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RESEARCH

Beyond dispersal limitation: drivers of fine-scale population structure in two common solitary wild bees

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Abstract

In landscapes shaped by intense agriculture, even common bee species may face limits to their dispersal capacity. We explored how spatial isolation and land-use types influence the genetic population structure of two generalist mining bees – *Andrena haemorrhoa* and *A. nigroaenea* – which differ in body size and putative dispersal potential, yet share similar ecological niches. Using a network of isolated wetland patches as a model for fragmented habitats, we hypothesized that body size, spatial isolation, and landscape features, such as intensive crop production, affect genetic structure. We expected the larger-bodied *A. nigroaenea* to show less genetic differentiation, given its presumed higher dispersal potential, while gene flow in the smaller *A. haemorrhoa* would be constrained by landscape resistance and isolation. Using nine microsatellite markers per species, we found low genetic differentiation, with no consistent link between body size and genetic structure. Genetic clusters did not align with groupings based on spatial proximity, suggesting that factors beyond geographic isolation may shape genetic structure. Landscape resistance, i.e. species-specific habitat permeability, showed a weak influence on gene flow, more evident in *A. haemorrhoa*, indicating some, albeit limited landscape impact on dispersal. Despite evidence for inbreeding, both species maintained high allelic richness. Our results highlight how species life-histories, ecological factors, and landscape features interact to shape population structure. Despite considerable landscape fragmentation, generalist bees showed little spatial genetic structure, emphasizing the value of scattered high-quality habitat patches and corridors for supporting gene-flow, especially in smaller-bodied species.

Introduction

Wild bees are key pollinators in natural and agricultural systems, essential for entomophilous plant reproduction and crop production. The awareness of the decline in wild bee diversity and the associated loss of critical pollination services has significantly increased over recent decades (Potts et al. 2010; Hallmann et al. 2017; Lima et al. 2022). At the same time, the major anthropogenic threats to wild bee populations are loss and fragmentation of natural habitats caused by major land-use changes, including rapidly advancing urbanization and expansion of intensive farming (Kremen et al. 2002; Winfree et al. 2009). In such fragmented environments, competition for nesting and foraging habitats considerably increases. For bees, as central place foragers that transport resources back to their specific (nest) site (Bell 1990), larger inter-patch distances may impose disproportionately higher energetic costs to cover distances between foraging and nesting habitats (Zurbuchen et al. 2010). Particularly under agricultural intensification, access

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to floral and nesting resources becomes increasingly limited as habitat isolation proceeds, especially for ground-nesting bees that are restricted to field edges and must travel greater distances in search for floral rewards than in less intensified landscapes while experiencing intense local competition near their nests (Everaars et al. 2018). For mining bees, intensive cultivation measures, including soil modification critically constrain the availability of suitable nesting sites (Jha and Kremen 2013). Dorian et al. (2024) recently highlighted the urgent need for population-level studies to better inform conservation efforts and broaden the conceptual scope, particularly regarding movement patterns, habitat selection, and phenology. Yet, despite extensive research on European bee fauna, key knowledge gaps persist, with over half of the species lacking sufficient data in terms of spatial distribution and abundance (Nieto 2014). Hence, mechanisms that enable wild bee species to disperse in human-altered landscapes remain poorly understood (Ghisbain et al. 2021; Reeg et al. 2022). Some efforts have been made to identify key ecological and life-history traits that distinguish threatened from non-threatened species in terms of population persistence (occurrence) and capacity for dispersal (distribution). For instance, Moens et al. (2023) used wild bee species distribution models to highlight specialization, habitat and host selectivity, and adaptation to extreme climatic conditions as primary determinants of species endangerment. Notably, their findings demonstrated a negative response of both specialist and generalist species to intensive land use, with pastures and croplands being largely avoided.

Given the challenges of directly tracking small, highly mobile individuals, dispersal potential has largely been inferred from population genetic structure, with a particular focus on specialist wild bees (Zayed and Packer 2007; Exeler et al. 2008; Černá et al. 2013; Dellicour et al. 2015). Comparative analyses of specialist and generalist wild bee populations have yielded divergent findings, with some studies identifying a positive correlation between specialization and genetic differentiation (Zayed et al. 2006), while others report no clear pattern (Lecocq et al. 2017) or a negative association (Sousa et al. 2023). Although previous studies have investigated gene flow in generalist bee species (e.g. (Jaffé et al. 2016; Samad-zada et al. 2023; Sousa et al. 2023; Suni and Hernandez 2023), relatively few have explicitly focused on dispersal limitation within these generalists in highly fragmented landscapes at fine-resolution scale; for example, Darvill et al. (2010) used population genetic structure to infer dispersal differences between two common bumble bee species in an island system. High dispersal capacity has been suggested to evolve in species with strong foraging specialization (Salle et al. 2007). In line with this, small generalist wild bee species have been shown to be more negatively affected by habitat loss than small specialists, suggesting that behavioral flexibility does not always translate into greater movement capacity or gene flow (Bommarco et al. 2010). Hence generalist bee species — despite their widespread distribution — may still face dispersal limitations. More broadly, intensified habitat fragmentation has been reported to restrict movement and gene flow across wild bee species, particularly in temperate regions where resource patches are scarce and unevenly distributed (Kelemen and Rehan 2021). However, dispersal limitation is often rather linked to intrinsic traits that restrict gene flow, such as philopatry, where offspring tend to nest in the same site as their mother (López-Uribe et al. 2015; Ballare and Jha 2021), size-constraint flying capacity (Greenleaf et al. 2007; Wright et al. 2015; Sydenham et al. 2017), or limited social behavior and communication abilities (Kendall et al. 2022), rather than foraging or nesting specialization alone. In highly modified landscapes, even common generalists may reach their dispersal capacity threshold, with larger bees expected to travel considerably farther distances than smaller ones (Greenleaf et al. 2007). While this assumption is widely used, recent work has questioned the consistency of body size as a predictor of dispersal and gene flow in bees (e.g., (Hernandez and Suni 2024), highlighting the need for empirical testing across different ecological contexts and species. To explore this, we examined the effects of spatial isolation and landscape composition in two generalist solitary mining bees with largely overlapping ecological niche, but differing in body size and, consequently, presumed dispersal capacity. *Andrena nigroaenea* (Kirby, 1802) and *Andrena haemorrhoa* (Fabricius, 1781) are solitary ground-nesting bees that are broadly polylectic, univoltine (Wood and Roberts 2017; Westrich 2019), and nest singly or in aggregations in sandy to loamy soils, occurring in a wide range of habitats. Mating occurs in spring and early summer, with protandrous males patrolling along host plants (Jones 1930; Barrows 1978) or at non-resource rendezvous sites low over the ground in search for emerging females (Paxton 2005). Adult activity spans a few weeks, during which individuals mate, build nests, provision several brood cells, and lay eggs. A female may occasionally build several nests in her short lifetime, but does not overlap with the subsequent generation. *Andrena nigroaenea* is presumably monandrous, as post-mating odors in females suppress further male mating behavior (Schiestl and Ayasse 2000). Like many of their apoidean relatives, both species are central-place foragers, requiring nesting sites and food resources within their flying ranges (Bell 1990; Dyer 1998).

