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On the spatial clustering of behavioural phenotypes: matching movement tactics with landscape structure in a large herbivore

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In the wild, individuals consistently differ in movement and space use behaviours, depending on their personality. This variation can lead to personality–habitat associations and spatial structuring, potentially generating individual niche segregation. We explored the link between personality and landscape composition and structure in a population of free-ranging roe deer *Capreolus capreolus*, predicting that 1) individuals with similar movement tactics would occupy similar ecological niches, which should result in 2) the spatial clustering of personalities in heterogeneous landscapes with personality-alike individuals being closer to each other in space than by chance. Using GPS and activity data from 263 roe deer, we calculated five movement-based personality traits. We evaluated the association between movement phenotypes and habitat by comparing the among-individual similarity in movement behaviour to their similarity in home range composition and structure. Additionally, we conducted spatially-explicit analyses to quantify the spatial clustering of these traits. Our results reveal that individuals with similar daytime use of open habitats, an indicator of boldness, occupy the same ecological niche with respect to woodland availability and habitat homogeneity, leading to strong spatial clustering in this trait. In contrast, home range size, average movement speed and road diurnality (i.e. an individual's propensity to get closer to a road during daytime), were spatially structured only at a small-scale. Additionally, we found no spatial structure in activity level, and neither activity nor road diurnality were associated with landscape composition and structure. Matching movement-based personality traits with landscape features revealed spatial clustering of personalities. This non-random distribution could have implications for managing wild ungulate populations, segregating ecosystem services (e.g. nutrient fluxes) and disservices (e.g. road collisions) across the landscape.

Keywords: boldness, habitat, landscape composition, landscape heterogeneity, movement syndrome, personality-environment association

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Introduction

Movement and space use behaviours play a crucial role in wild animals, acting as the first line of behavioural adjustment through which individuals cope with environmental changes (Buchholz et al. 2019). Yet, not all individuals within a population exhibit the same movement and space use behaviours and there are often marked differences in behavioural expression within a single population. Among-individual differences in average behaviour that are consistent over time and across situations are termed personality (Réale et al. 2007) and may covary in behavioural syndromes (Sih et al. 2004). Specifically, movement syndromes have been identified that link several movement, activity and space use behaviours (Hertel et al. 2019, 2020, Khazar et al. 2025), characterising consistent individual movement tactics. Hence, a given individual cannot exhibit the entire spectrum of behavioural responses to varying environments, but rather is constrained by its personality (Sih et al. 2004), leading to the co-existence of behavioural phenotypes in a population that are potentially non-randomly distributed across environments generating a phenotype–environment covariance.

At least three non-exclusive mechanisms could potentially be at the root of the observed phenotype–environment covariance (Nicolaus and Edelaar 2018). First, behaviours such as movement and space use tactics are labile traits that can be flexibly adjusted depending on local conditions (Tuomainen and Candolin 2011): an individual with a given genotype can adaptively alter its phenotype as a response to varying environmental cues (Ghalambor et al. 2007), leading to a phenotype–environment association. Observed personality differences in the wild could thus solely result from landscape heterogeneity. Second, the personality-matching habitat choice hypothesis posits that personality differences drive variation in habitat preference, so that individuals with similar personalities or movement tactics occupy similar local habitat contexts (Carrete and Tella 2010). For example, there is increasing evidence that individuals who disperse, leaving their natal home range to settle in a spatially distinct adult range, choose their habitat depending on their behavioural phenotype, effectively matching their adult home range composition and structure to their personality (Davis and Stamps 2004, Jacob et al. 2015). Finally, personality–habitat associations could also occur due to the natural selection of certain personalities in specific habitats. In a heterogenous landscape, individuals may have a different fitness depending on the habitat that they occupy (Lapiedra et al. 2018). In this microevolutionary scenario, different personalities experience higher survival and/or reproductive success in different habitats (Dingemanse et al. 2004, Monestier et al. 2015). Assuming movement and space use behaviours have a genetic basis (e.g. non-zero heritability, Gervais et al. 2020), this could lead to individuals occupying only a small portion of the population or species' niche (i.e. individual niche specialisation; Costa-Pereira and Shaner 2025) in the absence of any behavioural plasticity or individual choice. For example, in free-ranging bank voles *Myodes glareolus*, bold individuals not only differed in the size of their home range and their movement patterns compared to shy individuals, but different personalities also expressed divergent microhabitat preferences, resulting in individual ecological niche specialisation (Schirmer et al. 2019). In their study on dunnocks *Prunella modularis*, Holtmann et al. (2017) identified the mechanism behind the observed personality–habitat association in the population as personality-matching habitat choice rather than behavioural plasticity. Consequently, regardless of the mechanism at play, when a population inhabits a heterogenous landscape, personality-dependent niche specialisation could in turn generate spatial niche segregation, whereby personalities become geographically segregated so that clusters of individuals with similar personalities can be observed (Spiegel et al. 2017). This spatial clustering of movement tactics across a heterogenous landscape could create hotspots of interaction or isolation between individuals, further impacting crucial population processes by, for instance, modifying patterns of predation risk (Quinn et al. 2012), parasite transmission (Boyer et al. 2010), resource exploitation (DiNuzzo and Griffen 2020) or connectivity (Kowalski et al. 2019).

