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

Damien R. Farine^{a,b,c}, Ben C. Sheldon^{*a}

^a Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom.

^b Department of Collective Behaviour, Max Planck Institute for Ornithology, Universitätsstrasse 10, 78457 Konstanz, Germany.

^c Department of Biology, University of Konstanz, Universitätsstrasse 10, 78457 Konstanz, Germany.

* Corresponding author:
damien.farine@orn.mpg.de

22 ABSTRACT

23

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

36

37 INTRODUCTION

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

50

51 Population social structure (the patterns of connections that emerges from
52 interactions among individuals, often represented using social networks) is

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

76

77 A major challenge in identifying extrinsic factors that drive population social
78 structure is the need to have information about the movement of individuals in
79 space, the patterns of social connections among the majority of individuals in a
80 population, and information about the habitat in which they live. Recent
81 technological advances have eased the logistical constraints of sampling many
82 individuals moving across large areas ^{25, 26, 27}. In particular, passive integrated
83 transponder (PIT) tags are cheap electromagnetic tags that can be fitted to many

84 individuals at once ²⁸, thus overcoming the challenges associated with studying
85 entire animal communities. Because PIT tags do not rely on battery power to emit a
86 signal, but instead are detected by affecting the magnetic field in radio frequency
87 identification (RFID) antennas, they provide the unprecedented ability to track
88 individuals across years and life stages. Further, advances in the analytical tools,
89 such as social network analysis ²⁹ and community detection algorithms ³⁰, are
90 facilitating greater insight into patterns of social structure. However, although
91 technological advances have underpinned a boom in the study of animals' social
92 networks ³¹, much less effort has focused on identifying key mechanisms that form
93 communities and shape social structure at the scale of populations.

94

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

107

108 RESULTS

109

110 *Quantifying individual movements*

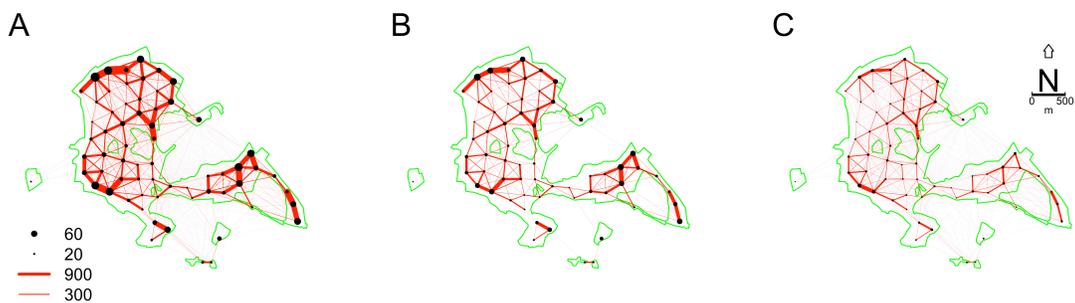
111 To determine whether individuals moved freely through Wytham Woods, or if
112 movement patterns are shaped by features of the habitat, we first quantified the
113 daily movement rates between different feeding stations. Our population consisted
114 of a total of 5163 unique PIT-tagged individuals (see Methods), of which 3051 were

115 great tits (*Parus major*), 3960 were blue tits (*Cyanistes caeruleus*), 403 were marsh
116 tits (*Poecile palustris*), 232 were coal tits (*Periparus ater*), and 110 were nuthatches
117 (*Sitta europaea*). We detected the presence and group membership of birds using a
118 grid of 65 bird feeders filled with unhusked sunflower seed, and studied the
119 population over 4 winters.

120

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

135



136

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

140 same day. The size of the points represents the average number of individuals
141 observed at each feeding station. The green outline represents the outline of
142 Wytham Woods and four small external woodplots.
143
144 *Testing the predictors of movement propensity*
145 Habitat structure is likely to shape movement patterns by birds during the winter in
146 several ways. First, for arboreal species, individuals are more likely to move through
147 the forest than over open ground, and thus the distance between foraging patches
148 needs to be calculated through the forest and thus the presence of open areas is
149 likely to have some impact on the spatial patterns of movements. Second, within the
150 forest, the understory structure of the habitat could create preferred areas of
151 movement by providing shelter from predators. Finally, additional factors such as
152 local traditions could maintain consistent movement pathways, when generations
153 mix and where social learning occurs. We compared the patterns of movement
154 observed across years, and relate these to spatial distance and habitat features. To
155 avoid the potential confounding effect of population density in our statistical
156 analyses, we re-defined edges in the movement network as the probability that an
157 individual detected at either site moves between them on a given day (see
158 methods). Edge weights ranged from 0 representing no movement between
159 adjacent sites to 0.83 representing that each individual detected had an 83% chance
160 of moving between the two sites on a given day (Figure S4). For each pair of sites,
161 we also estimated the density of understorey vegetation between them using data
162 collected at 100m intervals throughout Wytham Woods³² (see methods). Because
163 Wytham Woods is unevenly shaped, we also calculated distance between feeding
164 sites as *forest distance*, which is the shortest line without leaving boundaries of the
165 forest. To enable direct comparison between each predictor variable, we scaled each
166 predictor to zero mean and unit variance.
167
168 Weighted multiple regression quadratic assignment procedure (MRQAP)³³ revealed
169 that the movements by birds between feeding stations were significantly more
170 similar from year to year than expected by chance, even when accounting for forest

171 distance and habitat structure (see Table 1, Figure 2). In all years, birds were
172 significantly more likely to move between ‘close’ feeding stations than distant ones,
173 and were also more likely to move between feeders that were separated by higher
174 understory habitat density. However, the propensity to move between feeders
175 observed in previous years was consistently the strongest predictor of future
176 movements. The coefficient values for movements predicted by the previous year
177 are typically an order of magnitude larger than those of other predictor variables,
178 suggesting that some undetected factors are driving patterns of movements by birds
179 across this woodland. Because for many feeding stations the distance and forest
180 distance are very similar (see Figure 2), we also tested whether birds were less
181 likely to move between feeding sites that were separated non-forest by calculating
182 the difference between forest distance and Euclidian distance. We found that birds
183 moved less between feeders with a larger difference in distance (i.e. the path
184 through the forest was much longer than the straight-line path), suggesting that
185 birds are avoiding crossing open fields (Table 2).