We used a system of isolated wetland patches in an intensively used agricultural landscape that provide foraging and putatively nesting resources for wild pollinators. The natural isolation of these semi-natural habitats mimics

habitat fragmentation that mining bees may experience in other environments, providing a model system to study their dispersal across fragmented landscapes. Both Andrena species are abundant and among the dominant pollinators in this area (Haß et al. 2012; Lozada-Gobilard et al. 2021), a pattern consistent with similar landscapes across their mid-European range (Szczepko-Morawiec et al. 2024).

We specifically hypothesize that: (1) body size influences dispersal ability and genetic structure, with the larger-bodied *Andrena nigroaenea* exhibiting lower genetic differentiation across the landscape than *Andrena haemorrhoa*, as increased body size is expected to enhance flight capacity and dispersal potential; (2) spatial clusters based on maximum homing range delineate population genetic structure and define patterns of genetic divergence; and (3) geographic and least-cost distances predict genetic differentiation, with spatial separation and landscape resistance constraining gene flow in both species, though to a lesser extent in the larger *A. nigroaenea*, such that landscape structure and isolation shape functional connectivity among local populations.

Methods and Materials

Sample collection

Sampling of the two focal Andrena species occurred in 2017 as part of a larger sampling of pollinators in the 'Agroscapelab Quillow' (Lozada-Gobilard et al. 2021), an open research platform of 168 km^2 located in North-East Germany (Fig. 1a). The area is characterized by a landscape mosaic of intensively cultivated areas, interspersed with waterbodies and rural settlements. Sampling campaigns were performed during the peak flowering season in May and June at 36 small glacial wetlands, i.e. kettle holes (Fig. 1, Appendix S1, Tab. S1). Surrounded by large, intensively farmed land and abundant throughout the area, these semi-natural wetlands function as isolated islands, providing critical resources for numerous plant and animal species, including wild bees. Kettle holes were distributed across a 15 × 11 km area). Sites were selected to assess spatial-genetic structure under an isolation-by-distance framework, with an average inter-patch distance of 7.2 ± 4.2 km (mean ± SD; range: 70 m–15.6 km) (Lozada-Gobilard et al. 2021). At each site, four color traps were placed in the cardinal directions, a method ensuring high pollinator sample coverage (Westphal et al. 2008; Lozada-Gobilard et al. 2021). Traps were collected after one week, and specimens from each kettle hole were pooled. While sampling included both sexes, male specimens were scarce. In addition, population genetic analyses focused on diploid females, as haploid males, due to the species' haplodiploid system, do not inform about heterozygosity or Hardy–Weinberg expectations. Samples were preserved in ethanol, identified by an expert (Dr. Christoph Saure; Museum of Natural History Berlin), and subsequently dry-mounted and stored at 4 °C. Specimens are archived in an entomological collection at the University of Potsdam.

Estimating homing ranges

In wild bees, flight distance and dispersal capacity are reported to be positively correlated with body size. We use the intertegular distance (ITD), i.e., the distance between the two wing bases (tegulae) on the thorax, which is strongly correlated with dry body mass, as a proxy for body size (Cane 1987; Kendall et al. 2019). Body size differs between the species, with *A. nigroaenea* being notably larger (average 13–15 mm) compared to *A. haemorrhoa* (10–12 mm; Westrich (2019). Accordingly, we expected intertegular distance (ITD) measurements to differ between the species. This was confirmed by our own ITD data (Appendix S1, Tab. S2). The maximum intertegular distance (ITD) was determined in a subset of 15 specimens of each *Andrena* species from the collection using *imageJ* software (Schneider et al. 2012). We used the *BeeIT* package which implements empirically derived equations from Greenleaf et al. (2007) to estimate the potential maximum dispersal range based on maximum ITD, thereby assessing the upper limit of gene flow across populations.

Molecular methods

Genomic DNA was extracted from the thorax of dry-pinned *A. haemorrhoa* and *A. nigroaenea* specimens using a modified low-salt CTAB (MoLSC) benchtop protocol (Arseneau et al., 2017). The protocol was optimized by extending the incubation time in water at 58 °C to 90 min. Microsatellite genotyping was performed using nine loci for *A. haemorrhoa* and nine loci for *A. nigroaenea*, originally developed for two congeneric species by Mohra et al. (2000), and Paxton et al., 1996, respectively: *AJ01*, *AJ25*, *AJ26*, *vaga27*, *vaga01*, *vaga03*, *vaga06*, *vaga26*, and *vaga20* (*A. haemorrhoa)*; and *AJ01*, *AJ25*, *vaga05*, *vaga06*, *vaga08*, *vaga13*, *vaga21*, *vaga25*, and *vaga27* (*A. nigroaenea;* Appendix S1, Tab. S3). Loci selection was based on primer testing in a subsample during a pilot study. For multiplexing, the forward primers were fluorescently labeled (FAM, VIC, NED, PET) and grouped into three and four Polymerase Chain Reaction (PCR) sets, respectively (Appendix S1, Table S4 b-c). For each sample, 1 µl of extracted DNA was combined with the MyTaq DNA Polymerase Kit (Bioline) and species-specific microsatellite primers (Appendix S1 Table S4