The European roe deer *Capreolus capreolus* is an especially abundant and widespread species of ungulate that exhibits high individual flexibility in behaviour (Lorenzini et al. 2022). Adult roe deer display marked spatial fidelity after the establishment of their home range (Andersen et al. 1998), the area an animal uses for its routine activities (Burt 1943). When and where they have the choice, roe deer can use habitats ranging from closed forests to open agricultural plains and natural meadows, with marked inter-individual differences in space use within populations (Morellet et al. 2011, Bonnot et al. 2015). Personality traits have been identified in this species, with individuals displaying varying coping styles (i.e. response to stress, Monestier et al. 2016), related to space use and movement behaviours (Bonnot et al. 2015, 2018) that correlate into a movement syndrome (Khazar et al. 2025). Hence, based on the movement-based personality traits and the movement syndrome previously described in a European roe deer population inhabiting a highly heterogeneous landscape (Khazar et al. 2025), we tested the hypothesis of an association between personality, or behavioural type, and landscape composition and structure. Using an extensive long-term monitoring data set of 263 wild roe deer in south-western France, we predicted that 1) individuals with a similar movement phenotype would use similar ecological niches (i.e. similar home range compositions and structures, supposing that the home range reflects several dimensions of an individual's ecological niche), resulting in 2) clusters of personality-alike individuals that are closer to each other in geographic space than by chance.

Material and methods

Study site

The study site 'Vallées et Coteaux de Gascogne' is a long-term research area located in southwestern France in Aurignac

(43°13′N, 00°53′E) that spans 19 000 ha. The landscape is highly fragmented, composed of a mosaic of different habitat types, whether open such as agricultural fields and meadows, or closed, with two large forests and several smaller woodland patches. The remainder of the area consists of hedgerows and scattered human habitation interconnected by a dense road network (Hewison et al. 2009). A detailed characterization of land use within the study area was developed using aerial imagery from IGN's BD ORTHO (Institut Géographique National, https://geoservices.ign.fr/bdortho). The landscape harbours varying levels of risk for roe deer, with open habitats that can be considered risky, notably when human disturbance is high during daytime (Bonnot et al. 2013), and closed forests that offer refuge from potential threats. Within the study area, we captured and monitored roe deer in seven local capture sites with contrasting habitat composition and structure (i.e. including predominantly forested, mixed and very open sites; Fig. 1).

Data collection

The data for this study was obtained from the long-term monitoring of a free-ranging roe deer population. Since 2005, individuals have been captured annually during winter (November–March) using drive netting in each of the capture sites. Individuals were tranquilized with acepromazine (Calmivet 0.3cc, Montané et al. 2003) and kept in wooden retention boxes (see Bonnot et al. 2017 for details on capture methods). Each animal was assigned to an age category based on tooth examination: juvenile (less than 1 year old), yearling (1–2 years old), or adult (more than 2 years old, Hewison et al. 1999), and sexed. Roe deer were equipped with GPS collars, programmed to drop-off automatically

