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Methods

The individualized niche in motion: Quantifying individual specialisation with movement data

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Abstract

Individuals of the same species often differ consistently in their use of resources, their responses to environmental gradients, and their movement decisions. Between-individual variation across niche axes has been shown to have important ecological consequences. However, practical frameworks that translate modern tracking data and space-use patterns into operational, comparable measures of individual specialization in habitat use remain limited. The individualized niche concept has inherited the plasticity of the ecological niche concept, and its quantification is considered a laborious task. Here, a workflow that estimates realized and potential individualized niches from movement data using mixed-effects resource selection functions and niche multidimensional hypervolumes is presented. The workflow combines random-intercept and random-slope resource selection functions with relative selection probabilities and ecological niche indices. The outputs of resource selection functions are used to create a kernel density-estimated hypervolume, and individualized niches are quantified using niche breadth and pairwise niche overlap indices. In addition, repeatability estimates are used to capture consistent among-individual differences and allow direct comparisons between realized and potential niche components. The workflow is implemented exclusively in the programming language R. A case study using publicly available northern lapwing (*Vanellus vanellus*) tracking data illustrates how the workflow can integrate multiple environmental variables, including earthworm abundance, human presence, pesticides, management, soil variables, and vegetation, to characterize individualized niches. The proposed workflow is transferable across taxa of mobile organisms and can facilitate the study of niche specialization and population-level heterogeneity across scales.

Key words: glmmTMB, individual specialization, intraspecific resource partitioning, Jaccard similarity, landscape ecology, Movebank, remote sensing, species–habitat relationships

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Introduction

The ecological niche is a foundational concept in the field of ecology, central to understanding species interactions and environmental relationships. Over time, its definition has evolved, reflecting shifts in ecological theory and perspective. Early uses of the term were imprecise, often referring generally to a species' ecological position, habitat, or requirements. The first formalized definitions of the niche were proposed by Elton (1927) and Grinnell (1928). Elton (1927) conceptualized the niche as the functional role of a species within a community, emphasizing its interactions with other species, an interpretation widely employed

in community and functional ecology. In contrast, Grinnell (1928) defined the niche as the physical space in which a species lives—the habitat or spatial position of a species within the environment. These definitions laid the groundwork for subsequent theoretical developments. The most commonly used definition of the ecological niche was introduced later by Hutchinson (1957), who defined the concept as a hypervolume in an *n*-dimensional environmental space. Moreover, Hutchinson distinguished between bionomic and scenopoetic variables, which roughly correspond to biotic and abiotic factors.

Literature reviews of the niche concept appeared relatively early in the ecological literature (Hutchinson 1978), and its definition has remained a subject of considerable debate. Hurlbert (1981) compiled a list of more than 20 different definitions of the ecological niche, which was recently extended with additional conceptual approaches (Takola and Schielzeth 2022). Despite subtle differences among the existing definitions, there is one characteristic that most have in common: their species-level (or above-species-level) focus. A few exceptions, such as the definitions provided by Roughgarden (1972) and Hutchinson (1957), recognize the existence and importance of intraspecific variation and showcase the use of the niche concept at the population or individual level (Fig. 1).

Historically, intraspecific variation was considered noise around an ecological "optimum." However, later foundational work, coupled with technological and methodological advancements, has shed light on the ecological importance of intraspecific variation (Uchmański and Grimm 1996; Bolnick et al. 2002; Araújo et al. 2007). It is now known that many species exhibit distinct phenotypes that are linked to age, sex, or behavioral differences. The study of individual-level variation is necessary to better understand the dynamics of ecological systems and facilitate causal inference in global-change dynamics and conservation biology (Xuereb et al. 2021; Jeltsch et al. 2025).