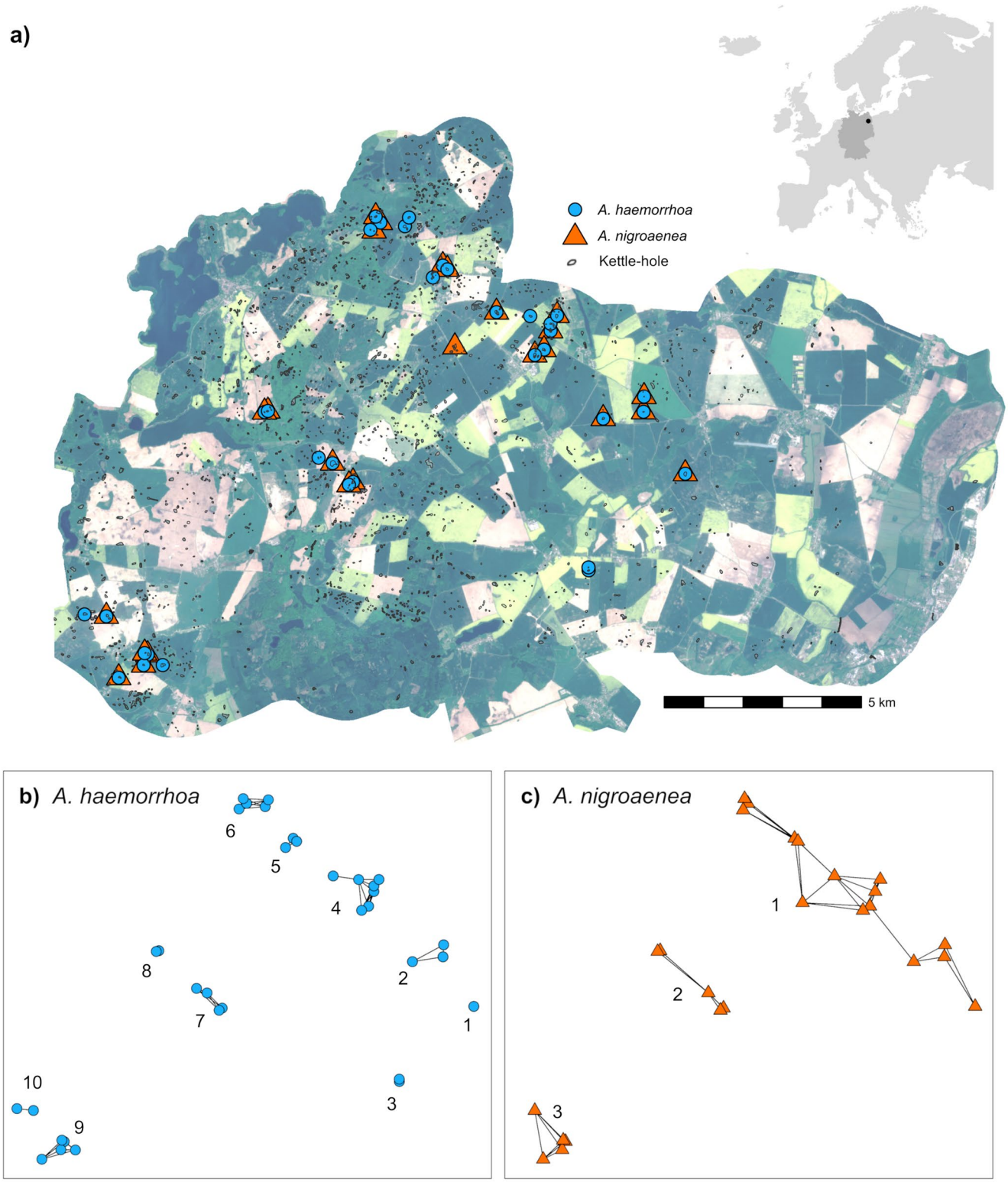

Fig. 1 (**a**) Geographical outline of the research area 'Agroscapelab Quillow' in the Uckermark (Northern Germany) and locations of individual kettle holes surveyed. Light blue circles and orange triangles represent sampling sites where *Andrena haemorrhoa* and *Andrena nigroaenea* occurred, respectively. All kettle holes present in the area are contoured in black. (**b**, **c**) Connection networks illustrate site connectivity, i.e. spatial clusters (indicated by numbers), based on neighbor-distance and species-specific maximum homing distance, which were inferred from intertegular distance (ITD) measurements reflecting body size (ITD_{Max}: *A. haemorrhoa* ≈ 2.7 mm; *A. nigroaenea* ≈ 3.3 mm)

a-c) in a total reaction volume of 25 µl. PCR amplifications were performed in a Biometra $T_{Gradient}$ thermocycler under the following conditions: an initial denaturation at 95 °C for 5 min; followed by 3 cycles of denaturation at 95 °C for 30 s, annealing at 60 °C for 1 min, and extension at 72 °C for 45 s. This was succeeded by 32 cycles of denaturation at 95 °C for 30 s, annealing at the locus-specific temperature (52–57 °C; Appendix S1, Tab. S3) for 1 min, and extension at 72 °C for 45 s. A final extension step was conducted at 72 °C for 10 min, followed by a hold at 16 °C. PCR products were analyzed on a 3500 Genetic Analyzer (Applied Biosystems Hitachi), and allele scoring was performed using GeneMapper software (Version 5.0, Applied Biosystems).

Data analysis

Hardy–Weinberg, linkage disequilibrium and genetic diversity

All analyses were conducted separately for each *Andrena* species. Spatial population clusters were defined based on species-specific homing distances by clustering sampling sites that fell within each species' estimated maximum foraging range, using neighborhood-by-distance calculations implemented in the *sp* and *stats* packages (v.2.1-4, Pebesma and Bivand 2005; R Core Team 2022) in R version 4.2.2. To ensure marker reliability, we assessed null allele frequencies, tested for Hardy-Weinberg equilibrium (HWE), and examined linkage disequilibrium (1,000 permutations) across at each locus using *PopGenReport* and *pegas* package (v.3.0.7, Paradis 2010; v.1.1 Adamack and Gruber 2014), as well as Arlequin (v3.5, Excoffier et al. 2005). Descriptive statistics, including observed and expected heterozygosity (H_O, H_E), rarefied allelic richness (A_R), and the inbreeding coefficient (F_{IS}) were calculated using the *hierfstat* package (v.0.5–11, Goudet 2005), with significance of F_{IS} tested in Arlequin (n_{perm}=1,000).

Population structure

Population structure was analyzed using Discriminant Analysis of Principal Components (DAPC) (*adegenet*, v.2.1.10, Jombart 2008; Jombart et al. 2010), which partitions genetic variation into between-group and within-group components based on K-means clustering, maximizing discrimination between pre-defined groups. DAPC does not assume a population genetic model, making it particularly suitable for haplodiploid mating systems (Jombart et al. 2010; Grünwald & Goss 2011). The optimal number of principal components (PCs) was determined via cross-validation (xvalDapc(), 1,000 replicates, *adegenet*), i.e. the number of PCs achieving the lowest mean squared error in cluster assignment prediction. Population structure was visualized using scatterplots of the first two discriminant axes. DAPC barplots were generated to illustrate cluster distribution across individuals and pre-defined spatial clusters. Pairwise F_{ST} and G'_{ST} were calculated with the *diversity* package (Keenan et al. 2013), considering both, clusters defined by maximum homing distance, and DAPC-inferred genetic clusters. G'_{ST} was included alongside F_{ST} as it provides a standardized measure of differentiation that accounts for high within-population heterozygosity (Hedrick 2005). Corresponding confidence intervals (95%) were estimated using 10,000 bootstrap replicates. Global F_{ST} and G'_{ST} were computed using the *hierfstat* and *mmod* package (Winter 2012), respectively. We further assessed genetic differentiation among spatial clusters performing an analysis of molecular variance (AMOVA) in Arlequin using 20,000 permutations.

Isolation by distance and resistance

To evaluate whether landscape corridors facilitate gene flow, we compared Euclidean distance (ED) with Least Cost Path (LCP) distance. Euclidean distance was calculated as the shortest straight-line distance between sampled sites using the *sp* and *stats* packages. LCP distance was estimated in *gdistance* (v.1.6; Van Etten 2017), incorporating habitat resistance values based on biotope maps of the federal state of Brandenburg, Germany (2013) and dispersal preferences of *A. haemorrhoa* and *A. nigroaenea*. For LCP estimation, habitat types were classified based on their suitability for dispersal and occupation by each *Andrena* species (Hofmann et al. 2019; Moens et al. 2023; Szczepko-Morawiec et al. 2024). Studies indicate that *A. haemorrhoa* predominantly inhabits semi-natural environments, including grasslands, ruderal areas, gardens, parks, and both production- and semi-natural forests, while avoiding densely urbanized landscapes. In contrast, *A. nigroaenea* is occurring in highly urbanized areas and prefers semi-natural forests. However, both species are unlikely to occupy or disperse through open water habitats or intensively managed cropland and pastures (Hofmann et al. 2019; Moens, Szczepko-Morawiec et al. 2024). Jha (2015) assigned resistance values approximately 10 times as high to cropland and open water as to semi-natural habitat, parameter settings that demonstrated high predictive power for genetic distances in bumblebees. Among habitats where dispersal is generally possible, Rayfield et al. (2010) suggested a narrower scaling to reflect relative differences in dispersal costs among habitats. Following these authors, resistance values were assigned to habitat types to reflect species-specific movement constraints as follows: For *A. haemorrhoa*, open hedgerows, field copses and groves, and ruderal areas were given the lowest resistance

value of 1, followed by grasslands and forests with a value of 2. Urban areas were assigned a resistance value of 3, fens and bogs a value of 4, and open water and cropland the highest resistance value of 10. The classification for *A. nigroaenea* was similar, but with adjustments to reflect its greater tolerance for urbanized environments, setting urban areas to 1 and lower tolerance to production forests, setting forest to 3. Accordingly, a resistance value of 1 represented least resistance, while 10 represented maximum resistance. The Least Cost Path was calculated as the path of least resistance between locations. We compared *Bruvo's* genetic distance (*poppr*, v.2.9.6, Kamvar et al. 2014) against both Euclidean and Least Cost Path (LCP) distances using Mantel tests with 10,000 permutations in the vegan package (v.2.6-4, Oksanen et al. 2022).