186

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

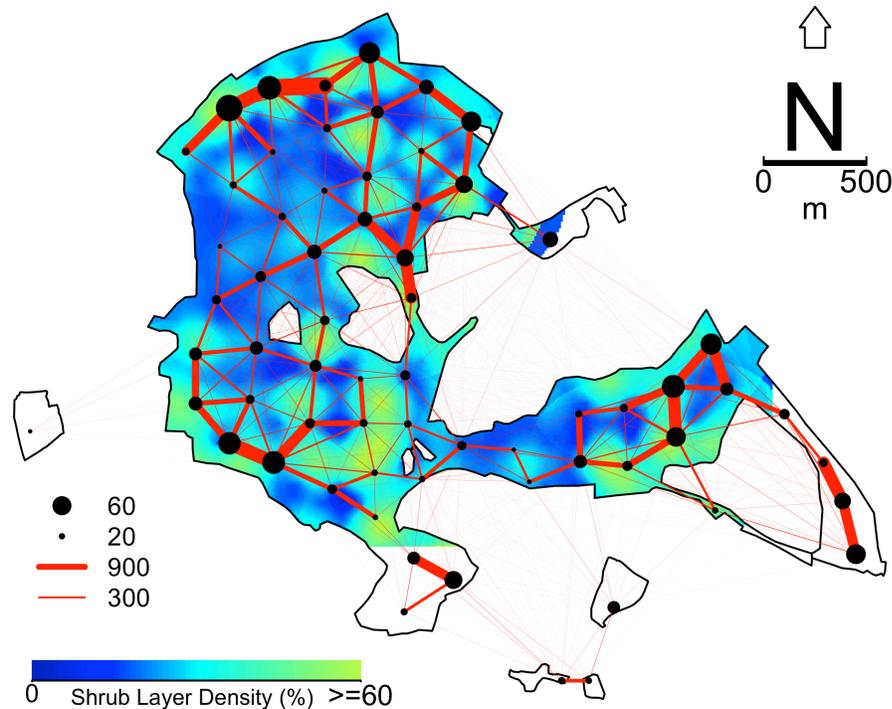
194

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

195

196

197



198

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

202

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

209

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

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213

214 *Quantifying community structure*

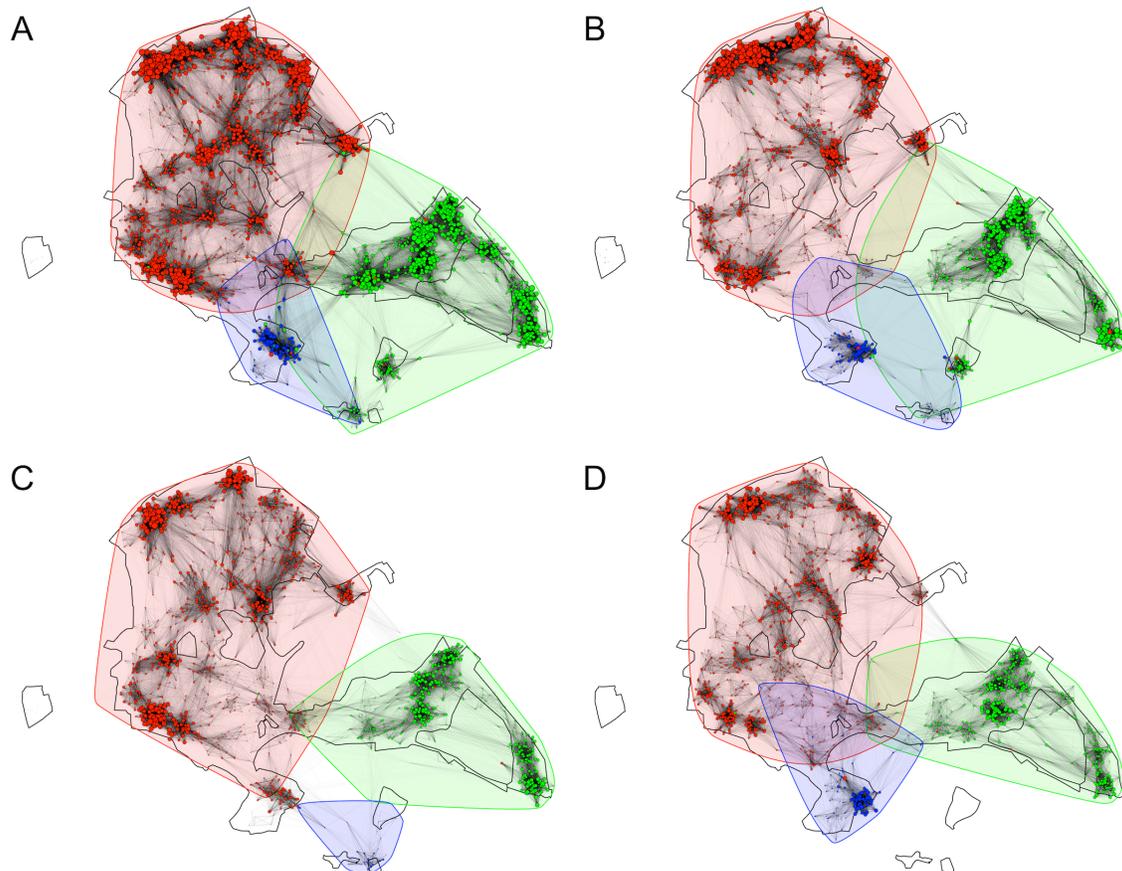
215 Population-level social structure can have significant implications for population
216 processes. For example, high levels of clustering can reduce the spread of disease
217 within populations³⁴. Thus far, we have shown that both social and habitat features
218 are likely to contribute to where animals move. Here we investigate how these
219 patterns contribute to the emergent structure of the population. From the
220 detections of individuals at feeding stations, we inferred flock membership and
221 social network structure (see methods) using well established approaches
222 developed for this population^{7, 12, 13, 14, 29, 35, 36, 37, 38}. We then inferred communities in
223 the social networks using the edge betweenness community detection algorithm in
224 the R package *igraph*³⁹, and explored the between-year stability of individual co-
225 membership to the same community (see Methods).