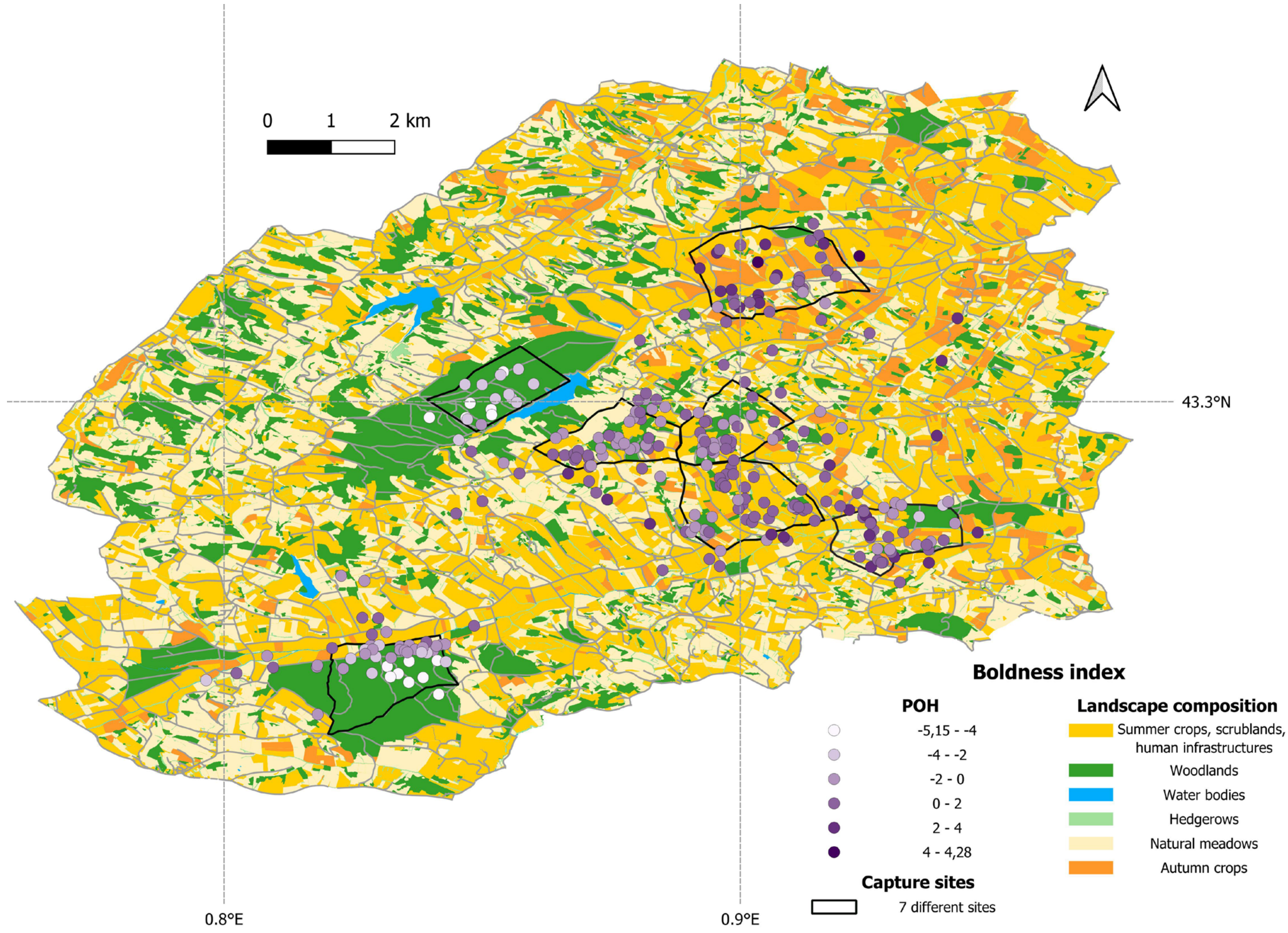

Figure 1. Map of the study site, with the barycentres of the GPS locations for each individual and their associated value for the random intercept of the model describing the probability of using open habitats during daytime (P_{OH}). The seven capture sites are delimited by black lines and the woodland and water features are highlighted in green and blue respectively. Features that are shown in different nuances of orange/yellow correspond to open habitats. This comprises autumn and summer crops, scrublands, natural meadows, hedges and human infrastructures. Grey lines show the road network in the area. The random intercepts are graded, from white for low values of P_{OH} (individuals with a very low probability of using open habitat during daytime) to dark purple (high P_{OH}). The spatial clustering of individuals is readily apparent, particularly in the two large forests, as well as in the more open areas of the landscape.

after 48 weeks for retrieval in the field, and individuals were then released on site.

Pre-processing of the telemetry data

Between 2005 and 2023, roe deer were equipped with Lotek GPS 3300, Vectronic Plus-1C, or Vectronic Vertex GPS collars fitted with activity sensors that recorded activity levels (ranging from 0–255, Bonnot et al. 2020, Benoit et al. 2023b) every 5 min along two axes (X and Y). We programmed the collars with two tracking schedules: continuous GPS fixes every 6 h (four fixes per day at UTC 00:00, 06:00, 12:00 and 18:00 h) throughout the year, from January or February, depending on the date of capture, to December (or earlier in the event of premature termination of tracking due to animal mortality, collar dysfunction, etc., see the Supporting information for the distribution of sampling months over the year) and high-frequency fixes every 10 min during a 24-h period from noon to noon, approximately once a month. We removed aberrant locations based on the method described by Bjørneraas et al. (2010). Individuals monitored for less than a month or with fewer than 50 recorded fixes were excluded from the dataset. Locations from the first seven days post-capture were removed to avoid bias due to temporary changes in spatial behaviour caused by capture (Morellet et al. 2009). This data processing phase resulted in a sample of 321 individuals, consisting of 201 females and 120 males.

Movement traits calculation

To evaluate the spatial structure of movement behaviour in roe deer, we calculated five movement traits using GPS and activity data, that were computed monthly, generating up to 11 repeated measures per individual and year. These traits were previously identified as personality traits, as they are repeatable and vary among individuals in wild roe deer (see Khazar et al. 2025 for more details). On average, we obtained 1125 GPS fixes per individual (SD = 545; range = 141–3733) with the 6-h schedule, 1783 GPS fixes per individual (SD = 1161; range = 151–15 443) with the 10-min schedule and 84 940 activity records per individual (SD = 47 183, range = 361–285 534). The calculation of the traits below was based on a total sample of 2294 individual-months, including 263 individuals with no missing values for any of the five movement traits.

All calculations and analyses were performed using R ver. 4.4.1 and RStudio (www.r-project.org).

- The probability of using open habitats during daytime (P_{OH}) is a space use personality trait linked to boldness (Bonnot et al. 2015). Indeed, open habitats offer abundant food resources, but are perceived as high-risk, particularly during daytime. To measure open habitat use during daytime, we focused on GPS fixes recorded at noon only (note that we removed fixes at 06:00 and 18:00 h as they would alternatively fall during the day or the night depending on the season, resulting in unbalanced sampling across the year). For each individual and month, we divided the number of fixes in open habitats (i.e. every habitat type that is not forest) at noon by the total number of fixes at noon, regardless of habitat type. The probability of using open habitats during daytime ranges from 0 to 1, with bolder individuals typified by a value closer to 1.
- The diurnality of the distance to roads (D_{road}) also serves as an index of boldness in roe deer. We considered individuals that ventured closer to roads during the day compared to their nighttime distance to roads to be bolder, as roads can be perceived as a risk and a significant source of disturbance by roe deer (Padié et al. 2015). We used GPS fixes recorded at noon and midnight to estimate the average distance to roads during daytime and nighttime, respectively. The diurnality of the distance to roads, describing an individual's propensity to be near a road during daytime, when traffic is more intense, relative to its habitual behaviour over the 24-h cycle, was then calculated monthly as follows:

$$\frac{\text{Distance to roads during daytime} - \text{Distance to roads during nighttime}}{\text{Distance to roads during daytime} + \text{Distance to roads during nighttime}}$$

The diurnality of the distance to roads ranged between −1 and 1, with bolder individuals typified by a value closer to −1.

