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Unexpected landscape-scale contemporary gene flow and fine-scale genetic diversity in rural hedgehogs

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Abstract

Agricultural intensification is one of the major forces driving populations of many traditionally common native species into smaller, fragmented populations which are prone to isolation and loss of genetic diversity. Identifying the spatial extent and characteristics of rural systems that support gene flow and promote genetic diversity for these species is thus essential for their long-term conservation. Here we used asymmetric autosomal genetic structure between sexes to investigate current gene flow among four neighbouring suburban populations of hedgehogs (*Erinaceus europaeus*) in England, which are separated by agricultural land. Contrary to expectations, we found that individuals belonged to a single genetic population despite the populations being separated by unoccupied agricultural land. Spatial autocorrelation was significant in adult female hedgehogs, but non-significant in adult males, revealing male driven contemporary gene flow between local populations. The results suggest that male hedgehogs are capable of moving between population patches separated by at least 3 km across the agricultural matrix. This finding is crucial to aid the development of a conservation strategy for hedgehogs as, for the first time, it shows the extent that previously assumed isolated populations across a perceived inhospitable landscape are connected by current gene flow. Higher within patch relatedness, and lower allelic richness were found from smaller suburban patches, largely reflecting local population size, indicating an early stage of genetic diversity loss due to habitat loss and associated fragmentation. Our study illustrates that considering current gene flow and local genetic diversity together is important to better understand habitat effects on genetic variation and to inform future conservation management.

Keywords Contemporary gene flow · Sex-biased dispersal · Genetic diversity · Metapopulation dynamics · Agroecosystem · *Erinaceidae*

Introduction

In recent decades, agricultural intensification and the subsequent loss and fragmentation of rural habitats have had severe impacts on the distribution and abundance of many previously common species (Tilman et al. 2017). This is particularly relevant in Western Europe, where such changes in farmland have led to substantial declines and range fragmentation for many common species including birds (Donald et al. 2001; Rigal et al. 2023), amphibians (Petrovan and Schmidt 2016; Băncilă et al. 2023), and butterflies (Habel et al. 2022). Understanding current gene flow between local populations can provide insights into the scale and extent

over which functional population connectivity can exist (McMahon et al. 2014). However, this is challenging as the genetic structure of the population is often difficult to detect, being masked by stronger historical gene flow that may have long since disappeared (Milligan et al. 2018; Lucena-perez et al. 2020). Thus, methods used widely to infer contemporary gene flow, such as assigning individuals captured from distinct populations to their natal population, typically lack power where there is minimal variation in genetic structure (Proctor et al. 2020). Also, relatively large overall population size limits the power of traditional individual pairwise genetic pedigree methods via the detection of closely-related pairs of individuals to inform ongoing

gene flow, as such individuals are often difficult to capture or detect (Taylor 2015).

A potential method for overcoming these issues that is applicable to species exhibiting sex-biased dispersal is through inferring asymmetric genetic structure between sexes (Li and Kokko 2019), using biparental inherited autosomal genetic markers. When species show sex-biased dispersal, contrasting genetic structure patterns between males and females is possible to be detected. However, this is only possible where gene flow occurs between local populations, as the signal of this asymmetric sex-biased genetic structure is lost in just one generation if gene flow ceases (Prugnolle and de Meeus 2002). Consequently, this method has the potential to reveal current gene flow, whilst bypassing the confounding effects of historical gene flow. For example, a strong social genetic structure was found in female African striped mice (*Rhabdomys pumilio*) living along a 7 km dry riverbed, whereas only weak structure, was found in the dispersing males, the latter indicative of coming from one population (Solmsen et al. 2011). The contrasting structure patterns between the males and females suggest that gene flow was occurring between populations of African striped mice, albeit largely from the wider-ranging males. However, the method remains largely untested, especially for populations that are separated by unoccupied landscapes where the signal of sex-biased genetic structure might be less visible if inter-patch movement is highly restricted (Prugnolle and de Meeus 2002).

The West-European hedgehog (*Erinaceus europaeus*) is considered a model species in agroecosystems for informing rural habitat connectivity (e.g., Moorhouse et al. 2014) and evaluating agri-environment schemes (e.g., Hof et al. 2012; Pettett et al. 2017). The species has undergone significant population decline across its geographic range (e.g., Roos et al. 2012; Hof and Bright 2016; Taucher et al. 2020), with rural habitat loss and fragmentation thought to be the principal drivers (Wilson and Wembridge 2018). Recent studies also suggest that rural hedgehogs have a patchy and discontinuous distribution (Williams et al. 2018), and where present in rural environments, they tend to occur in small populations near residential buildings (Schaus et al. 2020) where they will occasionally use the surrounding agricultural matrix (Parrott et al. 2014; Hof et al. 2012). As hedgehog home ranges are relatively small (e.g., 0.12 km^2 for females and 0.22 km^2 for males; Pettett et al. 2017) and their dispersal ability is poorly understood, questions remain about their ability to move between suburban centred populations separated by a largely uninhabited agricultural matrix (Yarnell et al. 2014). If hedgehogs are unable or unwilling to traverse the agricultural matrix, and the suburban populations are indeed isolated, they are likely to experience increased genetic drift and a subsequent loss of genetic diversity and lowered population viability (Reed and Frankham 2003; Spielman et al. 2004).