226

227 To investigate population social structure at different scales, we cut the social
228 network into k communities, where ranged from 2 to 65 (the latter representing the
229 total number of locations with a feeding station). If communities are structured
230 exclusively by extrinsic factors, we expected a drop in the stability of co-membership
231 by individuals as we created more fine-scale communities. For example, if a
232 population is spread across three isolated patches of woodland, then we expect that
233 birds will always occur within the same three communities (one for each woodland)
234 each year. By contrast, if communities are structured socially, then we expected
235 smaller communities (local cliques) to be more stable. For example, for a territorial
236 pair-living species living in a lattice-like uniform environment, an algorithm will be
237 able to isolate each pair when identifying $k=N/2$ communities, whereas the
238 communities detected for smaller k values will be essentially random. When applied
239 to our social network data, we uncovered two scales that maximized the propensity
240 for pairs of individuals that were observed in the same community to be re-
241 observed in the same community in the following year. When social networks were
242 partitioned into 2 or 3 communities (Figure 3), individuals observed in the same
243 community in one year and observed again in the following year re-occurred in the
244 same community approximately 90% of the time. These communities largely

245 represent the geometry of Wytham Woods, with two core habitats (north-west and
246 the east), and a small wood to the south that is only attached by a narrow neck of
247 vegetation representing a third community.

248



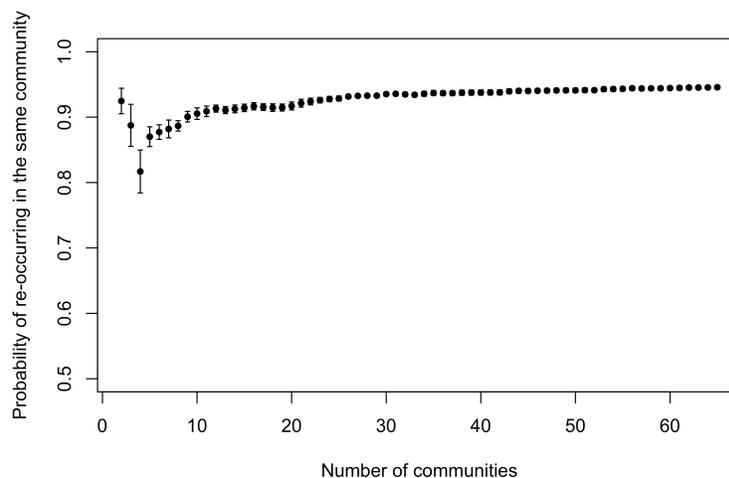
249

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

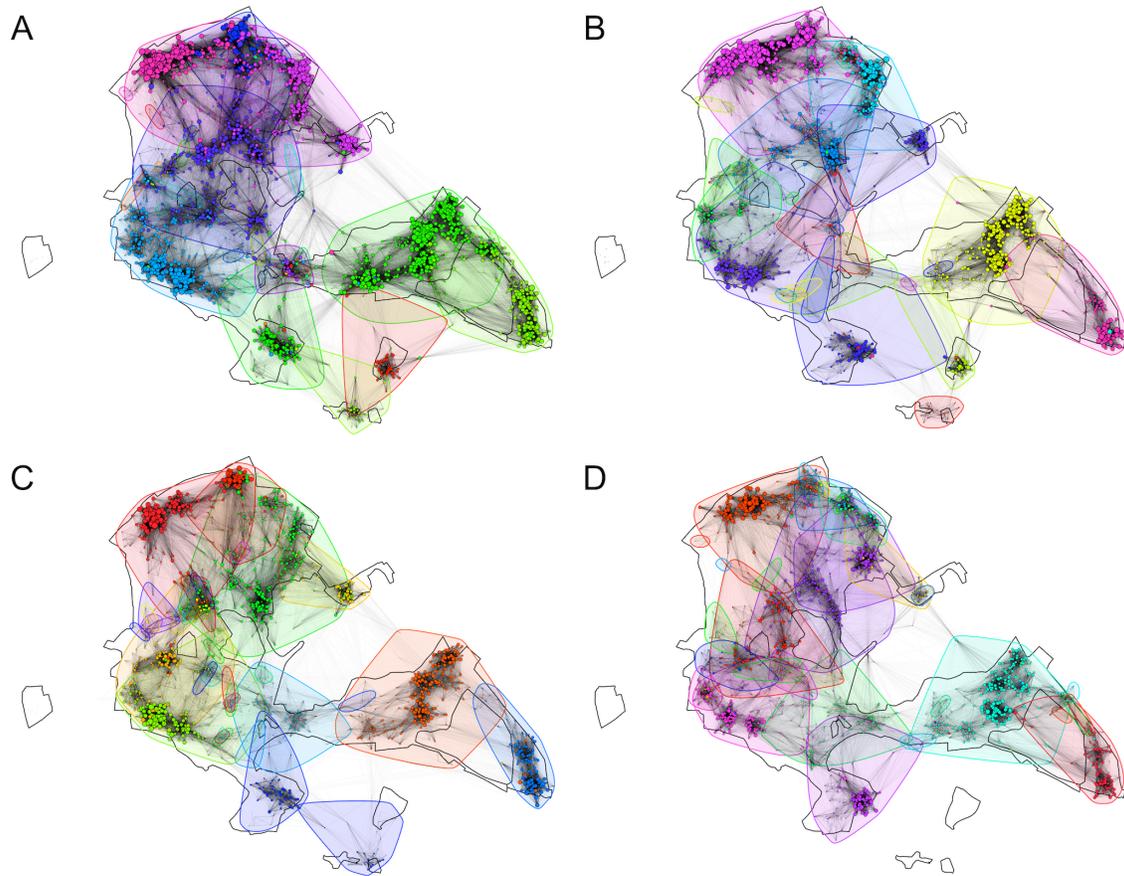
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255 Specifying the algorithm to detect 4 communities significantly decreased the
256 probability of individuals being re-observed in the same community (no overlap in
257 the 95% confidence intervals in Figure 4), suggesting that there is no stable 4th
258 community. Partitioning the network further by specifying the algorithm to detect
259 more than 4 communities then increased probability that two individuals occurring