- Home range size (HR size) has been linked to the propensity of an individual to engage in exploration and activity (Villegas-Rios et al. 2017). We excluded individual-months with less than ten locations (Börger et al. 2006) from the analysis and estimated home range size with the kernel method at the 90% isopleth (Worton 1989) with the *hr_kde* function ('amt' package, Signer et al. 2019), using the reference smoothing parameter (ad-hoc method defined by Worton 1989 and Signer et al. 2019). To exclude individuals with non-sedentary movement, for which home range calculation is invalid (Börger et al. 2008, Patin et al. 2020), we calculated the net squared displacement (NSD) over time for each individual-month. The NSD is used to classify movement trajectories as non-stationary (e.g. dispersion, migration, nomadism) or stationary (Börger and Fryxell 2012). We visually checked NSD distributions to classify individual-months as stationary or not (Bunnefeld et al. 2011). We thus excluded 96 individual-months (50 different individuals; see the Supporting information for the yearly distribution of removed months), ensuring that the home range size estimates used in the analyses were statistically meaningful. Monthly home range size ranged between 1 and 668 ha, with a mean value of 66 ha, with more explorer individuals having a larger home range.
- Average movement speed (AVG_{speed}), used to index an individual's overall mobility level (Gervais et al. 2020), was calculated using GPS data from the 10-min schedule. We determined step length and duration between consecutive locations using the 'amt' package. To ensure representative monthly values, we excluded 24-h periods with fewer than 20 h monitored and individual-months with fewer than 40 steps recorded. Movement speed was

calculated by dividing the step length by its duration, and the average monthly speed was then computed. Monthly average movement speed ranged between 0.02 and 0.87 km h^{-1}, with a mean value of 0.20 km/h, with more active individuals having a higher speed of movement.

- The mean daily overall dynamic body acceleration (ODBA) indexes the general level of activity in terms of energy expenditure (Benoit et al. 2023a, 2023b). Values of activity recorded on the X and Y axes were summed to obtain an activity level between 0 and 510 for each 5-min interval over the whole monitoring duration. These values were then averaged over the month and then multiplied by 288 (the number of 5-min intervals in a 24-h period) to obtain a mean daily value. We removed months with less than 50 values of activity recorded. Monthly ODBA ranged between 1173 and 43 246, with a mean value of 13 571, with more active individuals having a higher mean daily ODBA.

Home range composition and structure

To describe individual home range composition, we used digitalized homogenous polygons extracted from IGN's BD ORTHO database. We categorised habitats into eight classes based on annual field observations: autumn crops (corn, sunflower, sorghum), summer crops (all other crops, including artificial meadows), natural meadows, woodlands, scrublands, hedges, roads and other manmade structures (such as human dwellings and parking areas). For roads, buildings and hedges, we computed the mean distance of an individual's range to each of these features. This involved sampling 10 000 random spatial points within each individual home range (*st_sample* function, 'sf' package, Pebesma 2018) and computing their distances to the nearest road, hedge or manmade structure. By averaging these values per individual, we obtained individual average distances to roads, hedges and human infrastructures. For woodlands, autumn crops, summer crops, natural meadows, and scrublands, we calculated their relative availability within each individual home range by taking the proportion of each habitat relative to the total home range area. Moreover, to describe the homogeneity of individual home ranges in terms of habitat composition (hereafter 'habitat homogeneity'), we calculated a contagion index (based on the above eight habitat categories and using the *lsm_l_contag* function, 'landscapemetrics' package, Hesselbarth et al. 2019), with values close to 100 indexing a very homogenous home range and values close to 0 a highly heterogenous home range.

Finally, to statistically summarize this information describing individual home range composition and structure, we performed a principal component analysis on the above nine metrics, using the *dudi.pca* function ('ade4' package, Dray and Dufour 2007). Results of the PCA analysis are given in the Supplementary material. The first axis explained 46% of the variance, with the proportion of woodland loading strongly on it. This first axis (hereafter PC1) indexes the degree of anthropisation, with positive values indicating home ranges that are in closed and homogeneous habitat, further away from human infrastructures, versus negative values indicating highly heterogeneous home ranges, with less woodland and more cultivated fields, and that are closer to human infrastructure. The second (17%), third (14%), fourth (10%) and fifth (9%) components revealed no additional structure in the data, with none of these four axes standing out (Supporting information), hence we decided to only use the first axis PC1 in subsequent analyses.

Statistical analysis

Movement syndrome and behavioural types

To identify individual behavioural types for each of the movement traits, we used a multivariate Bayesian mixed effect model, with the five movement traits as separate response variables. We controlled for sex, age class (yearling or adult at capture) and mean monthly day length (i.e. seasonal phenology) for each trait to remove confounding effects that could artificially inflate the repeatability of traits (Nakagawa and Schielzeth 2010). We also included the year of monitoring and the identity of the individual as random effects on the intercept to control for repeated observations per year and individual, respectively. We used a binomial family distribution with a logit link function for the probability of using open habitats during daytime and a Gaussian family distribution with an identity link function for the four other response traits. ODBA and home range size were log-transformed and average movement speed was square-root transformed to linearize the data. All continuous fixed effects and response variables were scaled to facilitate model convergence. The model was run over four chains, for 300 000 iterations with a 100 000 warm-up, a thinning parameter of 200 ('brms' package, Bürkner 2017), and uninformative priors. For more details on the model see Khazar et al. (2025). In subsequent analyses, we used the random intercepts extracted from this mixed effect model as a measure of the individual behavioural types and kept the full posterior distributions to propagate uncertainties (Houslay and Wilson 2017).

