., with contributions to the data collection by R.R., C.J.G. and D.R.F. R.R. performed most data analyses, with involvement of C.J.G. in the eigenvector analyses. The SNP genotyping and quality control were organized and

performed by J.S., A.W.S. and I.D.C. Gathering events were quantified by D.R.F. R.R. drafted the manuscript. All authors provided comments on the manuscript, and read and approved the final manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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