Individuals differ in their genotype, morphology, life strategies, dietary habits, or behavior. Multiple studies have focused on examining the behavioral phenotypes (also known as personalities) of different animals and the characteristics of each phenotype (Stamps and Groothuis 2010; Wolf and Weissing 2012; Carter et al. 2013). The field of behavioral ecology focuses on examining these phenotypes within the context of survival and fitness (Smith and Blumstein 2008; Brehm and Mortelliti 2024; West et al. 2025). Consistent individual behavioral differences have been observed in cognition (Bračić et al. 2022), antipredator behavior (Hahn et al. 2023; Winter et al. 2023), breeding behavior (Gladow et al. 2025), and infochemical composition and responses to infochemicals (Müller et al. 2020). Individual niche variation has consequences for inter- and intraspecific dynamics (Dingemanse et al. 2004; Moran et al. 2022; R et al. 2024; Enne et al. 2026), an observation known as the Niche Variation Hypothesis (Van Valen 1965). The Niche Variation Hypothesis suggests that the width of a species' niche is driven by among-individual variation, and this relationship has been empirically demonstrated across multiple taxa (Bolnick et al. 2007). Consequently, individual-level differences are relevant to population-level dynamics and species coexistence (Schirmer et al. 2020).

The term individualized niche emerged at the beginning of the 2010s to describe individual niche specialization or individual niche differences (Fig. 1). Following Hutchinson's distinction between the fundamental and realized ecological niches, an individualized niche can be distinguished as either a realized or potential individualized niche (Takola and Schielzeth 2022), representing the

environmental space where an individual is or could be found, respectively. Behavior is an integral part of individualized niches and can predict resource use in voles (Erixon et al. 2025). Individualized niches emerge through three mechanisms: niche choice, niche construction, or niche conformance (Trappes et al. 2022; Krüger et al. 2026). Experimental studies have shown the prevalence of these mechanisms across multiple animal groups (Singh et al. 2024). For example, early-life experiences shape the individualized niches of guinea pigs, zebra finches, and fire salamanders at later developmental stages through (social) niche conformance (Oswald et al. 2020; Lilie et al. 2022; Mutwill et al. 2023; Rystrom et al. 2024; Liebermann-Lilie et al. 2025; Schulte et al. 2025). Many insect species are known for their niche-construction strategies (Jakobs et al. 2019; Lo et al. 2025; Schulz et al. 2025), while niche choice has been observed in common voles, salamanders, and insects (Petruzzi et al. 2006; Erixon et al. 2025; Nabutanyi et al. 2025). In addition, morphological and developmental variation can give rise to variation in niche choice (Cabon et al. 2025). Individualized niches can emerge through intrinsic factors (e.g., condition) or external factors, such as the social environment, ecological opportunity, or interspecific dynamics (Araújo et al. 2011; Moran et al. 2022; Winter et al. 2023; Kaiser et al. 2024) and have important consequences for the indefinite persistence of species (Bolnick et al. 2003).

Various attempts have been made to quantitatively estimate individualized niches. Depending on the purpose of the study, researchers draw on a variparaxis of analytical methods and modeling approaches (Lowe and Ingram 2023; Trappes et al. 2025). Individual differences in habitat selection have been studied using resource selection functions (RSFs), mixed-effects models, reaction norms, and repeatability analyses, showing that, in some species, individuals consistently choose different habitat types (Aarts et al. 2008; Leclerc et al. 2016; Cuscó et al. 2018; Newediuk et al. 2022). In addition, individual variation increases when resources are of unequal quality (Kikuchi and Reinhold 2021). Resource acquisition and energy dynamics affect the survival of individuals, as well as interspecific dynamics (Costa-Pereira et al. 2019; Szangolies et al. 2024), highlighting the importance of exploring habitat-use patterns at the individual level, also known as spatial personalities (Stuber et al. 2022).