Ecological niche specialisation: association between movement types and habitat

Because the home range is the area that an individual uses for its routine activities, we supposed that among-individual differences in home range habitat composition and structure should reflect among-individual differences in individual ecological niche, notably in terms of environmental conditions, resources and habitat. The temporal dimension of an individual's ecological niche is not explicitly considered but is partially accounted for in the movement syndrome (i.e. in the probability of using open habitats during daytime and the diurnality of the distance to roads). To assess whether individuals that had similar movement phenotypes also had similar home range habitat composition and structure, and thus evaluate the degree of association between landscape structure and movement phenotype, we calculated between-individual Euclidean distance matrices for each movement trait, as well as for the movement phenotype on the overall movement syndrome (i.e. including the five movement traits). These movement-based distance matrices quantify the proximity of individuals in terms of movement behaviours. To define individual ecological niches, we also calculated between-individual distance matrices in terms of home range habitat composition and structure. Notably, we calculated a distance matrix for each of the following landscape descriptors: the proportion of woodland, the mean distance to roads, habitat homogeneity, as well as the individual coefficients on the first PCA axis of home range composition. Additionally, we computed environmental distances among individuals using all nine landscape composition descriptors calculated to obtain a distance matrix that simultaneously included all the dimensions of home range composition and structure. These environmental distance matrices quantify the proximity of individuals in terms of habitat composition and structure. To assess the correlations between the among-individual movement and environmental distance matrices, we performed a Mantel test with 1000 permutations using the *mantel* function ('vegan' package, Oksanen et al. 2007). We performed these analyses on every draw of the multivariate model, meaning that we used every value of the posterior distribution (4000) of the random intercepts to index the movement phenotype and thus propagate uncertainty between analyses (Houslay and Wilson 2017). The strength of the correlation can be interpreted as the degree of ecological niche specialisation, where a higher value indicates a very strict specialisation (individuals with similar movement types are constrained to a specific niche), whereas a lower value indicates more among-individual variation in ecological niche across individuals with the same movement type. To summarise, we compared six movement distance matrices to five home range description matrices, leading to a total of 30 Mantel tests and thus 30 correlations between matrices.

Spatial clustering of movement phenotypes in the landscape

To assess the spatial clustering of movement phenotypes in the landscape, we used two complementary approaches in spatial analysis: Geary's C (Geary 1954) as a measure of similarity, here in terms of movement behaviour, between an individual and its nearest neighbours and semivariograms. Geary's C offers a global statistic that captures the degree of local spatial autocorrelation, while considering the impact of landscape on individual proximity (i.e. neighbours in forest habitats will be spatially closer than neighbours in open habitats, due to differences in home range size, Lovari et al. 2017). In contrast, semivariograms provide a continuous, distance-based measure of spatial structure to determine the scale over which trait similarity is significant. Geary's C describes the spatial clustering of behavioural types, while the semivariogram evaluates the spatial scale at which this clustering occurs.

To evaluate the level of segregation of phenotypes in space, we calculated the barycentre of all GPS coordinates for each individual and associated it with its behavioural type. To identify spatial structure in movement traits, we first calculated the Geary's C for the entire posterior distribution (4000 draws) using the *geary.test* function ('spdep' package, Bivand 2022). A value of 1 represents the null hypothesis of no spatial structure in a given trait, values between 0 and 1 indicate positive spatial autocorrelation, while values between 1 and 2 indicate negative spatial autocorrelation. Secondly, we calculated semivariances and semivariograms for each movement trait to obtain the matrix of distances between individuals. We used the *variogram* function ('gstat' package, Pebesma 2004) and computed the spatial envelope using 100 permutations. This spatial envelope represents the null hypothesis of no spatial structure in the trait studied and is calculated by randomly permuting coordinates between individuals (i.e. modifying randomly the association between coordinates and behavioural type). We derived credibility intervals for semivariance values by performing the calculations over the 4000 draws of the multivariate model. To reject the hypothesis of spatial independence in a trait, semivariance values must lie outside of the calculated envelope.

Results

Association between movement types and landscape composition

We found significant positive correlations between the probability of roe deer using open habitats during daytime and all the landscape descriptors. This indicates that individuals with similar home range composition and structure had a similar probability of using open habitats during daytime. The strongest correlations were with the proportion of woodland (Mantel correlation statistic, hereafter r, of 0.71 [0.67, 0.75]), habitat homogeneity ($r=0.60$ [0.55, 0.65]) and the overall home range composition and structure indexed by the first PCA axis (PC1, $r=0.57$ [0.52, 0.60], Table 1). We also found a positive correlation between the overall movement syndrome and all landscape descriptors (Table 1), meaning that individuals with a similar home range composition and structure had a similar movement syndrome. Additionally, individuals with similar woodland availability in their home range were also more similar in terms of home range size and average movement speed, as indicated by the strong association of the proportion of woodland in the home range with both home range size ($r=0.18$ [0.13, 0.25]) and average movement speed ($r=0.12$ [0.05, 0.19]). However, the association of both home range size and average movement speed with habitat homogeneity (respectively, $r=0.15$ [0.08, 0.20] and $r=0.11$ [0.04, 0.18], Table 1) and PC1 (respectively, $r=0.13$ [0.08, 0.19] and $r=0.10$ [0.04, 0.17], Table 1) was weaker. Finally, we found no significant correlations of either the diurnality of the distance to roads or the activity level (ODBA) with any of the landscape descriptors. This indicates that individuals with a similar home range composition and structure did not express a similar behaviour with respect to the diurnality of the distance to roads or ODBA.