Spatial principal component analysis

To detect potential (cryptic) spatial genetic structure linked to homing distances, we performed a spatial principal component analysis (sPCA, *adegenet*, v.2.1.10, Jombart 2008). For this, Moran's *I* was used to assess spatial autocorrelation, applying the neighborhood-by-distance method and integrating maximum homing distance to weight network connectivity. Monte Carlo tests (10,000 iterations) evaluated the statistical significance of global and local spatial structures. Finally, the scores of the first principal component were mapped onto sampling coordinates to visualize spatial genetic patterns.

Results

Genotyping and sampling summary

Based on the survey of 36 kettle-holes, we genotyped 214 female individuals of *A. haemorrhoa* from 34 locations and 137 female individuals of *A. nigroaenea* from 25 locations (Appendix S1, Tab. S1, Appendix S2). ITD measurements with maximum values of ≈2.7 mm (ITD_{Mean}=2.4±0.04) for *A. haemorrhoa* and ≈3.3 mm (ITD_{Mean}=2.8±0.08) for *A. nigroaenea* resulted in assumed maximum homing distances of 1227 m and 2339 m, respectively.

Spatial clustering and linkage disequilibrium

Consistent with these estimates, neighborhood-by-distance clustering resulted in ten aggregations, i.e. spatial clusters, in *A. haemorrhoa* and three in *A. nigroaenea*, comprising groups of 8–48 and 63–87 individuals, respectively (Fig. 1b, c). Global tests for linkage disequilibrium (L_D) indicated significant results in one and three out of 36 locus pairs, respectively, however, after *Bonferroni* correction none of the values remained significant at an experiment-wise error rate of 0.05, indicating no evidence of physical linkage among any pair of loci (Appendix S1, Fig. S1).

Hardy–Weinberg equilibrium and null alleles

Significant deviations from Hardy–Weinberg equilibrium (HWE) were observed in some spatial clusters, affecting up to 4 of 9 loci in *A. haemorrhoa* and 6 of 8 loci in *A. nigroaenea* (Appendix S1, Fig. S2). However, no loci consistently deviated from HWE expectations, as would be expected in the presence of abundant null alleles or allelic dropouts. Null alleles were detected at low frequencies across all loci, suggesting minimal impact on genotype calling (Table 1). Therefore, all loci were retained for further analyses.

Genetic diversity and heterozygosity

In *A. haemorrhoa*, observed heterozygosity (H_O) ranged from 0.38 (AJ01) to 0.85 (vaga06), while. expected heterozygosity (H_E) varied between 0.41 (AJ01) and 0.92 (vaga03). Significant heterozygote deficits, as indicated by positive F_{IS} values, were detected at vaga03 (F_{IS} = 0.169) and vaga20 (F_{IS} = 0.230). Allelic richness (A_R) spanned from 2.2 (AJ01) to 8.6 (vaga03). In *A. nigroaenea*, H_O ranged from 0.40 (vaga21) to 0.81 (vaga05), and H_E from 0.54 (vaga21) to 0.89 (vaga05). In *A. nigroaenea*, all loci exhibited significant heterozygote deficits, with F_{IS} values ranging up to 0.264 at vaga21, indicating elevated levels of inbreeding. Allelic richness varied between 1.0 (AJ25) and 5.5 (vaga04). Summary statistics at the lower scale (i.e., across locations, without pooling individuals to spatial clusters) revealed only minor deviations, suggesting that inbreeding due to potential Wahlund effects is unlikely (Appendix S1, Table S5). Additionally, considering null alleles were detected at low frequencies across loci, their influence on FIS estimates is likely limited.

Genetic clustering and population structure

K-means DAPC identified population genetic structure in both *Andrena* species, with the highest support (BIC) for K=4 genetic clusters (Fig. 2, Appendix S1, Fig. S3). While genetic clusters exhibited partial overlap (Fig. 2a, b), most individuals were assigned with high probability (Fig. 2c). Notably, linking DAPC assignment to geographic location and spatial cluster (Figs. 1 and 2c) not only highlights the apparent lack of correlation between genetic assignment and spatial cluster, but also indicates low admixture at finer geographic scales, even between adjacent kettle holes.

Table 1 Genetic diversity metrics estimated for each locus, pooled across all Spatial clusters, for 214 *Andrena haemorrhoa* and 137 *Andrena Nigroaenea* individuals. Metrics include observed heterozygosity (Ho), expected heterozygosity (He), inbreeding coefficient (F_{IS}), allelic richness (A_R), number of alleles (n.all), and null allele frequency (Null.all). Asterisks indicate significant deviations of F_{IS} from Hardy–Weinberg expectations

Locus	H_O	H_E	F_{IS}	A_R	*n*.all	Null.all
A. haemorrhoa						
vaga27	0.6316	0.7004	0.072	5.342	16	0.042
AJ25	0.4082	0.5271	0.187	3.072	7	0.101
vaga01	0.8375	0.8762	0.057	7.524	15	0.030
AJ26	0.5465	0.6466	0.044	4.166	8	0.067
vaga03	0.7713	0.9237	0.169*	8.569	21	0.071
vaga26	0.6150	0.6792	0.072	4.063	8	0.004
vaga20	0.7146	0.8850	0.230*	8.312	19	0.091
AJ01	0.3817	0.4104	−0.015	2.201	3	0.028
vaga06	0.8463	0.8564	−0.055	7.142	16	0.007
A. nigroaenea						
vaga27	0.5209	0.6253	0.141*	4.393	7	0.054
vaga04	0.5983	0.7160	0.129*	5.494	8	0.053
vaga21	0.4036	0.5400	0.264*	3.743	5	0.097
AJ01	0.5084	0.6563	0.248*	5.483	8	0.106
vaga13	0.5772	0.7087	0.150*	5.389	9	0.064
vaga08	0.7016	0.7653	0.094*	4.998	5	0.039
vaga25	0.5136	0.5595	0.126*	3.922	4	0.044
vaga05	0.8085	0.8932	0.107*	1.276	15	0.050
AJ25	0.5836	0.7740	0.202*	1.050	15	0.093
vaga06	0.6316	0.8338	0.210*	1.045	17	0.103

Assigning individuals to groups based on their predominant DAPC cluster (k = 4) still revealed low global differentiation ($G'_{ST\,A.haemorrhoa}$=0.008, $G'_{ST\,A.nigroaenea}$=0.05). Additionally, running DAPC with lower k values (e.g., k = 2, k = 3) produced a similar scattering of genetic clusters across locations and spatial clusters (Appendix S1, Fig. S4).