260 in the same community in one year and both observed in the following year again
261 re-occurred in the same community. Thus, the patterns of social organization at
262 both the population scale (2-3 communities) and at a local scale (>50 communities)
263 were extremely stable year-to-year. This result suggest that multiple levels of
264 community structure exist in this population. Partitioning the network into larger
265 number of communities did not result in one community per feeding station, instead
266 several large communities were maintained and many small ones were created
267 (Figure 5). Finally, we found no evidence that the composition of species in
268 communities changed based on how many communities were created (Figure S5).
269 Thus, the partitioning of the network into more (smaller) communities did not
270 segregate individuals into species-specific clusters, and so stable community
271 structure at a local scale was not explained by simple species-level processes.
272



273
274 **Figure 4:** The social network for each year of the study partitioned into 3
275 communities. Each point represents one individual, and its colour represents the
276 community it is assigned into. The size of each point represents its weighted degree
277 (larger points have more and/or stronger connections to other individuals). Points
278 are drawn at the average location that the individual was observed, with a small
279 amount of jittering added to reduce the overlap between individuals observed in the
280 same location.
281



282

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

290

291 *Linking movement patterns to community structure*

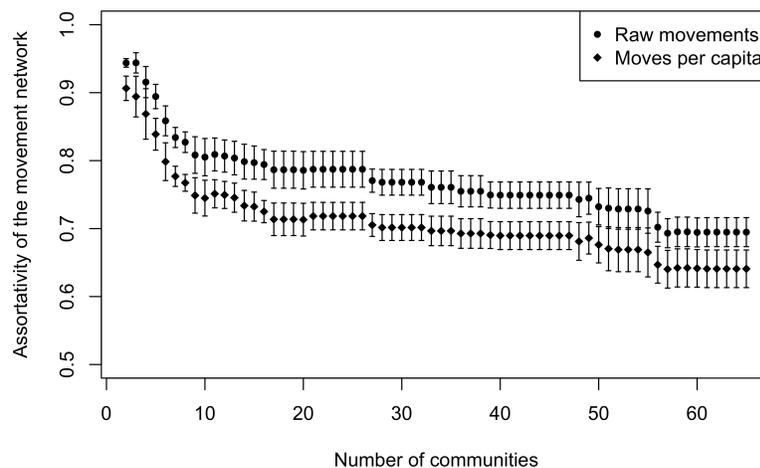
292 What drives the consistent patterns of community structure in the social network of
293 this population? Understanding how communities emerge in the social networks is
294 important for determining which behaviours (i.e. mechanisms) group-living could
295 act on as agents of selection. Uncovering the processes that drive community
296 structure becomes notably more complex when studying species where individuals

297 form fission-fusion groups, as no single individual is likely to be responsible for the
298 global patterns of connection. Instead social structure arises from the interactions
299 among all individuals taken together. One plausible mechanism that is likely to
300 underpin some aspects of community structure is the patterns of movements.
301 Individuals living at two locations with frequent movements of individuals between
302 them will be more likely to be connected in the social network, and therefore more
303 likely to be in the same community and share similar social environments.

304

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

316



317

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

324

325

326 DISCUSSION

327

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

341

342 The link between extrinsic habitat factors and community structure in animal
343 populations has been investigated before. For example, community and sub-
344 community structure in Galapagos sealions *Zalophus worlabaeki* are largely driven
345 by the structure of male territories⁴¹. However, territorial behaviours are unlikely
346 to play a major role in structuring the winter population of birds in Wytham Woods
347 because the majority of individuals were great tits and blue tits, which are both non-
348 territorial during the winter. In non-territorial wintering golden-crowned sparrows

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

357
358 A potentially important feature that we extracted in our study was differential
359 movement patterns between classes of individuals. We found that juveniles typically
360 made more long-distance movements than adults. This pattern, which is likely to
361 arise from juvenile dispersal behaviour, has a number of implications for social
362 processes. To overcome strong seasonal changes in the environment, juvenile tits
363 rely on learning from adults ⁴³. As they move through the landscape, juveniles copy
364 the adults in their local environment, and a recent study demonstrated that tits
365 exhibit a strong conformist (copy the local majority) social learning strategy ¹².
366 However, stability in local community structure means that local traditions
367 (behaviours that differ among different social groups in a population) can easily
368 become entrenched ¹². Juveniles could therefore play an important role in
369 facilitating transfer of new information into social groups. At the same time,
370 juveniles are likely to come into contact with a greater number of individuals, and
371 thus could play an important role in spreading diseases or pathogens across
372 communities (as suggested in humans ⁴⁴).