Table 1. Mantel test results of correlation between matrices of environmental distances and matrices of distances in movement traits. Significant correlations (highlighted in bold) were identified when the credibility intervals (calculated by performing the analysis on the 4000 draws of the posterior distribution) did not include 0. Strong positive significant correlations (> 0.4) are shown in blue and weak or moderate ones (< 0.4) in red. Positive correlations indicate that individuals that have similar movement behaviour tend to occupy the same ecological niches, while negative correlations indicate that individuals that have similar movement behaviours occupy ranges that are more dissimilar in their habitat composition than expected by chance. P_{OH} corresponds to the probability of using open habitats during daytime, D_{road} to the diurnality of the distance to roads, HR size to the home range size, AVG_{speed} to the average movement speed and ODBA to the activity level.

Movement trait						
Landscape descriptor	P_{OH}	D_{road}	HR size	AVG_{speed}	ODBA	Movement syndrome
Proportion of woodland	**0.71 [0.67,0.75]**	−0.02 [−0.05,0.02]	**0.18 [0.13,0.25]**	**0.12 [0.05,0.19]**	−0.01 [−0.03,0.007]	**0.58 [0.54,0.62]**
Mean distance to roads	**0.06 [0.03,0.08]**	−0.02 [−0.05,0.02]	0.03 [−0.03,0.09]	0.001 [−0.03,0.05]	−0.01 [−0.04,0.02]	**0.04 [0.006,0.07]**
Habitat homogeneity	**0.60 [0.55,0.65]**	−0.04 [−0.07,0.004]	**0.15 [0.08,0.20]**	**0.11 [0.04,0.18]**	−0.02 [−0.04,0.003]	**0.49 [0.44,0.54]**
First PCA axis (PC1)	**0.57 [0.52,0.60]**	−0.03 [−0.06,0.01]	**0.13 [0.08,0.19]**	**0.10 [0.04,0.17]**	−0.007 [−0.03,0.02]	**0.46 [0.42,0.50]**
All landscape descriptors	**0.32 [0.29,0.35]**	−0.01 [−0.04,0.03]	**0.08 [0.02,0.14]**	**0.05 [0.004,0.11]**	−0.02 [−0.04,0.003]	**0.26 [0.22,0.29]**

Spatial clustering of movement phenotypes in the landscape

We found that neighbouring roe deer are more similar in their use of open habitat during daytime than expected by chance, as shown by the significant positive spatial autocorrelation observed for the probability of using open habitats during daytime (Geary's C of 0.35, Table 2). This spatial structuring exists across all scales within the study area, i.e. not only are neighbours more similar in their probability of using open habitats during daytime, but the degree of similarity decreases progressively with increasing distance between individuals (Fig. 2). This results in individuals with equivalent probability of using open habitats during daytime values occurring in distinct clusters within the landscape (Fig. 1). The diurnality of the distance to roads, home range size and average movement speed also exhibited significant positive spatial autocorrelation, as indicated by the Geary's C for these traits (respectively 0.71, 0.76 and 0.77, Table 2). The spatial structuring of these traits occurred at low spatial scales (less than 1 km, Fig. 2), even though the wide credibility intervals and the overlap with the envelope indicate that this spatial autocorrelation is weak. Finally, there was a weak negative spatial autocorrelation for ODBA (Geary's C value of 1.09; Table 2). That is, although close neighbours tend to be more dissimilar in terms of their ODBA than expected by chance, the degree of similarity did not depend on the geographical distance between individuals across the study site (Fig. 2).

Discussion

Differences in movement-based personality traits can lead to among-individual variation in habitat preference and niche specialisation (Schirmer et al. 2019), generating spatial clustering of personality traits in the landscape (Spiegel et al. 2017). In this study, we found that roe deer with similar movement traits, particularly those linked to risk-taking, indeed occupied similar ecological niches. Furthermore, we found that individual types were strongly segregated in terms of their boldness across the landscape, forming clusters that may align with spatial structure in landscape composition. In contrast, the spatial structure found for other movement traits, such as activity, exploration and home range size, was weak and occurred at a very small scale, suggesting local behavioural adjustments or fine-scale spatial niche segregation that do not scale up at the landscape level. However, the lack of phenotype–environment association for certain movement traits (notably activity and the diurnality of the distance to roads) indicates that trait inter-correlation within a broader movement syndrome (Khazar et al. 2025) does not preclude trait-specific responses to landscape heterogeneity.

Individual movement types are associated to landscape composition and structure

We found an association between most movement-based personality traits and home range composition and structure. Individuals with similar levels of boldness and exploration

Table 2. Geary's C values for each of the movement traits. The Geary's C measures the spatial autocorrelation among matrices of traits. A value of 1 indicates no significant autocorrelation, thus, to reject the hypothesis of spatial independence, credibility intervals should not include 1. A value below 1 (in blue) indicates positive spatial autocorrelation, i.e. neighbouring individuals are more similar in their movement traits than expected by chance, while a value above 1 (in red) reflects negative autocorrelation. The credibility intervals for each movement trait were obtained by calculating the Geary's C on each draw of the posterior distribution of the multivariate model. P_{OH} corresponds to the probability of using open habitats during daytime, D_{road} to the diurnality of the distance to roads, HR size to the home range size, AVG_{speed} to the average movement speed and ODBA to the activity level.