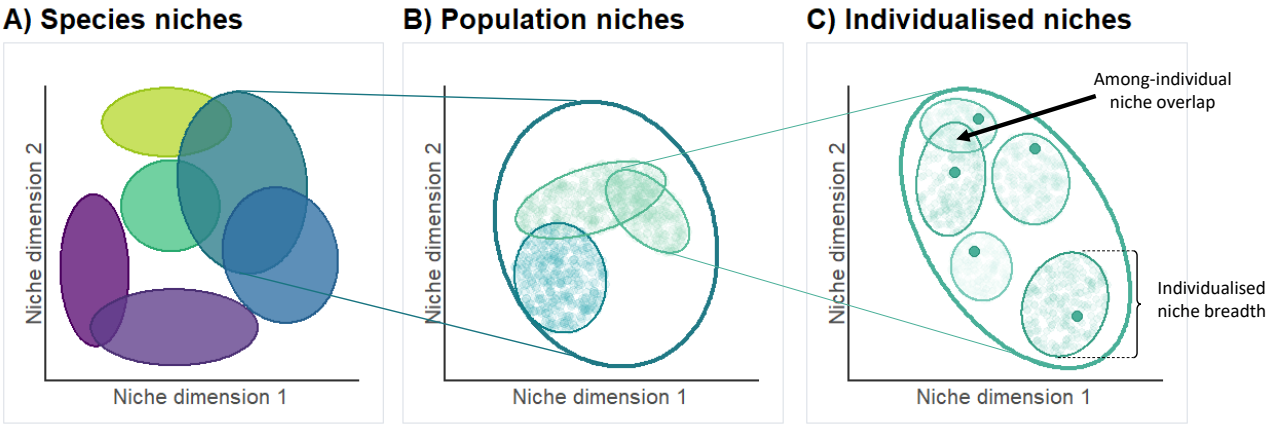

Figure 1. Heuristic representation of the different niche levels. **A.** A community can be represented as a set of species in which each occupies a different niche. **B.** A species can be represented as a set of metapopulations with different niches. **C.** A population consists of multiple individuals with different individualized niches (the potential niche is shown with transparent dots, and the realized niche is shown with bold dots). Adapted from Takola and Schielzeth (2022).

Tracking data shed light on new scientific questions (Nathan et al. 2022; Trappes 2023; Beltran et al. 2025), and RSFs are particularly useful for studying individual specialization (Carlson et al. 2021). Existing approaches for quantifying individual variation in resource use, such as conditional logistic models combined with kernel-density hypervolumes (Carlson et al. 2021), individual-level RSFs combined with random forests (Bastille Rousseau and Wittemyer 2019), and species- and season-specific RSFs combined with individual hypervolumes to assess specialization, nestedness, and clustering (Caldwell et al. 2026), provide valuable tools for detecting statistical differences among individuals in environmental use or selection. The first study frames individual niches in relation to the Grinnellian niche, building the environmental niche model using tracking and accelerometer data; the second draws on Hutchinson's hypervolume concept but analyzes heterogeneity in selection behavior using random forests; and the last uses only observed habitat use to create hypervolumes. However, these approaches generally operationalize individualized niches empirically through patterns of realized use or behavioral response rather than using concepts such as the realized and fundamental (or potential) niches.

The aim of this paper is to provide an operational workflow for the individualized niche concept based on movement data. Takola and Schielzeth (2022) defined the concept using schematic diagrams and empirical examples, whereas the present study translates that concept into a movement-data workflow for empirically estimating realized and potential individualized niches. In other words, the present paper provides an integration of existing statistical tools and hypervolume exploration methods with a published formal definition of the individualized niche and proposes a practical application based on GPS tracking data. Quantitative frameworks that systematically analyze intraspecific variation can help build cross-scale conceptual bridges. The workflow is demonstrated using movement data from northern lapwings (*Vanellus vanellus*) in Western Europe.

A proposed workflow to estimate individualized niches

Overview

The aim of the proposed workflow (Fig. 2) is to quantify individualized niches and produce quantitative outputs that can be further used in ecological studies. It incorporates tools from ecological niche modeling, behavioral ecology, and spatial ecology. It can be implemented entirely in the R programming environment (R Core Team). The workflow has three stages: data preparation, analysis, and output generation.

Data structure and preprocessing

Data preparation includes the generation of used and available points from GPS tracking data. The recorded GPS locations correspond to used locations, and the available locations can be generated randomly within a specific radius, depending on the organism's dispersal rates. Subsequently, these points should be overlaid with all selected environmental variables. The resulting dataset is the input for all further analyses. Each row of this dataset corresponds to a used or available position of a particular individual. Environmental predictors can be measured,