373
374 By investigating the stability of community structure at different scales, we found
375 evidence that tits in Wytham Woods live in a multi-level community structure.
376 Multi-level community structure occurs when animals form small groups, or
377 clusters, of individuals with whom they associate most strongly, and a larger groups
378 composed of individuals with whom they associate loosely or indirectly. There is
379 increasing interest in multi-level community structure as it can have major

380 implications for how social processes occur^{45, 46, 47, 48}. Multiple factors can shape the
381 movement (or not) of individuals among social units. These factors can be broadly
382 split into two categories: social factors (such as relatedness^{49, 50, 51}, cultural
383 similarity⁵², or species identity⁴⁵) and habitat factors (features of the environment
384 that modulate how individuals move, and thus whom they encounter). Although
385 recent studies have begun teasing apart social versus habitat factors that determine
386 the patterns of contact among individuals with different phenotypic characteristics
387³⁷, little is known what drives the emergence of global population-level structure.
388 Cantor et al⁵² recently used simulations to suggest that multi-level communities can
389 emerge when individual segregate into clans formed around similar cultural
390 behaviours. In our study, we found evidence that both habitat and social factors
391 contribute to multi-level community structure. The general geometry of Wytham
392 Woods introduced a repeatable set of large-scale communities (Figure 3).
393 Environmental features (notably habitat density) that promote or hinder movement
394 by individuals (Figure 2) can shape whom individuals encounter. Together, these
395 features are likely to play a major role in how the population is broadly structured.
396 In addition, by studying birds that form mixed-species communities, our study
397 highlights that complex interaction patterns, such as associations among kin or
398 cooperation, are not pre-requisites for multi-level structure to emerge. Instead,
399 social mechanisms, such as social preference³⁷ and phenotypic drivers³⁵, determine
400 who individuals affiliate with, while the woodland geometry and habitat density
401 determine who individuals can come into contact with.

402

403 The presence of multi-level community structure can have implications for
404 evolutionary dynamics of populations. First, restricted movement can reduce gene
405 flow and lead to divergence in the evolutionary trajectories of sub-parts of each
406 population. Garant et al.²⁴ demonstrated that differential dispersal reinforces local
407 variation in selection for nestling body mass. In their study, they found that trends
408 in genotypic variance for body mass in nestlings were very different in the eastern
409 sectors of Wytham Woods and the northern sectors. These two areas represent the
410 two largest population-level communities we found in our study. Second,

411 individuals in the same community will have more similar social environments than
412 individuals occurring in different communities. Thus, any social effects arising via
413 the social environment, such as indirect genetic effects⁵³, could accelerate patterns
414 of divergence within single populations. Finally, the social environment itself can act
415 as an agent of selection^{18,54}, and therefore processes that shape social structure are
416 likely to impact the overall strength and direction of selection experienced by
417 populations.

418

419 Together the findings from our study highlight how stable social structure can be
420 maintained in populations as a consequence of both social affiliations and features
421 of the habitat that individuals live in. The combination of strong clustering together
422 with some random movements in networks can facilitate the spread of disease or
423 information through the network³⁴. This prediction is supported by evidence from
424 the rapid spread of a recent disease⁵⁵ and of novel traditions¹² in this population.
425 At the same time, consistent population social structure can lead to phenotypic and
426 genotypic divergence²⁴, with potential implications for how animals can adapt to
427 changing environmental conditions. Integrating information about animal social
428 structure with data on both pulse and long-term selective events could yield novel
429 insights into the evolution of social behaviour. However, as our study highlights,
430 determining the capacity for populations to respond to selective pressures will
431 require an understanding of a range of different drivers shaping their social
432 structure.

433

434

435 DATA COLLECTION METHODS

436

437 *Study location, study species, and population dynamics*

438 The study was undertaken in Wytham Woods, Oxfordshire, UK (51° 46' N, 01° 20'
439 W), a 385ha area of broadleaf deciduous woodland surrounded by open farmland.
440 Pairs of birds hold territories during the breeding season (April – June), but form
441 loose fission-fusion groups during the winter, flocking with unrelated individuals

442 that forage for ephemeral food sources. Flocks often contain multiple species³⁸, and
443 our study also includes data on the five most common flocking species: blue tits,
444 marsh tits, coal tits, and nuthatches. Tits are generally short-lived—great tits have a
445 mean life span of 1.9 years. This short generation time results in high annual
446 population turn-over and inter-annual variation in population sizes. Very good
447 breeding conditions lead to large population sizes, whereas poor breeding
448 conditions result in fewer juveniles and a much reduced population size.

449

450 *Understorey habitat density*

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

461

462 *PIT-tagging birds*

463 All birds in the study were caught in either a nest box (as parents and as chicks) or a
464 mist-net (approximately half the population are birds that immigrate). Each bird
465 was fitted with uniquely numbered British Trust for Ornithology metal leg ring, and
466 a uniquely-coded passive integrated transponder (PIT) tag (IB Technologies, UK)
467 that was fully enclosed in a molded plastic ring fitted to the other leg. Each PIT tag
468 contains a unique code that can be recorded by antennae (see next section), and
469 these were then matched to the bird's ring number. We ceased fitting PIT tags to
470 coal tits from October 2012 as the tags were aggravating pox lesions on birds legs
471 during a naturally-occurring epidemic. For each bird that was caught and tagged, we
472 recorded the age and sex (where possible following⁵⁶).