The isolation of populations and their likelihood of losing genetic diversity will depend on the distance between populations and the size of the populations. A lack of suitable habitat will also play a role in shaping the within-population genetic variation, leading to reduced genetic diversity at local scales. This is because smaller patches can only accommodate lower effective population sizes and, consequently, local populations will experience higher levels of genetic drift and retain lower levels of genetic diversity (Keyghobadi 2007). However, very few studies have considered the effects of landscape structure on genetic diversity within populations (Dileo and Wagner 2016). In hedgehogs, whilst much work has focused on hedgehog genetic structure, genetic diversity remains insufficiently understood (Rasmussen et al. 2020).

Interpretation of previous studies on hedgehog gene flow is also hampered by ascertainment bias in analysis, historical gene flow (Araguas et al. 2022), and the unknown wider genetic population structure across its geographical range. For example, Becher and Griffiths (1998) showed population differentiation between eight populations within a 15 km radius in Oxfordshire but could not identify if natural barriers to intrinsic dispersal or human induced habitat fragmentation were the cause. In Zurich, hedgehog population structure might be confounded by sampling biases caused by sampling closely related individuals (Braaker et al. 2017; Barthel et al. 2020). Furthermore, a population in central London was found to have low genetic diversity, but whether this was due to current isolation, historic or recent founder effects remains unknown (O'Reilly 2016).

Here, we used nuclear autosomal genetic data from hedgehogs residing in four local suburban sites with varying local hedgehog population sizes to investigate contemporary gene flow across a perceived inhospitable agricultural matrix. We expected that if gene flow between local populations still occurred, asymmetric genetic patterns structure between sexes, due to sex-biased dispersal, might be detectable. Otherwise, if gene flow between local populations ceased, asymmetric genetic patterns structure between sexes should be lacking, and genetic structure between local populations might become detectable. We used different methods to infer genetic structure. We also investigated relatedness patterns, and genetic diversity, both within and across sites, to evaluate the effects of habitat composition on the genetic variation in the hedgehogs.

Methods

Study area and sampling design

Hedgehogs were sampled from four suburban centers (Farnsfield, Halam, Kirklington, and Southwell) in rural Nottinghamshire, England (Fig. 1). The spatially-varying distribution of the hedgehogs within our study is representative of most rural hedgehog populations in England as: (1) sites were <10 km apart from their nearest neighbour, and hedgehogs have been sighted in 91.4% of 10×10 km grids across England (Hof and Bright 2016) and (2) sites were largely separated by agricultural land which takes up 69% of land cover in England (National Statistics 2022). The sites had varying local hedgehog population sizes, and differing amounts of preferred suburban and grassland habitats (Fig. 1; Table S1; Table S2).

Between 2020 and 2021, 276 hedgehog samples were collected from a ~ 1 km² area in each suburban population. The majority of samples ($n=247$) were hairs plucked from live hedgehogs during systematic spotlight transects. Additional soft tissue samples mainly from ears ($n=29$) were collected from road killed hedgehogs within the suburban

centers. Geographic coordinates, sex, and age information were recorded where possible (Supplementary Table S7). For hedgehogs with multiple captures, the midpoint between sampling coordinates was taken as the location of that hedgehog's sample. 'Juvenile' hedgehogs were defined as those born that calendar year. All tissue samples were stored in 50 ml of absolute ethanol in screw-topped rubber-sealed falcon tubes and transferred to a -20 °C spark-proof freezer as soon as possible until DNA extraction.