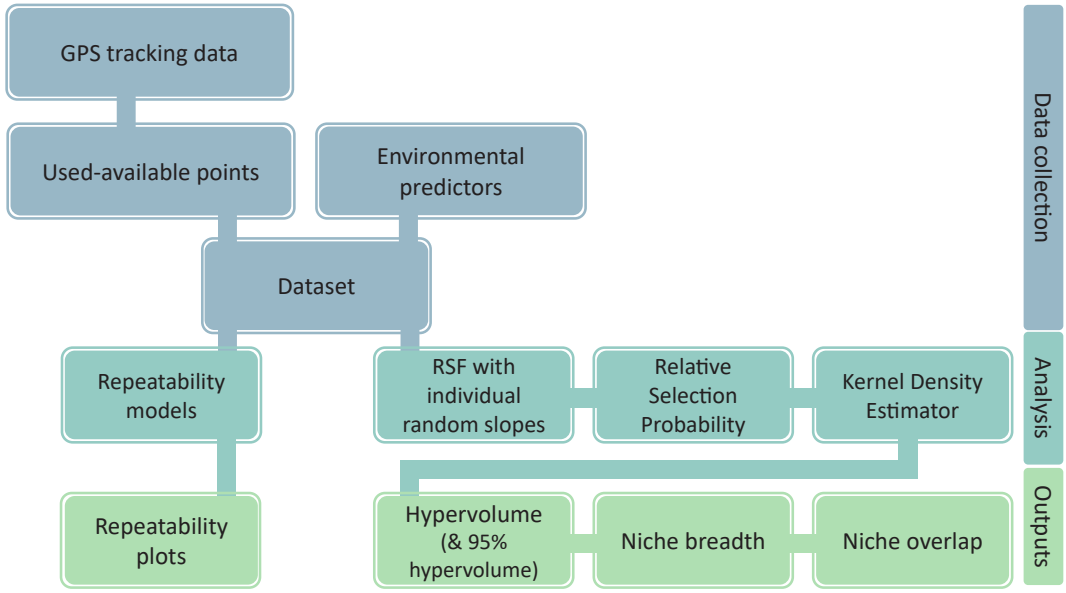

Figure 2. Graphical representation of the proposed workflow.

inferred, or calculated—usually with the aid of remote-sensing tools—for each location and then grouped based on resource type (e.g., food, soil, and weather).

Mixed-effects RSFs with random slopes per individual

After compiling the dataset, the first step is to implement a mixed-effects resource selection function (RSF) for each resource-type group using a binomial model with a logit link in glmmTMB (McGillycuddy et al. 2025). The response variable of all models should be binary (available vs. used locations), and each model should contain the predictors relevant to the corresponding resource type, along with random intercepts and random slopes for each individual. The random intercepts are used to capture baseline differences among individuals, whereas random slopes are included to estimate individual variation in the strength of selection along each environmental gradient. The model results represent (i) population-average effects that describe selection and (ii) individualized deviations that quantify consistent among-individual differences in selection along specific environmental axes.

For each resource domain, a binomial generalized linear mixed model was fitted to distinguish used from available locations. The response variable was the use–availability status of each sampled location. For animal α at location *j*, the response variable was

$$Y_{a,j} = Bernoulli\,(p_{\alpha,j}),$$

where $Y_{a,j} = 1$ denotes a used location and $Y_{a,j} = 0$ denotes an available location. The parameter $p_{\alpha,j}$ is the probability that location j was used by animal a.

This probability was modeled using a logit link, such that the probability of use was related to the linear predictor on the log-odds scale

$$\text{logit}\,(p_{a,j}) = \eta_{a,b}.$$

Thus, $\eta_{a,j}$ represents the predicted log-odds of use for location j by animal a.

The linear predictor included the fixed effects of the environmental predictors, an individual-specific random intercept, and individual-specific random slopes for selected predictors

$$\eta_{a,j} = \beta_0 + \sum_{k=1}^{K} \beta_k x_{a,j,k} + b_{0,a} + \sum_{k \in S} b_{k,a} x_{a,j,k}.$$

Here, $x_{a,j,k}$ is the value of environmental predictor k at location j for animal α, K is the total number of predictors in the model, and S is the subset of predictors for which random slopes were fitted (i.e., the group of variables corresponding to a specific niche type). The coefficient β_0 is the fixed intercept and β_k is the fixed effect of predictor k. The term $b_{0,a}$ allows the baseline probability of use to vary among animals, whereas $b_{k,a}$ allows the strength and direction of selection for predictor k to vary among animals.