473

474 *Data collection*

475 We placed 65 automated feeding stations in a evenly-spaced grid covering the
476 entirety of Wytham Woods and small isolated patches of woodland nearby.
477 Commercial bird feeders (Jacoby Jayne, UK) were fitted with a radio frequency
478 identification (RFID) antenna on each of the lower two access holes and other access
479 holes were blocked. The antennae recorded the unique PIT tag code, time and date
480 for each visit by a marked bird. For the duration of the study, the feeding stations
481 were scheduled to open and begin logging at 6am on Saturday mornings, and shut
482 after dusk on Sunday evening. Feeders were in place December to February in the
483 winter 2011-12 (13 weeks), from December to early March of winters 2012-13 and
484 2013-14 (14 weeks each), and for January and February in the winter of 2014-15 (8
485 weeks). This data collection resulted in 49 unique weekends and 98 complete data
486 logging days over the 4 winters. In latter years, 6 feeders covering two external sites
487 were replaced for a separate experiment, and thus the data were not included in
488 these analyses.

489

490 *Inferring flocks and flock membership*

491 The data logged from the PIT tag detections produces bursts of detections in the
492 temporal data stream. These vary in length depending on the size of the flocks
493 present which increases during the course of the day,⁵⁷. We used a recently-
494 developed statistical method called Gaussian Mixture Models⁵⁸ to extract the start
495 and end times for each distinct flock. This machine-learning method statistically fits
496 Gaussian curves of varying sizes to each burst in the data and allocates each record
497 to the distribution, or 'gathering event', into which it falls. Gaussian Mixture Models
498 provide a more robust estimation of the social network structure than alternative
499 methods⁵⁹.

500

501 *Constructing movement networks*

502 From the logging data, we recorded every case of movement by a bird from one
503 feeding station to another within the same day (a total of 83071 movements over 4

504 winters), and used these to create movement networks that quantify the
505 connectedness between each pair of feeding stations in the study. We used daily
506 sequential detections to maximize our chances of correctly inferring direct
507 movement pathway (e.g. moving between locations A and D via locations B and C)
508 and minimizing our chances of incorrectly inferring movement pathways (e.g.
509 estimating only a direct movement between A and D). Because the number of
510 movements are inherently linked to number of individuals present at a specific pair
511 of feeders, we also created a network describing the rate of movement between
512 feeders, where the rate was defined as the probability that an individual at one focal
513 feeder would be observed moving to the other focal feeder within a day.

514

515 *Constructing social networks*

516 We defined edges in the social network using the simple ratio index: $E_{AB} =$
517 $\frac{x}{x+y_{AB}+y_A+y_B}$, where E_{AB} is the edge weight between individuals A and B , x is the
518 number of times they were detected in the same flock, y_{AB} is the number of
519 occasions they were both detected at the same time but not in the same flock, y_A is
520 the number of detections of A where B was not seen, and y_B is the number of
521 detections of B where A was not seen. The networks for each year were constructed
522 using *R* package *asnipe* ⁶⁰.

523

524 *Linking movements to community structure*

525 For each year's social network, we first split the network by specifying $k = 2$ to 65
526 communities (see main text). For each value of k , we allocated individuals to their
527 most common feeder, and for each of the feeding stations, select the community that
528 the majority of individuals present were members of. This enabled us to create a
529 community label for each feeding station (and for each value of k), and link these to
530 the network formed by the movement of individuals (Figure 1). To test whether the
531 movement network shaped the community structure in the network for a given
532 value of k , we quantified the assortativity coefficient of the network using
533 communities as discrete trait values ^{61,62}. Assortativity is the measure of how well

534 connected alike nodes are compared to how well connected dislike nodes are,
535 ranging from 1 (all edges connect nodes with the same traits) to -1 (all edges
536 connect nodes with different traits).