Genetic differentiation and variance partitioning

AMOVA did not yield significant genetic structuring among spatial clusters in both species (Table 2). Among-spatial-cluster differentiation accounted for only 0.55% (F_{ST}=0.005, p = 1.0) of total genetic variance in *A. haemorrhoa* and 0.56% (F_{ST}= 0.005, p = 1.0) in *A. nigroaenea*, with most variance occurring among individuals within spatial clusters (9.11% in *A. haemorrhoa*; 16.26% in *A. nigroaenea*), and the largest proportion of variance found within individuals, reflecting heterozygosity. Significant heterozygote deficits (FIS = 0.091 and 0.161, respectively; p < 0.001) suggest non-random mating within spatial clusters, rather than strong genetic structuring at the spatial level. Pairwise F ($F_{STmin} - F_{STmax}$, *A. nigroaenea* −0.007– −0.004; *A. haemorrhoa* = −0.017– 0.010) and G'_{ST} ($G'_{ST\,min} - G'_{ST\,max}$, *A. nigroaenea* −0.015– −0.006; *A. haemorrhoa* = −0.035– 0.049) statistics did not yield any significant differentiation between spatial clusters (Fig. 3). Generally, slightly negative G'_{ST} and F_{ST} values observed reflect statistical noise due to sampling variance and are commonly interpreted as zero, indicating an absence of detectable genetic differentiation.

Spatial genetic structure, isolation by distance and least cost path distance

Spatial PCA (sPCA) incorporating a neighborhood-by-distance weighted network detected no significant global or local spatial genetic structure in either species (*A. haemorrhoa:* r_G = 0.007, p = 0.618, r_L = 0.007, p = 0.519; *A. nigroaenea:* r_G = 0.012, p = 0.456, r_L = 0.01, p = 0.836). First PC score plots showed no evidence of a clinal or clustered genetic pattern, instead indicating diffuse genetic variation across the landscape (Fig. 4).

Euclidean distance showed no association with genetic distance in either species (Fig. 5a, b), suggesting that isolation-by-distance alone is negligible at the spatial scale examined. However, despite the lack of a clear spatial genetic structure, landscape resistance analyses revealed a weak, but significant correlation between genetic distance and least-cost path (LCP) distance in *A. haemorrhoa* (r = 0.06, p = 0.03; Fig. 5c), but not in *A. nigroaenea* (r = 0.06, p = 0.231; Fig. 5d), suggesting that landscape features may influence gene flow in *A. haemorrhoa*, but not in *A. nigroaenea*.

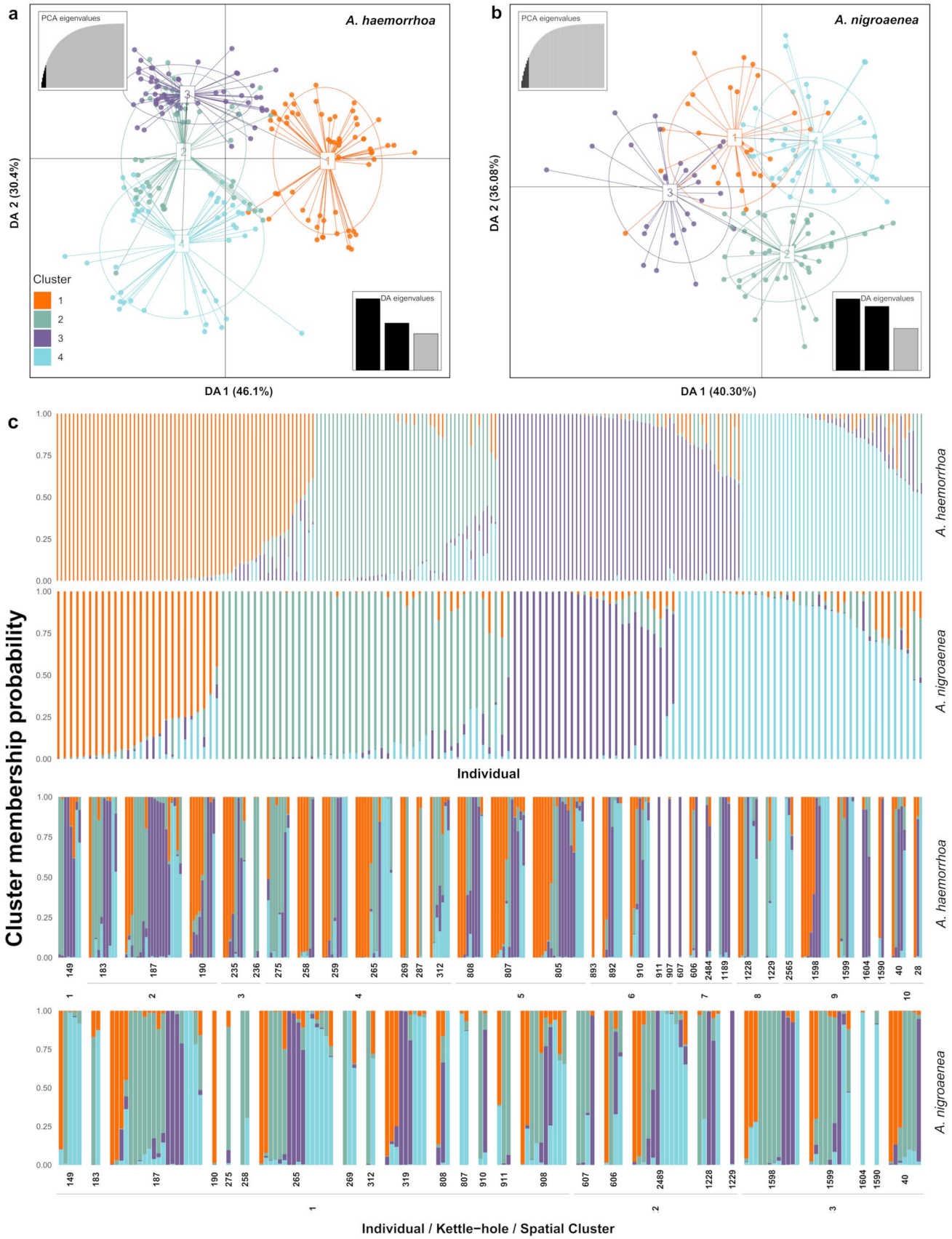
a
A. haemorrhoa
PCA eigenvalues
DA eigenvalues
Cluster
1
2
3
4
DA 2 (30.4%)
DA 1 (46.1%)
b
A. nigroaenea
PCA eigenvalues
DA eigenvalues
DA 2 (36.08%)
DA 1 (40.30%)
c
Cluster membership probability
A. haemorrhoa
A. nigroaenea
Individual
Individual / Kettle−hole / Spatial Cluster