For predictors with individual-specific selection slopes, the random slopes were modeled as

$$b_{k,a} \sim N\left(0, \sigma_0^2\right), \qquad k \in S$$

These terms allow animals to differ in their responses to selected environmental predictors. Predictors not included in S, the subset of predictors in a particular niche type, had only fixed effects and therefore shared a common population-level response across animals.

Although the predictor set differed among resource domains, all models followed the same structure. Interaction terms, where included, were treated as additional predictors in the linear predictor. Resource-selection predictions were obtained by converting the fitted linear predictor from the logit scale back to the probability scale

$$\hat{p}_{a,j} = \frac{\exp\left(\hat{\eta}_{a,j}\right)}{1 + \exp\left(\hat{\eta}_{a,j}\right)}.$$

Thus $\hat{p}_{a,j}$ represents the fitted probability of use for location j by animal α, conditional on the environmental predictors and the estimated individual-specific random effects. These predicted values were subsequently used as observation-level weights in the niche hypervolume analyses.

Relative selection probabilities (RSPs)

As described previously, for each resource group, the fitted mixed-effects RSF was used to predict an individual-specific linear predictor, η, for every used and available point. These predictions were derived from the full RSF model and therefore included both fixed effects and individual-level random effects. Thus, η represents the predicted relative selection score of each row for a given individual and resource group. This linear predictor was subsequently converted into a scaled relative selection probability (RSP) as follows

$$RSP_i = \exp\left(\eta_i - \max\left(\eta_i\right)\right),$$

Where RSP_i is the relative selection probability that each resource type (food, soil, and weather) will be chosen by an individual i and η_i is an individual's score

of the corresponding resource type, based on the output of the mixed-effects RSFs. This scaling sets the maximum predicted selection value for each individual to 1, while all other rows are expressed relative to that maximum. The resulting RSP values therefore represent individual-specific relative selection strengths rather than absolute probabilities of use and were used as weights in the subsequent individualized niche estimation.

Weighted hypervolumes of individualized niches

For each resource type, weighted hypervolumes can be created by transforming each ecological group into a standardized multidimensional environmental space. The weights used here are the normalized RSPs calculated from the RSF output for each individual. The hypervolume is calculated separately for each individual using Gaussian kernel density estimation and Silverman's bandwidth estimator. As a result, different points in the environmental space have different probabilities of being selected by each individual, allowing for among-individual variation. These plots serve as diagnostics of (i) separation among individuals, (ii) the degree of overlap among realized conditions, and (iii) whether high-selection subsets are concentrated or diffuse in environmental space.

For each resource type (r), an individual i and a niche component (c), the weight that is introduced in the hypervolume is

$$w_j = \frac{RSP_j}{\sum_{j=1}^{N} RSP_j}.$$

The weighted hypervolume of each individual is then

$$\hat{f}_{r,a,n}(x) = \sum w_j K_h (x - x_j),$$

where x_j represents the environmental predictor values for row/location j, w_j is the normalized RSP weight for that row, K_h is the Gaussian kernel with bandwidth h, and $\hat{f}_{r,a,n}$ is the weighted environmental density used to define the hypervolume.

Because the hypervolumes are constructed using a density estimate, their boundaries are continuous, potentially hindering the calculation of niche breadth. For the calculation of niche breadth, it is useful to convert the continuous boundaries to hard boundaries by selecting the region of the hypervolume that contains 95% of the probability estimates (Blonder 2018). The hypervolumes can be created either for one individual across time or separately for each season.

Based on the definition of individualized niches, a point in the environmental space belongs to the individualized niche only if it allows the focal individual to expect high reproductive success. As a result, not all of the environmental space used by an individual is part of the individualized niche hypervolume. Estimating an individual's expectation is more difficult than estimating fitness outcomes (see Bračić et al. 2025). However, multiple studies have linked habitat preferences to survival (DeCesare et al. 2014; Catlin et al. 2019) and fitness outcomes (McLoughlin et al. 2006), supporting the connection between high RSPs and high expected lifetime reproductive success (Gaillard et al. 2010; Uboni et al. 2017).