Movement trait	P_{OH}	D_{road}	HR size	AVG_{speed}	ODBA
Geary's C	**0.35 [0.31,0.38]**	**0.71 [0.65,0.77]**	**0.76 [0.71,0.81]**	**0.77 [0.69,0.85]**	**1.09 [1.05,1.12]**

(characterized respectively by the daytime use of open habitats; Bonnot et al. 2015, and home range size and average movement speed; Villegas-Rios et al. 2017), tend to occupy similar home ranges (Table 1), a proxy of the individual's ecological niche. The association was the strongest for boldness, suggesting that woodland availability, providing refuges for roe deer, highly influences individual niche specialisation. These results are not surprising, as the influence of landscape composition and structure on spatial behaviours has been previously shown in roe deer (Hewison et al. 2001), with individuals in more forested and homogenous landscapes using open habitats less during the day, when human disturbance and associated risks peak (Bonnot et al. 2013, De Groeve et al. 2020). Moreover, the degree of habitat openness may constrain exploration and foraging behaviours. Indeed, while open and heterogeneous habitats are characterised by richer resources that are clumped, woodlands have sparse and less nutritive resources for roe deer (Abbas et al. 2011). This disparity can explain the observed association between landscape composition and structure with movement speed and home range size. However, even though the intensity of habitat use intrinsically depends on its availability in the

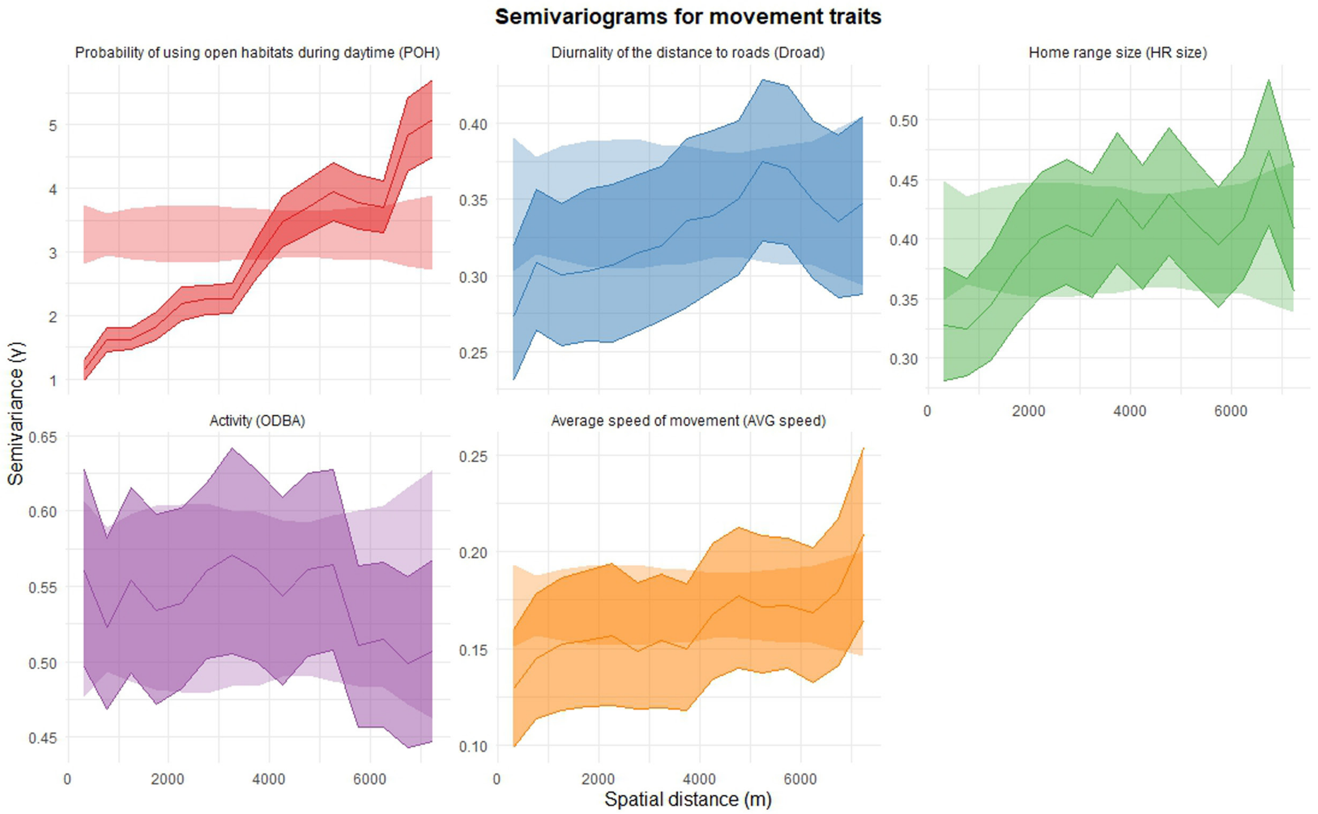

Figure 2. Semivariogram for each of the movement traits. These graphs represent the semivariance γ in movement traits depending on the distance between individuals in meters. The cutoff for the semivariance calculation was set to 7500 m, which is approximately half the diagonal of the squared box encompassing the whole study site (Fig. 1 for a map of the study site with scales). The envelope (lighter horizontal ribbon) was calculated using 100 permutations and indicates the values of semivariance that could be obtained under the null hypothesis of no spatial structure in the data. Thus, when the semivariance curve falls outside this envelope, the hypothesis of spatial independence can be rejected. The credibility intervals around the semivariance (darkerribbon around the curve) were computed by calculating the semivariance for each of the 4000 draws of the multivariate model. Note that the y-axis scales differ between plots.