Local hedgehog density (number of individuals per km²) was estimated based on spatial-capture-recapture as part of a wider research project (Moore 2023). Landscape composition was qualified using both node-based and link-based methods, with the former focusing on within-patch habitat availability and the latter inter-patch permeability (Dileo and Wagner 2016). For node-based landscape composition, the density (proportion) of suburban, grass, and arable land within a 1 km radius of each sampling location was calculated based on UKCEH Land Cover Map 2021 (Marston et al. 2022), with all types of grasslands included as 'Grass'. In addition, densities (proportions) of buildings and roads were calculated for the same area based on Ordnance Survey Open Built Up Areas v.1.0, 2022, and Ordnance Survey
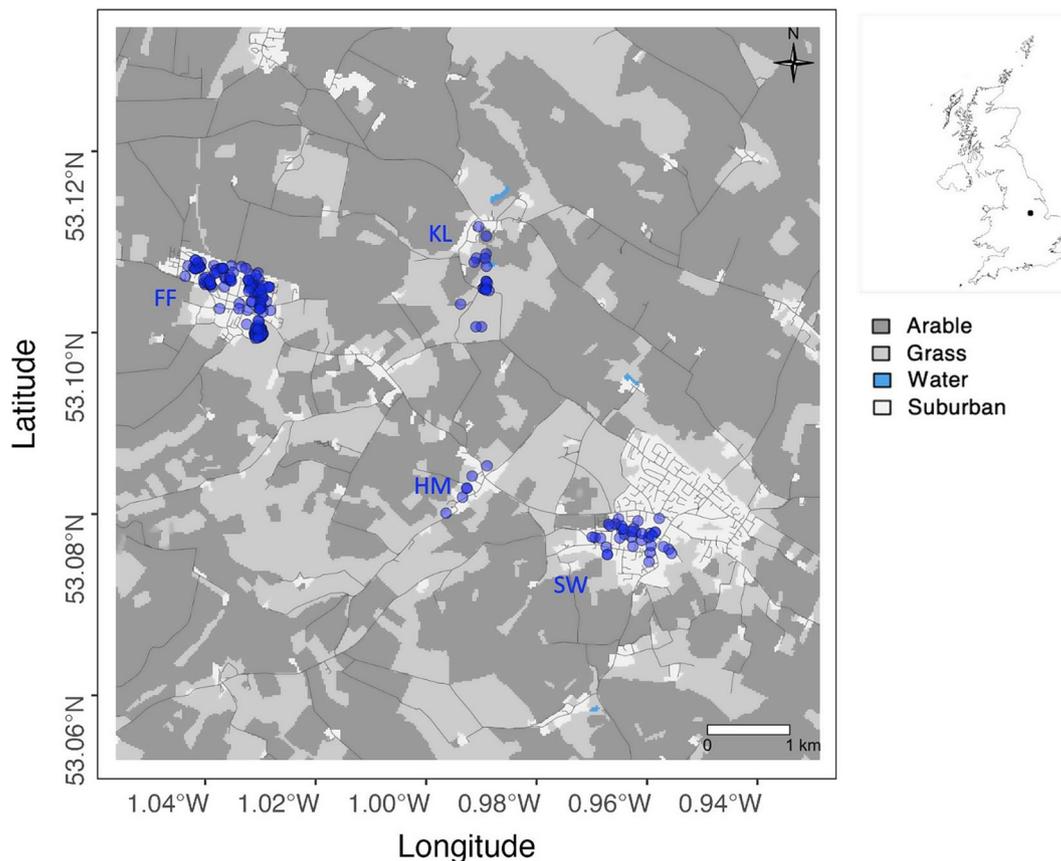

Fig. 1 Sampling locations of hedgehogs from 4 sites in Nottinghamshire, UK ($n=183$; only for those with coordinates available). Darker blue shaded points indicate geographically close or overlapped sam- ples. Grey lines indicate roads. *Abbreviations: KL: Kirklington; FF: Farnsfield; HM: Halam; SW: Southwell. Base map: UKCECH Land Cover Map 2020 (Marston et al. 2022); projection: EPSG:4326

Open roads v.2.4, 2023, respectively. As different base maps were used, some buildings and roads were included in the suburban category, thus densities (proportions) of these habitat compositions combined do not equal 1. The average landscape composition densities were calculated for each site to provide a within-site landscape composition (Table S1; individual-based landscape composition is included in Supplementary Table S8). For link-based landscape composition, densities (proportions) of the same variables were calculated within a 1 km buffer around lines drawn between pairwise site centroids (Table S2), using the same maps.

All hedgehog surveying and sampling were performed in accordance with ethical standards of the Animals (Scientific Procedures) Act, 1986, under a Natural England licence to capture and handle hedgehogs (2018-36011-SCI-SCI), and supported by Nottingham Trent University ethics committee (codes: ARE192014a and ARE192014b).

DNA extraction and genotyping procedures

DNA was extracted from all samples collected ($n=276$) using an ammonium acetate precipitation method (Nicholls et al. 2000). Twenty-eight hedgehog-specific primer pairs (Becher and Griffiths 1998; Henderson et al. 2000; Curto et al. 2019) were tested. The final analysis included genotype data from 14 primer pairs from 236 unique individuals (Detailed DNA extraction and genotyping procedures are included in Supplementary 1.2, 1.3; Genotype data are provided in Supplementary Table S7). Genetic markers being genotyped are nuclear loci, with genotyping for length variation of microsatellites.