537

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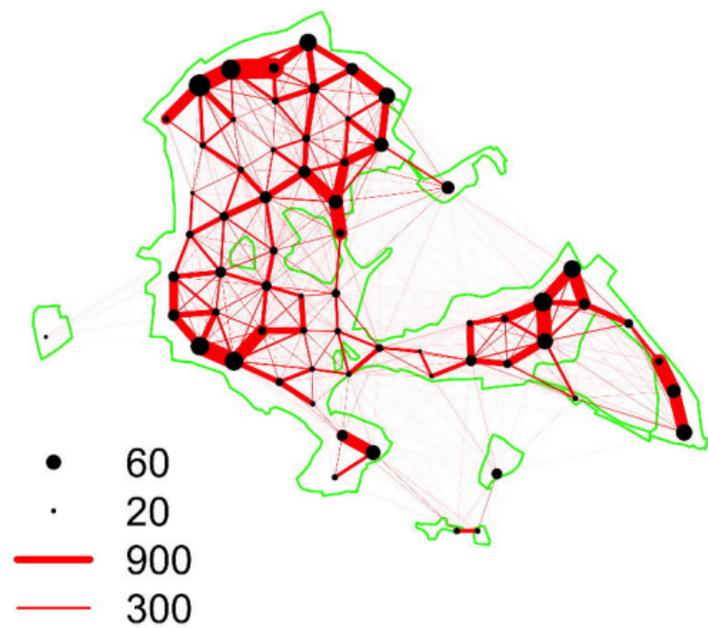
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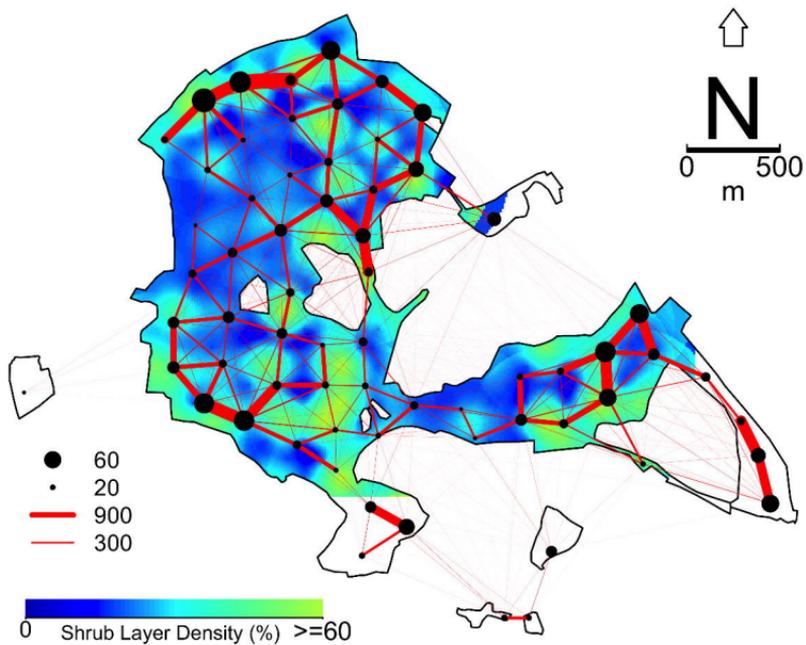
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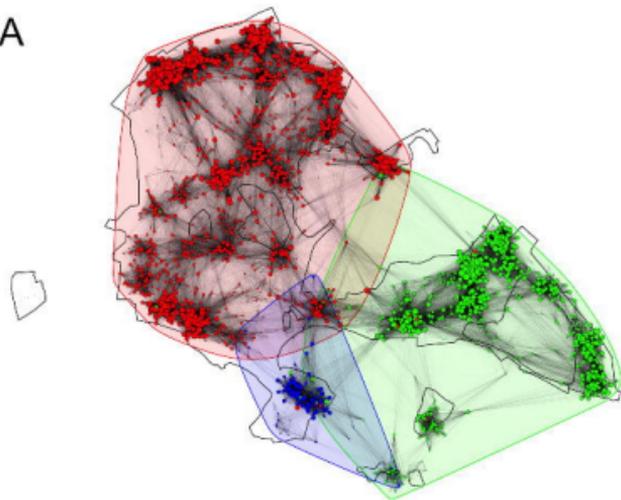
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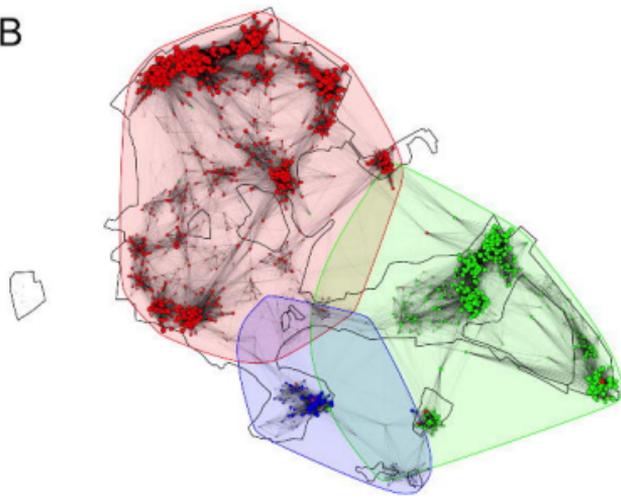
A**B****C**