Fig. 2 (**a**, **b**) Scatterplots from the discriminant analysis of principal components (DAPC) with assignment of individuals of each species to four genetic clusters ($G'_{ST\,A.haemorrhora}$=0.008, $G'_{ST\,A.nigroaenea}$=0.05), with the optimal number of clusters based on the lowest BIC from K-means clustering. (**c**) In DAPC bar plots, individuals (x-axis) are assigned to clusters with corresponding membership probabilities (y-axis). The upper two bar plots display individual genotypes ordered by prevalent cluster membership, while the lower bar plots classify them by sampling site (local kettle-hole ID by *ZALF*- Leibniz Centre for Agricultural Landscape Research) and spatial cluster arranged in decreasing longitudinal order. The color scheme in the bar plots aligns with that in the DAPC scatterplot. Species differ in body size (mean intertegular distance, ITD), which informed maximum homing distance estimates used to define species-specific spatial clusters

Discussion

Summary

This study investigated how body size, spatial clustering, and landscape structure shape genetic differentiation in two *Andrena* bees in an intensively used agricultural landscape. Both *A. haemorrhoa* and *A. nigroaenea* exhibited low genetic differentiation, though patterns varied with spatial grouping. While *A. nigroaenea* showed slightly lower differentiation across predefined spatial clusters, global G'_{ST} values between DAPC clusters were lower in *A. haemorrhoa*, suggesting that the observed differences may partially reflect the scale at which 'populations' were delineated. Spatial clusters based on homing range showed no correspondence with genetic structure. Conversely, we found well defined genetic population structure which was unrelated to spatial configuration of sampling sites. Landscape resistance weakly influenced gene flow, particularly in the smaller species *A. haemorrhoa*. These findings highlight species-specific responses to spatial and environmental constraints, which are further explored in the following sections.

Genetic diversity and inbreeding

Despite evidence of inbreeding, both species maintained relatively high allelic richness. Assortative mating mechanisms, such as female nest-site philopatry, likely increase frequencies of non-random mating (Paxton 2005; López-Uribe et al. 2015). However, the high allelic richness observed here is consistent with studies on the congener *Andrena vaga*, where inbreeding did not lead to reduced genetic diversity (Exeler et al. 2008). One possible explanation is that *Andrena* spp., like other solitary bees, maintain large effective population sizes (Romiguier et al. 2014) and reduced genetic drift, as all females can reproduce. This suggests that genetic diversity and inbreeding in the examined *Andrena* species may be largely shaped by intrinsic life-history traits. The observed inbreeding, in particular in *A. nigroaenea*, may however not lead to increased genetic load/inbreeding depression – a pattern also observed in other haplodiploid Hymenoptera - as haploid males, emerging from unfertilized eggs, purge deleterious alleles, reducing the overall impact of inbreeding compared to diploid organisms (Luna and Hawkins 2004).

Dispersal and genetic structure – influence of body size on gene flow

Larger-bodied bees were expected to have greater dispersal capacity and exhibit reduced genetic differentiation (Gathmann and Tscharntke 2002). The non-significance of pairwise G'_{ST} values indicates a lack of clear spatial population structure on the studied geographic scale in either species. Additionally, both DAPC analyses revealed clear genetic structure that however did not align with the spatial clustering of sampling sites. The absence of a clear contrast in levels of differentiation between the two species suggests that body size alone is insufficient to explain observed genetic patterns. This supports recent calls to move beyond purely morphological predictors and to consider how species-specific ecological traits and landscape context jointly shape population genetic structure (Hernandez and Suni 2024). Factors beyond geographic separation – such as mating strategies or microhabitat preferences – may influence genetic divergence. While foraging range can serve as a proxy for dispersal ability, it does not necessarily correspond to realized gene flow (Zayed et al. 2006). However, kettle holes provide essential floral resources for wild bees and since *Andrena* bees likely avoid large water bodies and intensively managed croplands, sampled individuals are expected to represent local genetic structure. We therefore assume a mechanism of male-biased natal dispersal as proposed by Paxton et al. (2005), a theory later supported in both solitary and social species. This was evidenced by stronger population structuring in maternally inherited mitochondrial haplotypes compared to nuclear loci (López-Uribe et al. 2014; dos Santos et al. 2016; Chapman et al. 2018) and higher female co-ancestry within local populations (López-Uribe et al. 2015). Garcia Bulle Bueno et al. (2022) found that males of a social bee, exhibit homing ranges up to 30 times larger than females, promoting gene flow across wider areas. Male-biased dispersal is well-documented in Hymenoptera and can mitigate genetic differentiation by enhancing connectivity among populations (Paxton 2005; Garcia Bulle Bueno et al. 2022). Some mechanisms underlying this pattern have been explored; for instance, Vereecken et al. (2007) found that male bees preferentially responded to female pheromones from geographically distant populations over those from their own in a solitary species. In contrast, females are typically highly philopatric, likely contributing to the observed population structure.

Table 2 AMOVA showing the partition of genetic variation. Populations consist of samples pooled according to Spatial cluster (nearest neighbor-distance assignment). Significance level is based on 20,000 permutations

Source of variation	Df	Sum of squares	Variance components	% variation	Fixation indices	*p*
A. haemorrhoa						
Among spatial clusters	9	3.102	0.018	0.55	F_{ST} = 0.005	1.0
Within spatial clusters	204	159.987	0.298	9.11	F_{IS} = 0.091	< 0.001
Within individuals		139.500	2.985	91.44		
Total	213	302.589	3.264		F_{IT} = 0.086	< 0.001
A. nigroaenea						
Among spatial clusters	2	4.657	0.017	0.54	F_{ST} = 0.005	1.0
Within spatial clusters	134	488.645	0.507	16.26	F_{IS} = 0.161	< 0.001
Within individuals	137	360.500	2.613	84.28		
Total	273	853.803	3122		F_{IT} = 0.157	< 0.001