Genetic structure and gene flow

Patterns of gene flow between sites were first investigated by analysing pairwise F_{ST} (Weir and Cockerham 1984), with all individuals included, using the package *hierfstat* (Goudet and Jombart 2022). Private alleles (alleles that are only found on one site) were identified using the package *adegenet* (Jombart 2017).

Patterns of gene flow were investigated further by undertaking an individual-based clustering analysis using the package LEA (Frichot and François 2015) as it is suggested to be more robust to Hardy-Weinberg equilibrium (HWE) assumptions (Frichot and François 2015) than commonly employed genetic clustering software like STRUCTURE (Pritchard et al. 2000) or ADMIXTURE (Alexander and Lange 2011). All individuals were included. Ancestry coefficients were calculated for each individual with K=2–4 where K is the number of assumed ancestry populations, and coefficients were compared.

Gene flow was then explored using two alternative genetic clustering methods: discriminant analysis of principal components (DAPC; Jombart et al., 2008), and spatial principal component analysis (sPCA; Montano and Jombart, 2017), using the package adegenet (Jombart 2008). In DAPC, we used four sites as prior populations to show how the genetic distribution of individuals was related to their original sampled sites. Then in sPCA, allele frequencies and their spatial autocorrelation were analysed on an individual, rather than population, basis. The analyses were run with both males and females combined and separated, with the former being indicative of the overall population structure across sites, and the latter the potential sex-biased structure. sPCA allows tests of global and local spatial structure, with high global structure indicating that individuals are genetically similar to their geographic neighbours, and high local structure indicating genetic dissimilarity on local scales (Montano and Jombart 2017). The genetic structure in sPCA was estimated from lagged scores summarizing genetic variability which also account for the geographic location of samples. The lagged scores of each component can be translated into a colour from the RGB colour channel such that the different shades of the red, green, and blue colour system give an indication of genetic differentiation with similar colours representing genetic similarity. In our analysis, the first two components were retained as suggested by the eigenvalues, and the results were plotted on 25 m land cover grids based on the UKCEH Land Cover Map 2021 (25 m rasterised land parcels, GB; Marston et al. 2022), using the package terra (Hijmans et al. 2023). To detect any influence of sex on genetic structure, analyses were undertaken separately for all hedgehogs, adult males only, and adult females only.

Relatedness

Relatedness was inferred using the package *related* (Pew et al. 2015), with group-based population simulations (Supplementary 1.5).

Genetic diversity

In order to characterize genetic diversity on different spatial scales, the following metrics were calculated across all sites overall, and for each site separately, using the package *hierfstat* (Goudet 2022): observed heterozygosity (H_O), expected heterozygosity (H_S = within sites; H_T = across sites), allelic richness (A_R), and inbreeding coefficient (F_{IS}), where high genetic diversity, indicative of increased gene flow, is associated with high heterozygosity and allelic richness, and a low inbreeding coefficient.

As considerable variance in genetic diversity was observed between sites, we investigated how this was impacted by sample size and habitat type, using two methods: (1) heterozygosity values were calculated as an effect of increased sample size using the package *hierfstat* (Goudet 2022); and (2) 6–10 samples from a 100 m radius around each sampling location were grouped, with locations with less than 6 samples excluded, and genetic diversity values calculated for each group using the package *sGD* (Shirk and Cushman 2011), and visualised using the packages *sf* (Pebesma 2018; Pebesma and Bivand 2023), and *tmap* (Tennekes 2018). All six samples from Halam were combined into one group.

All data analysis was carried out in R Statistical Software (v.4.2.2; R Core Team 2023).

Results

Data from 236 unique individual hedgehogs, genotyped using 16 markers, were included in the preliminary analysis. Loci EEU36H and W30 had low amplification success rates, and EEU36H was also not in Hardy-Weinberg equilibrium (HWE), possibly due to genotyping errors, thus were not included in the following analyses (although no obvious effects were found in the structure analyses either including or excluding both loci). The remaining 14 loci were potentially from 12 different autosomal chromosomes. For loci located on the same chromosomes, no consistent linkage-disequilibrium was detected between pairs of loci in more than 3 out of 4 sites. One locus (W10) showed a higher probability of the presence of null alleles but was retained

as no obvious effects were found in the following analysis. More information is provided in Supplementary 1.4.

Genetic structure and gene flow

F_{ST} values were low for all pairwise site comparisons, indicating that the local populations are not strongly genetically differentiated (all <=0.02; Table S5).

Individual-based clustering analyses failed to recover any discernible geographic population structure, with all sites containing a mixture of individuals assigned to each of the K population clusters, for each investigated value of K (Fig. 2).