landscape (i.e. the functional response, Morellet et al. 2011 for roe deer), individual variations in habitat selection do occur (Padié et al. 2015). This suggests that behavioural adjustments are possible for individuals, even when their behaviour is highly constrained by landscape features. Importantly, we focused here on movement behaviour within the home range (third order selection, Johnson 1980), but the choice of home range at settlement (second order selection) could be linked to an individual's behavioural type, in line with the personality-matching habitat choice hypothesis (Carrete and Tella 2010). Studying individuals that, over their lifetime, occupy different habitats with differing landscape composition and structure (e.g. dispersing individuals, or sedentary individuals experiencing environmental changes; Camacho et al. 2015) or experimentally manipulating the phenotype–environment association (Edelaar et al. 2008) could help disentangle the respective roles of plasticity in response to landscape composition and personality-driven habitat matching.

Finally, as for the use of open habitats during daytime, we observed an association between home range composition and structure and the overall movement syndrome. This is probably due to risk-taking in open habitats strongly driving the covariance in the movement syndrome (Khazar et al. 2025). On the other hand, there was no association of the diurnality of the distance to roads or individual activity level with home range composition or structure. Personality–habitat association is a crucial mechanism that can have strong impacts on individuals, for example, reducing intraspecific competition through niche segregation (Kobler et al. 2009). Such segregation may even lead to local population adaptation, notably when assortative mating or sexual selection occurs in the local populations (Schuett et al. 2010) or when dispersal between populations is low (Nicolaus and Edelaar 2018).

Spatial clustering of movement types in the landscape

Phenotype–environment covariance can lead to the spatial clustering of personalities in a heterogeneous landscape (Spiegel et al. 2017). As expected, given the observed association between movement traits, notably linked to risk-taking and habitat, we found a strong spatial structure in the probability of using open habitats during daytime, a boldness trait (Fig. 1). This means that across the landscape, individual roe deer with similar boldness are not only found in the same habitats but also are clustered in the same geographical locations. Boldness has been shown to be the personality trait with the most significant impact on performance (Smith and Blumstein 2008, Moiron et al. 2020). Therefore, following on from this, we might reasonably expect clusters of individuals with similar survival and/or reproductive success in the landscape that align with the spatial structure of open habitat use. For example, if boldness increases the risk of being hunted or victim of a collision, this could potentially lead to clusters of individuals which experience similar fates (Märtz et al. 2024). Moreover, if personalities are partly determined by genetic factors, which seems to be the case for some movement traits in roe deer (Gervais et al. 2020), this personality–habitat association could be driven by an evolutionary response, whereby certain habitats or environmental conditions select for specific personalities (differences in survival or reproductive success, see Monestier et al. 2015 for example). On the other hand, we also found some spatial structure (i.e. positive spatial autocorrelation; Table 2), in home range size, road diurnality and average movement speed, but at a very fine spatial scale (below 1 km, Fig. 1). This small-scale spatial structure could be driven by resource use within a given habitat (Hart and Marshall 2009) or variation in microhabitat features that we did not account for (Schirmer et al. 2019). Therefore, while boldness may reflect a stable, large-scale structure of ecological niche specialisation, these traits may be more context-dependent, with individuals flexibly adjusting these behaviours in response to local conditions (Rusch et al. 2023). In the particular case of the diurnality of the distance to roads, the fine-scale structure appears not to be explained by a personality–habitat association, since no association was found with any of the landscape features studied (Table 1). The observed spatial structure in this trait could be the result of other intrinsic factors, like relatedness (Bradburd and Ralph 2019). Indeed, Bonnot et al. (2010) found that individuals in close proximity were genetically more related, which is consistent with the high spatial fidelity (Lorenzini et al. 2022) and moderate natal dispersal in roe deer (34% of juveniles disperse, Debeffe et al. 2012). Individuals that are immediate neighbours have then a higher chance of being related and also exhibit greater similarity in some of their movement traits. Given the heritability of movement traits such as the distance to roads (Gervais et al. 2020), it is possible that the spatial structure observed in this trait partly reflects genetic relatedness among individuals. Finally, even though neighbouring individuals tended to be more dissimilar in their activity level than by chance (Table 2), this effect was weak and activity level was not associated with habitat, suggesting that this trait could be an individual characteristic (personality-based) that is constrained by other factors (physiology, locomotion or navigation capacity, Nathan et al. 2008), and that does not result in spatial clusters of individuals with similar activity levels.

In conclusion, while home range composition and structure may constrain some movement-based boldness and exploration behaviours, individuals still exhibit variations in personality within a common heterogeneous landscape. Overall, our results align with the conceptual framework proposed by Spiegel et al. (2017), showing that the association between individual differences in fine-scale movement behaviour and landscape composition and structure can lead to the spatial clustering of personalities within a heterogenous landscape. However, in our study, not all movement traits were associated with landscape features and spatially structured to a similar degree. Some movement traits may be more relevant to study than others when considering the spatial structure of personality traits and their consequences. The spatial structure of certain traits, such as boldness, should also be more likely to influence the distribution of ecosystem services or disservices (Hunter Jr et al. 2022, Uchida et al. 2024). Indeed, spatially structured personality traits in a landscape may have a major influence on individual and population processes such as foraging strategies (DiNuzzo and Griffen 2020), parasite transmission (Alexander et al. 2018) or population resilience towards environmental changes (Revilla and Wiegand 2008).

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Data availability statement

Data and the code used for analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sj3tx96jb (Khazar et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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