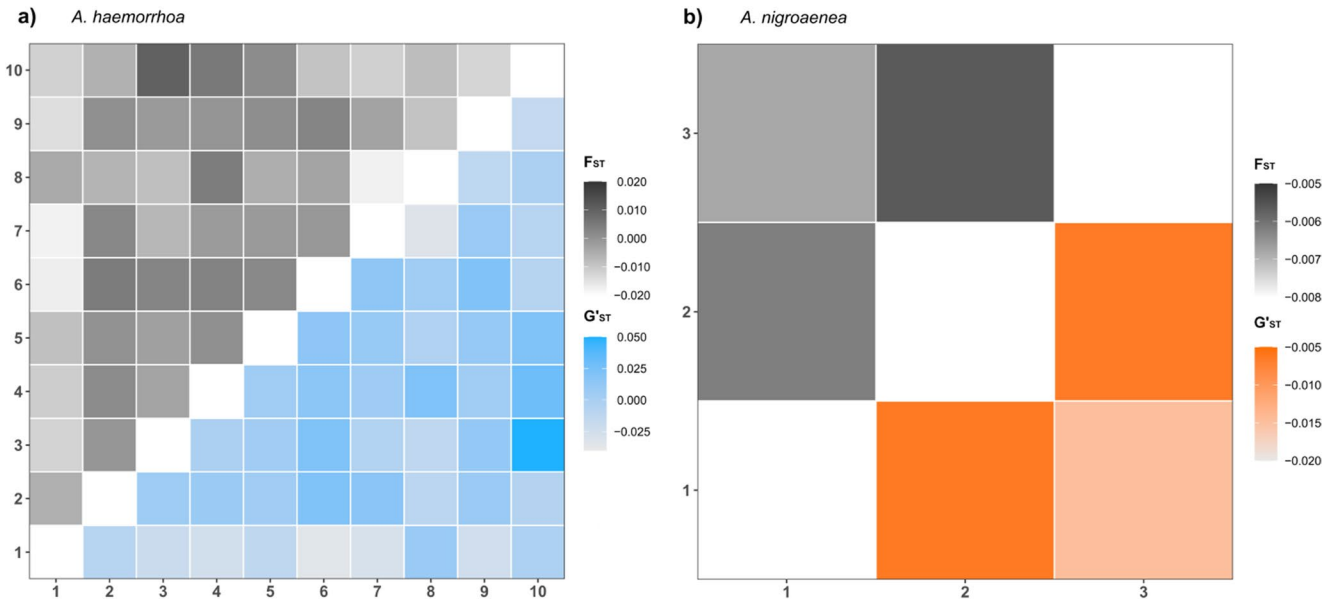

Fig. 3 Heatmaps illustrating pairwise F_{ST} (above the diagonal) and G'_{ST} (below the diagonal, adjusted for within-population heterozygosity; Hedrick 2005) among spatial sampling clusters of (**a**) *Andrena haemorrhoa* and (**b**) *Andrena nigroaenea*. All values are non-significant at α = 0.05

In line with this, our findings show that global F_{ST} values between DAPC clusters were low in both species, suggesting that while genetic structure is present, it is not pronounced. Another factor to consider is mating behavior, including pre-emergence intranidal mating with nest-mates. This is often linked with protandry – where males become reproductively active before females – promoting mating among siblings. This behavior has been observed in communal species such as *Andrena jacobi*, *Andrena agilissima*, and *Macrotera portalis* (Paxton and Tengö 1996; Paxton et al. 1999; Danforth et al. 2003) and could potentially explain the occurrence of distinct genetic clusters without spatial pattern. However, whether solitary species like *A. haemorrhoa* and *A. nigroaenea*, exhibit intranidal mating remains to be examined, as previous studies have underscored the role of social structure in shaping population structure and gene flow in bees (Danforth et al. 2003; Grüter and Hayes 2022).

Effects of landscape and isolation by distance

Our findings closely align with fine-scale population genetic studies on larger wild bees such as bumble bees, which show weak isolation by distance (IBD) and increased gene flow at scales below 10 km (Jha and Kremen 2013; Dreier et al. 2014). In contrast, clearer patterns of geographic genetic structuring and significant IBD tend to emerge at broader spatial scales, as highlighted by Lecocq et al. (2017), who found IBD in eight out of nine *Bombus* species across regional to continental extents based on inter-individual genetic distance. These findings underpin the importance of spatial scale in shaping patterns of spatial differentiation. The observed lack of a strong IBD pattern in our study suggests that gene flow occurs over distances of 15 km, sufficient to prevent spatial genetic structuring even in smaller-bodied species such as *A. haemorrhoa*. Least-cost

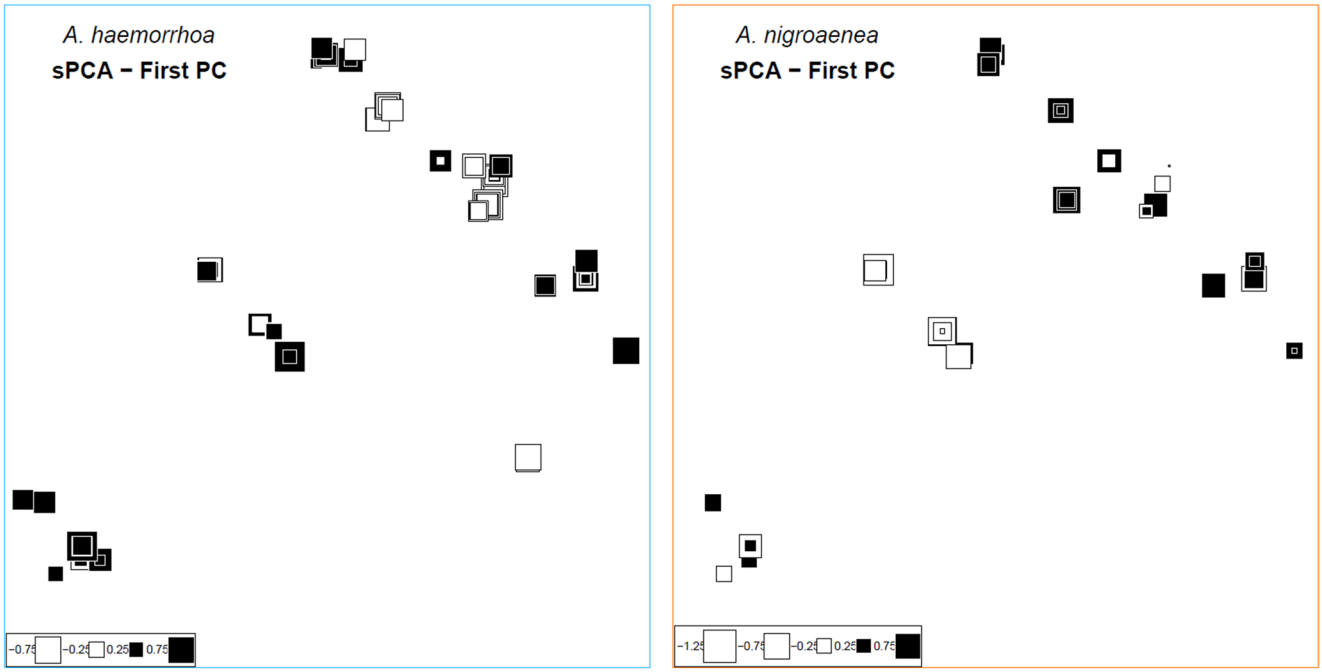

Fig. 4 Spatial principal component analysis (sPCA) results illustrating genetic population structure of (**a**) *Andrena haemorrhoa* and (**b**) *Andrena nigroaenea* in space based on the first (global) sPCA component. Individual scores are represented by squares, with black squares contrasting from white squares based on differentiation (i.e., negative vs. positive values), and square size indicating score magnitude. Mantel tests for global and local structure were insignificant in both species (*A. haemorrhoa*: $r_G = 0.007$, $p = 0.618$, $r_L = 0.007$, $p = 0.519$; *A. nigroaenea*: $r_G = 0.012$, $p = 0.4658$, $r_L = 0.01$, $p = 0.836$)

path (LCP) analyses indicated a weak but significant correlation between genetic distance and landscape resistance in *A. haemorrhoa*, suggesting that habitat features, rather than mere geographic distance, may influence dispersal. As optimal foraging theory predicts, mobile organisms should maximize energy gain while minimizing travel costs (Pyke 1984). Accordingly, previous studies have shown that effective distance – rather than Euclidean distance – better predicts genetic connectivity, as bees adjust their movement patterns based on habitat availability and resource distribution (Kendall et al. 2022). Again, we found no evidence that the larger *A. nigroaenea* is influenced by landscape resistance, suggesting that its increased dispersal capacity may mitigate the effects of limited resource availability in the study site. Also, species with limited dispersal capacity may cope with increased habitat fragmentation by increasing their movement range in resource-poor environments, as seen in butterflies and flies (Lander et al. 2011; Evans et al. 2020). However, if *A. haemorrhoa* exhibits shorter foraging ranges than *A. nigroaenea*, it may experience stronger genetic structuring in fragmented landscapes. The observed relatively weak landscape effects indicate that natural dispersal pathways (e.g., hedgerows, copses, groves, and meadows) could potentially facilitate connectivity, reducing the impact of habitat fragmentation (Bergholz et al. 2022). Additionally, body size interacts with landscape structure in complex ways. Recent studies suggest that landscape simplification can drive body size reductions in bees (Grab et al. 2019), which could in consequence create a negative feedback loop where smaller bees have lower dispersal ability, further reducing gene flow. Body size variation within and among populations may therefore affect landscape connectivity.