Findings from the DAPC analysis with the four study sites as prior populations showed the genetic distribution of samples roughly mirrors geography, suggesting an effect of geographic distance on the genetic divergence. But notably, samples from each site were not discretely clustered, instead showing considerable overlap across sites, indicating an absence of discrete, well-structured populations (Fig. 3).

Findings from the sPCA global structure analysis indicated that there was a significant positive spatial autocorrelation for individuals of all ages and sex ($\lambda=0.015$, $n=183$, $p<0.001$; Fig. 4A), indicating that individuals were more genetically-similar to their close geographic neighbours. When analysing adult males only, the positive spatial autocorrelation becomes non-significant ($\lambda=0.023$, $n=70$, $p=0.367$; Fig. 4B), whereas it is significant for adult females only ($\lambda=0.032$, $n=64$, $p=0.013$; Fig. 4C). Tests for negative spatial autocorrelation (decreased genetic similarity between close geographic neighbours) found no significant correlation ($p>0.05$) between genetic variation
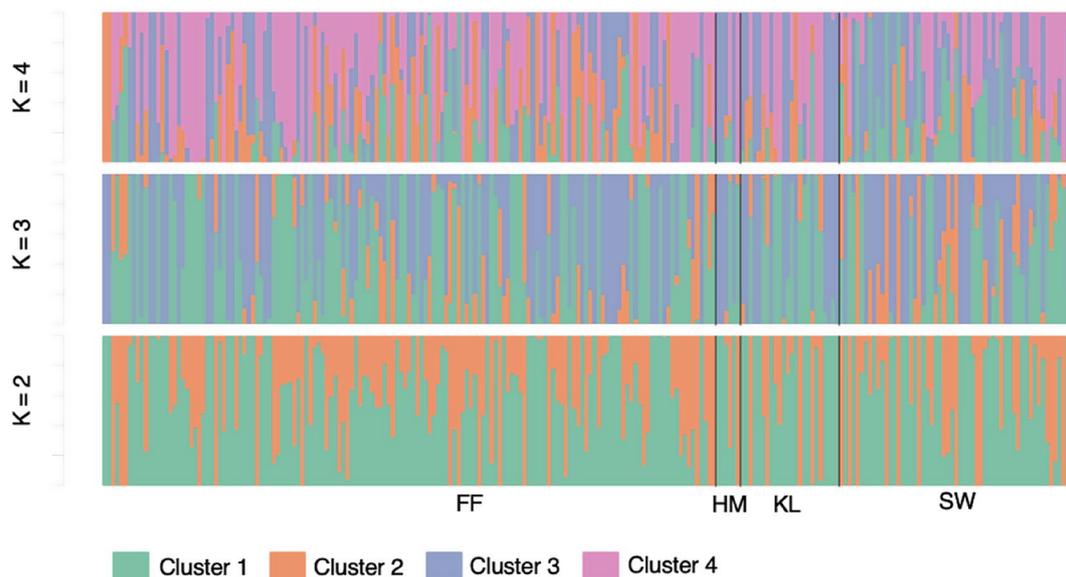