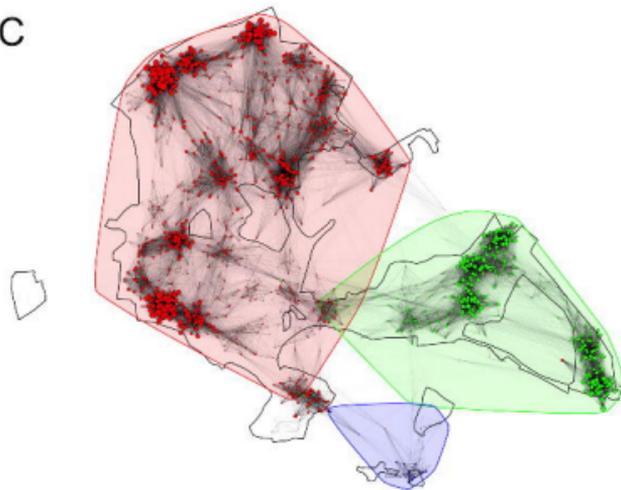
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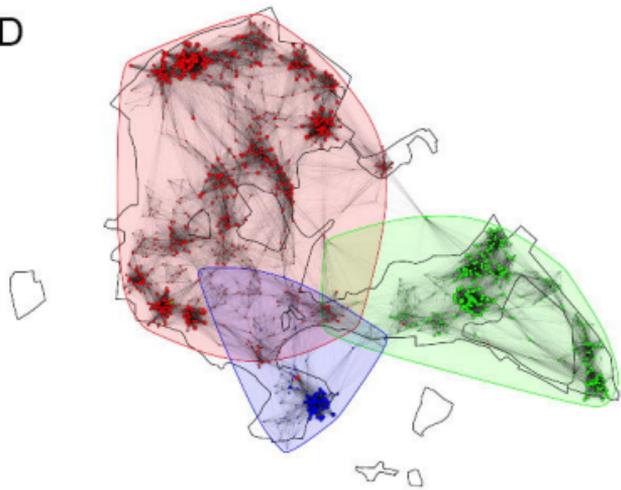
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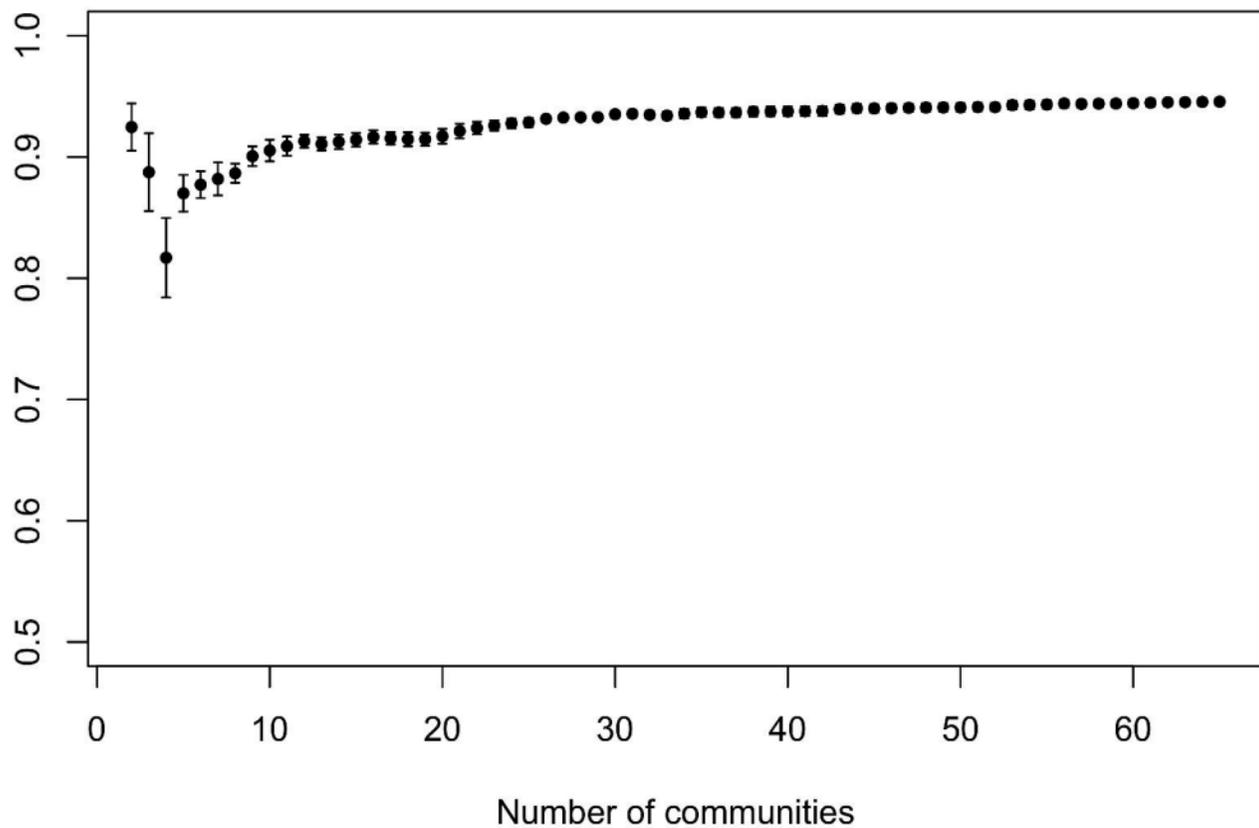
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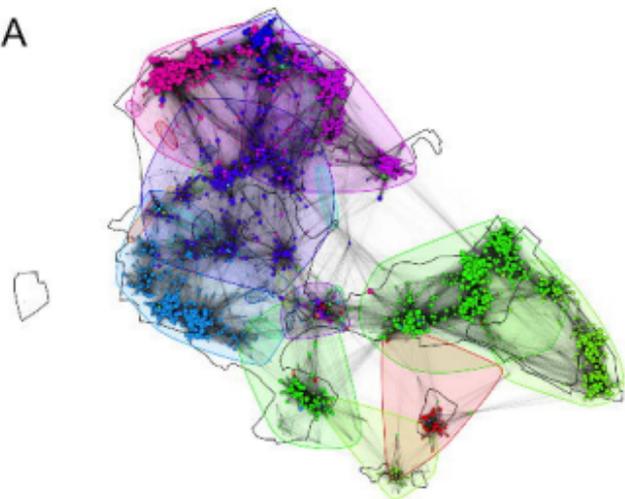
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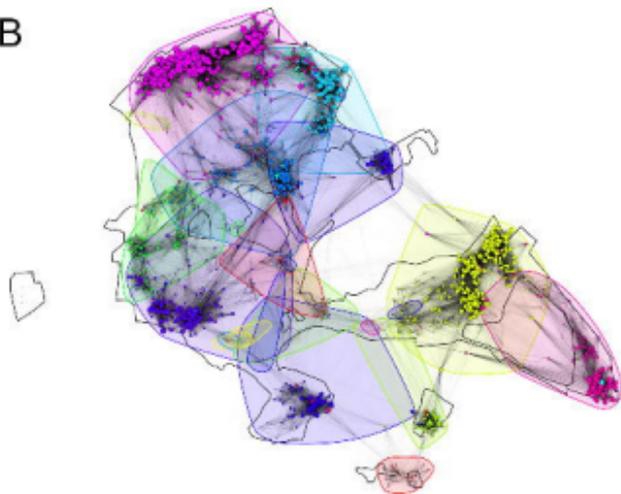
Probability of re-occurring in the same community



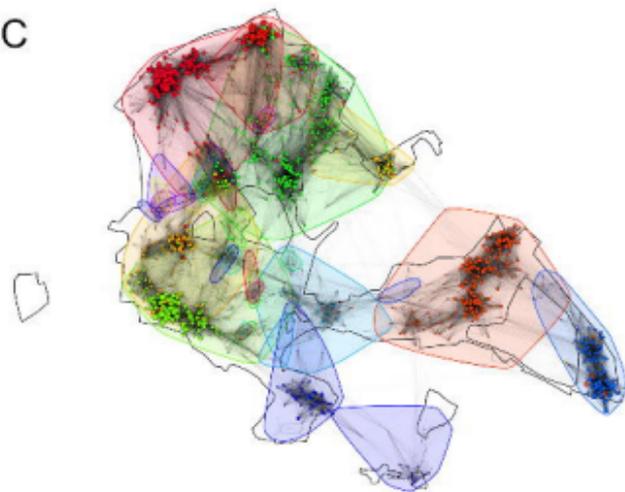
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