Conservation implications

Our findings emphasize the importance of understanding dispersal and genetic structure in solitary bees for conservation planning. While both species maintain gene flow across the study region, the small but significant IBR signal in *A. haemorrhoa* suggests that even moderate landscape resistance may impact smaller-bodied pollinators. This highlights the potential importance of preserving or enhancing habitat connectivity, especially under ongoing agricultural intensification. Multiple life-history traits shape the resilience of wild bee populations in heavily altered landscapes. Factors such as dietary breadths and seasonality can either amplify or buffer the impacts of limited dispersal ability (Bommarco et al. 2010). Thus, dispersal ability influences a population's vulnerability to habitat fragmentation and may partially account for variations in population declines. Here, ground-nesting bees in particular may benefit from

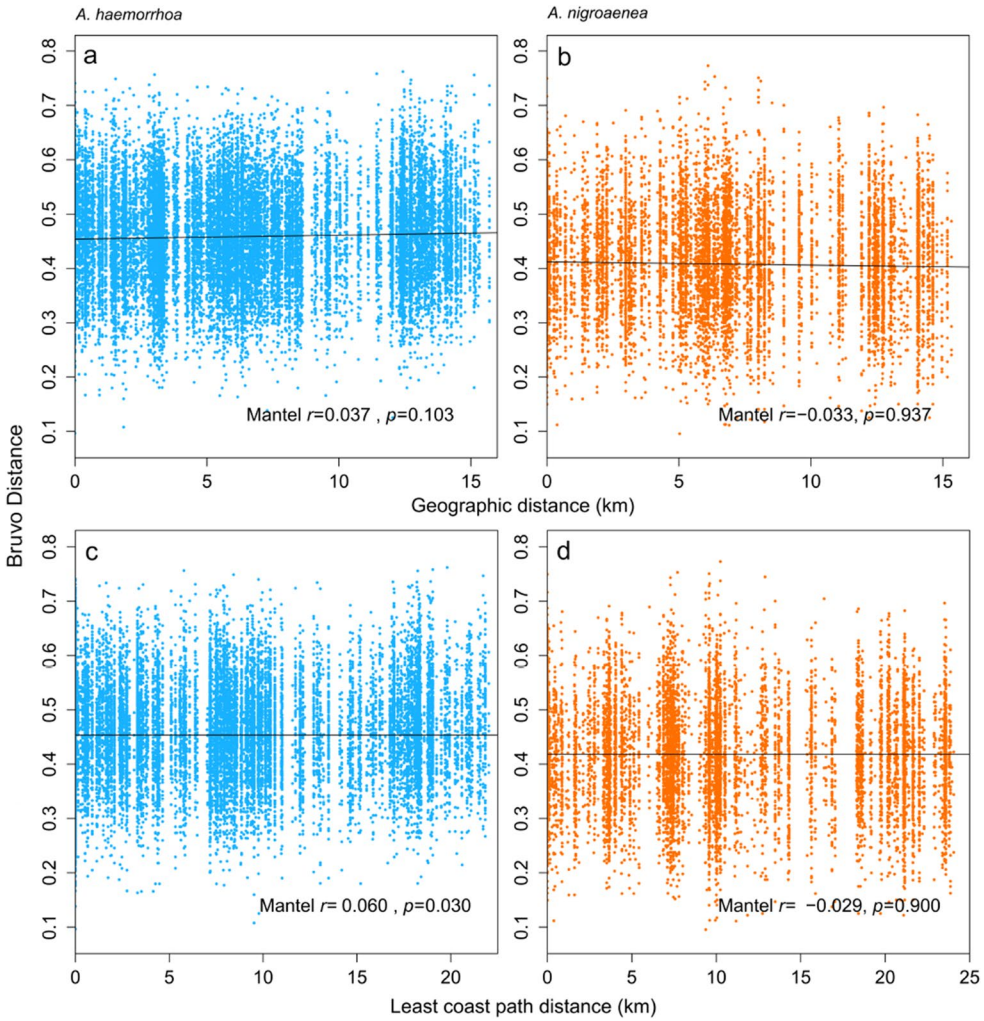

Fig. 5 Associations between geographic distance (**a**, **b**) and least cost path distance (**c**, **d**) with individual genetic distance (Bruvo) for *Andrena haemorrhoa* (a, c) and *Andrena nigroaenea* (b, d)

improved nesting conditions due to increased edge habitat around kettle holes (Everaars et al. 2018). Conservation should therefore focus on maintaining high-quality habitat patches and corridors that provide well-connected foraging resources to promote functional connectivity (Jha and Kremen 2013) in intensive agricultural or highly urbanized regions. Fine-scale studies that explicitly track gene flow and identify barriers will aid conservation by informing optimal landscape management strategies (Lozier and Zayed 2017). Combining genetic data with ecological modeling will further improve our understanding of how landscape changes affect pollinator populations, and ultimately communities (Schlägel et al. 2020; Smith et al. 2023). Additionally, population-level genetic studies can help identify vulnerable species by assessing genetic diversity trends and dispersal limitation (Cameron et al. 2011; Lecocq et al. 2017). While the microsatellite markers used in this study proved well-suited for detecting genetic differentiation and assessing gene flow in the investigated species, SNP-based approaches may offer valuable refinements in future landscape-scale studies in bees, particularly for detecting more subtle patterns (e.g. Parejo et al. 2018; Heraghty et al. 2023). Also mark-recapture approaches have become increasingly valuable for estimation local abundances, and could be extended to studying bee movement and dispersal, with recent advancements improving their efficiency and accuracy (Briggs et al. 2022). Amid ongoing wild bee declines, integrating genetic research into conservation strategies is essential for understanding, maintaining and enhancing pollinator biodiversity.

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Author contributions M.T., R.T., and S.L.G. conceived and designed the study. S.L.G. collected the samples. T.S and V.M carried out the laboratory work with support from A.E and M.T. M.T. and T.S. analyzed the data with input from R.T. M.T. created the figures and wrote the manuscript with contributions from R.T., T.S., J.J., S.L.G., V.M., and F.J. All authors have read and approved the final manuscript.

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Data availability All data supporting the findings of this study are provided in the supplementary materials: Appendix S1 (Appendix_S1.pdf) and Appendix S2 (Appendix_S2.xlsx).

Declarations

Competing interests The authors declare no competing interests.

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