Fig. 2 Genetic clustering for the 4 hedgehog populations, estimated using the package LEA ($n=236$). Cluster proportions are showing in y-axis (range: 0–1), and each bar represents one hedgehog, for K=2–4. *Abbreviations: KL: Kirklington; FF: Farnsfield; HM: Halam; SW: Southwell
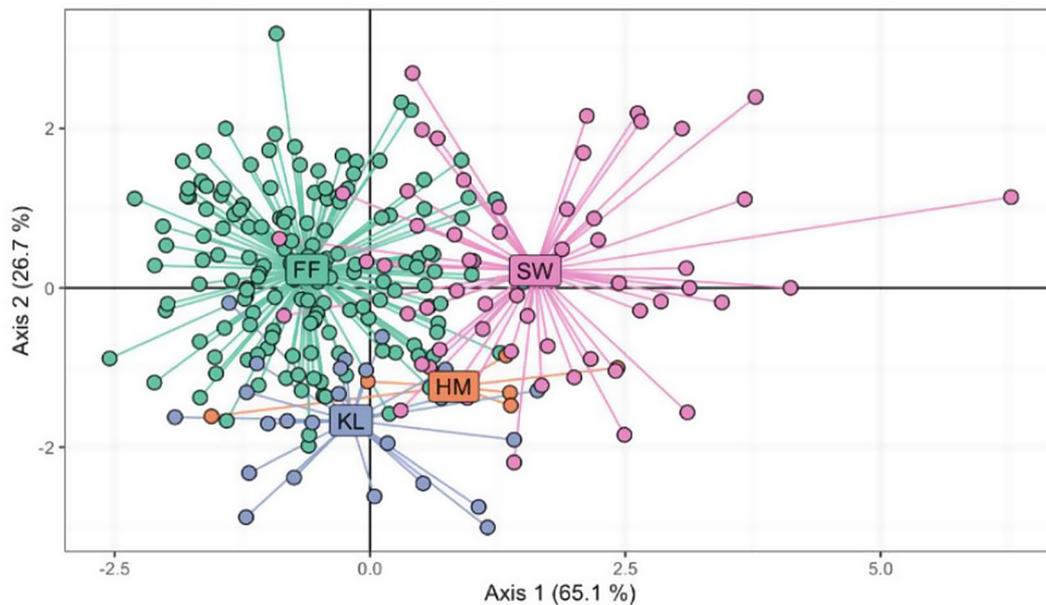
Fig. 3 Cluster analysis of genetic variation using DAPC ($n=236$), with the four study sites as the prior groups. Individual hedgehogs are represented by points and coloured by their sampled site (not genetic clusters). *Abbreviations: KL: Kirklington; FF: Farnsfield; HM: Halam; SW: Southwell
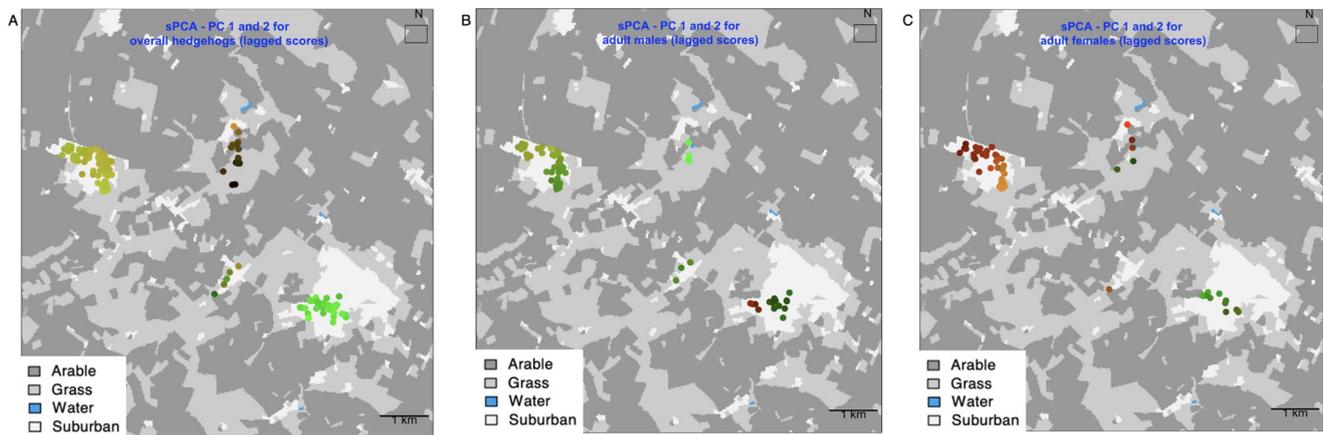

Fig. 4 Spatial genetic variation of hedgehogs inferred from the spatial principal component analyses (sPCA), using the first two principal components. Points represented individual hedgehogs, with the simi- larity in the colours indicating genetic similarity. A: all hedgehogs, B: adult males, C: adult females

and geographic distance for any of the hedgehog groups (all: $\lambda=0.009$, $n=183$; male only: $\lambda=0.021$, $n=70$; female: $\lambda=0.024$, $n=64$; Fig. 4), showing no genetic dissimilarity on a local scale. The difference in positive spatial autocorrelation between the sexes indicates that gene flow is currently being maintained across the study area, and this is mainly driven by the males.

Relatedness

Among the seven estimators of relatedness that were tested, lynchrd had a slightly higher Pearson's correlation coefficient (0.80) between observed and expected relatedness,

and thus was selected as the best estimator for subsequent analyses (Supplementary 1.5).

A total of 190 hedgehogs of known age were grouped as 'juvenile' or 'adult' and were taken as input in one run using the package *related*: the juveniles showed significantly higher relatedness within-group (observed relatedness $r=0.014$, $n=55$, $p<0.05$), and adults significantly lower relatedness within group ($r=-0.004$, $n=135$, $p<0.05$), than expected when being randomly mixed across age groups, indicating age effects on the relatedness potentially due to delayed natal dispersal and the lack of generation overlaps in juveniles. Thus, juveniles were excluded from the following analyses.
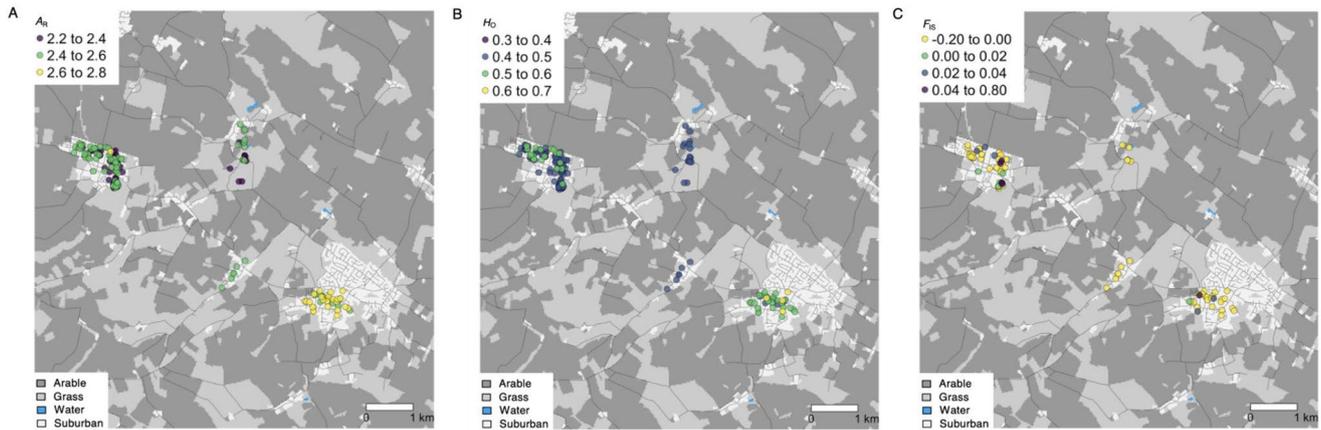
Fig. 5 Distribution of genetic diversity for groups of 6–10 samples within a 100 m radius of each sampling location ($n=183$). A: diversity allelic richness (A_R), B: observed heterozygosity (Ho), C: inbreeding coefficient (F_{IS})

When the adult individuals of both sexes combined were grouped into their four original sites (FF, HM, KL, SW), individuals from the same site showed significantly higher relatedness than expected when being randomly shuffled with individuals across sites ($n=135$, $p<0.05$) for each site except for HM which had low sample size ($n=4$), suggesting individuals from within-sites are more related than across sites. The two larger sites (SW and FF) had lower within-site relatedness than the two smaller sites (KL and HM), but relatedness values were low for all sites (Table S6). Then, to infer sex effects on the relatedness distribution, this analysis was run for adult males and adult females separately. A significantly higher within-site relatedness than expected when being randomly shuffled with individuals of same sex across sites were only found for females only at site FF ($n=47$, $p<0.05$), potentially reflecting a reduction in statistical power compared to the combined-sex analysis.

Genetic diversity

Genetic diversity parameters for each primer pair are included in Supplementary 1.4. Mean A_R (2.45; values from the four sites averaged) was 30% lower than overall A_R (3.5; samples from the whole area were taken as panmictic), showing severely reduced genetic diversity on local scales, which potentially reflects demographic change, whereas mean observed heterozygosity was close to overall heterozygosity, suggesting such demographic change happened in relatively recent times. Estimates of inbreeding coefficients were low (<0.1) for all sites (Table S6), but some locations showed higher inbreeding (within 6–10 individuals per location) (Fig. 5, C).

Values for observed heterozygosity (H_O), expected heterozygosity (H_S), and Allelic richness (A_R) were generally higher on larger suburban patches (Table S6, Fig. 5), and this is not due to sample size effects (Fig. S2), suggesting

that the hedgehogs were unevenly distributed across the study area, indicating an early stage of varied genetic diversity in relation to habitat type.

Discussion

In this study, we utilized the asymmetry in genetic variation between sexes as a powerful measure of current gene flow. This provided evidence of population-level, long-distance movement in a declining farmland mammal across a perceived inhospitable agricultural matrix. Smaller suburban patches had lower allelic richness and heterozygosity, reflecting local population size, indicating an early stage of varied genetic diversity due to habitat loss and the associated fragmentation.

The low F_{ST} values, no private alleles in any sites, and little evidence of differentiation in structure across the sites, indicate that the hedgehogs across the study area still belong to one genetic population. The genetic similarity observed here is in accordance with studies in urban Berlin (Barthel et al. 2020), and urban Helsinki (Osaka et al. 2022), which also suggested that their hedgehogs were not genetically differentiated. This is, however, in contrast to studies in rural Oxfordshire (Becher and Griffiths 1998), and urban Zurich (Braaker et al. 2017), in which distinct genetic differentiation patterns were observed. Nevertheless, the recent human-induced fragmentation, which is of direct conservation relevance, could not be concluded in these studies as influencing the observed genetic variation patterns as they were likely confounded by other factors, such as historical gene flow patterns. Such historical gene flow might obscure current fragmentation, leading to little to no genetic structure being detected. Conversely, where genetic structure is detected, it could be due to natural barriers and not

necessarily due to recent landscape changes (Milligan et al. 2018; Lucena-perez et al. 2020).

To better understand contemporary gene flow, we used asymmetric genetic variation between sexes. For species exhibiting sex-biased dispersal (Li and Kokko 2019), such as the hedgehogs, it is possible to detect contrasting genetic structure patterns between males and females using biparental inherited genetic markers. However, this is only possible where gene flow occurs between local populations, as the signal of this asymmetric sex-biased genetic structure is lost in just one generation if gene flow ceases (Prugnolle and de Meeus 2002). Consequently, this method has the potential to reveal current gene flow without the confounding effects of historical gene flow (Solmsen et al. 2011). We found a sex-biased difference in genetic variation, where the sPCA showed a significant positive spatial autocorrelation between allele frequency and geographical location in adult females ($\lambda = 0.032$, $n = 64$, $p = 0.013$; Fig. 4C), but not in adult males ($\lambda = 0.023$, $n = 70$, $p = 0.367$; Fig. 4B). This indicates that contemporary gene flow is occurring across the studied agricultural matrix, and is mainly driven by the movement of males.

This is the first evidence of the status of contemporary gene flow among local hedgehog populations on a landscape scale. Our results suggest that long-distance movement across the agricultural matrix (at least 3 km here) in hedgehogs might be more extensive and frequent than often suggested by spatial-capture-recapture, and GPS tracking studies which are often short-term, small-scale, and restricted to adult hedgehogs due to ethical considerations (Glasby and Yarnell 2013). For example, Pettett et al. (2017), estimated home ranges of adult females and males to be ~0.1, and ~0.2 km^2, respectively, and movements across agricultural matrix were rare. Our results suggest that hedgehogs require suitable corridors through which they can move between suburban population centres to maintain connectivity. Increasing the extent and quality of field margins (Moorhouse et al. 2014; Yarnell and Pettett 2020) and minimising road crossings that may act as barriers to hedgehogs (Moore et al. 2020, 2023) are likely to help facilitate such movement and reduce future risks of population fragmentation and isolation. Future studies should aim to use broad-scale population genetic structure to better understand matrix permeability, alongside the dispersal capabilities of hedgehogs, including what features and habitats they can navigate through so that they can be protected and maintained (Bowler and Benton 2005).

Low F_{st} values between all sites, and low average inbreeding coefficients within sites, potentially indicate a large population size of the hedgehogs on a metapopulation level. However, higher within site relatedness, and lower allelic richness were found on smaller suburban patches,

largely reflecting lower local population sizes, which suggests an early stage of genetic diversity loss in relation to small suitable habitat patches and associated fragmentation. Mean allelic richness across all four sites was lower than overall richness, while mean observed heterozygosity was close to overall heterozygosity, further suggesting the populations in this study were showing signs of recent habitat fragmentation. This is based on the theoretical prediction that allelic richness for neutral loci generally respond more strongly and rapidly to demographic change than heterozygosity when the population is experiencing recent decline and restricted gene flow (Barrandeguy and García 2021). Our results, thus highlight that for declining species which often show varied local density, variability in spatial patterns of genetic diversity can happen at a fine scale, even when some gene flow is still apparent and population differentiation is negligible. Similar results, i.e., reduced local genetic diversity despite large-scale gene flow, were also found in the declining common woodland birds in Australia (Harrisson et al. 2012). This suggests that although population differentiation is generally suggested to proceed faster than loss of genetic variation following habitat disruptions (e.g., Keyghobadi 2007), this might not always hold true, especially for species that are still with large population sizes, or that are mobile enough to maintain gene flow, but suffering different levels of local declines. Our results thus illustrate that considering current gene flow and local genetic diversity together is important to better understand habitat effects on genetic variation and to inform conservation management.

Conclusions

We have demonstrated several unexpected findings for the genetic status of a declining common mammal species across an agricultural matrix. The most important finding was that, despite the small size and high temporal stability of adult hedgehog home ranges, there is clear evidence that long-distance movement (at least 3 km) in hedgehogs is more frequent than previously thought based on home ranges. This finding is crucial to aid the development of a conservation strategy for hedgehogs as, for the first time, it shows the extent that previously assumed isolated populations across a perceived inhospitable landscape are connected by current gene flow. Higher within population relatedness, and lower allelic richness were found on sites with lower suburban land cover, largely reflecting local population size, indicating an early stage of reduced genetic diversity in relation to habitat loss and associated fragmentation. We suggest hedgehog conservation can aim to prevent further declines by identifying what features are needed to facilitate

hedgehog movement between population centres and facilitate improved connectivity and resultant gene flow.

Declarations

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