Quantifying individualized niches: breadth and overlap

Niche breadth (MacArthur and Levins 1967) and niche overlap (Jaccard 1901) are among the most important tools for studying relationships among species under the limiting similarity hypothesis. In the present study, niche breadth is the within-individual variation in potential and realized individualized niches, while niche overlap among individuals provides insights into intraspecific competition and niche partitioning along different environmental axes. They roughly correspond to the within-individual and between-individual variance components proposed by Roughgarden (1972).

Niche breadth can be calculated separately for potential and realized niches. The breadth of a potential niche is not necessarily larger than the breadth of the realized niche, contrary to the traditional definition of the fundamental and realized niches of species, in which the realized niche is always a subset of the fundamental niche. This notion has recently been challenged by the "zero-niche paradox" (Matthiopoulos et al. 2015), which describes cases in which animals can survive under conditions that do not belong to the fundamental niche of their species. Within the context of paired observations of used and available points, a realized niche breadth smaller than the potential niche breadth provides evidence of stronger individual specialization.

Niche breadth is defined here as the volume of each individual's 95% hypervolume, as described above, for each resource type.

The 95% hypervolume is defined as

$$H_{0.95} = \left\{ x : \hat{f}\left(x\right) \geq \tau_{0.95} \right\},$$

where $\tau_{0.95}$ is chosen so that the retained region contains 95% of the estimated probability density

$$\int_{H_{0.95}} \hat{f}\left(x\right) dx = 0.95,$$

Niche breadth is then the volume of that hypervolume:

$$B = Vol\left(H_{0.95}\right) = \int_{\mathbb{R}^d} 1\left[\hat{f}\left(x\right) \geq \tau_{0.95}\right] dx.$$

Niche overlap is defined here as the hypervolume overlap between two individuals. It is calculated separately for potential and realized individualized niches. The hypervolumes can also correspond to a specific season.

Jaccard overlap is calculated as

$$J = \frac{Vol\left(H_1 \cap H_2\right)}{Vol\left(H_1 \cup H_2\right)}.$$

If J = 0, there is no overlap between the two individuals, and if J = 1, the individuals have identical resource-use patterns.

The Sørensen overlap index gives greater weight to the shared component than the Jaccard index and is calculated as

$$S = \frac{2 * Vol\left(H_1 \cap H_2\right)}{Vol\left(H_1\right) + Vol\left(H_2\right)}.$$

Repeatability of individual resource use

Repeatability is a useful metric that quantifies the proportion of behavioral heterogeneity that can be attributed to between- and within-individual variance (Schielzeth and Nakagawa 2022; Nakagawa et al. 2026). Here, the R package rptR (Stoffel et al. 2017) is used to quantify the repeatability of the realized and potential individualized niches using 1,000 bootstrap replicates and 1,000 permutations to obtain empirical 95% confidence intervals. Comparing repeatability for used (realized) vs. available (potential) conditions provides a standardized test of individualized niche expression: higher repeatability under realized than potential conditions indicates stronger individual differentiation in use than expected from availability alone.

Implementation notes and limitations

The most important assumptions underlying the workflow are listed below.

i) Individuals move in landscapes that, on average, match their phenotype. There is no extensive phenotypic mismatch. In other words, an individual, on average, makes most decisions based on maximizing expected reproductive success through at least one surviving offspring.
ii) Across all individuals, higher relative selection probabilities correspond to environmental conditions that provide greater expected lifetime reproductive success.
iii) Individualization is supported when realized niches show greater among-individual structure than potential niches, as reflected by higher repeatability, reduced overlap, and narrower breadth in realized environmental space relative to available environmental space.

Case study: the individualized niche of northern lapwings (*Vanellus vanellus*) in Western Europe

Dataset

The dataset used in the present study to showcase the proposed workflow is the same dataset used in a previous study (Esguerra et al. 2025). Northern lapwing movement data are publicly available for Europe through the Movebank database (dataset ID: 1448409403; curator: Jelle Loonstra). The data cover an area spanning the Netherlands, Belgium, England, France, and Spain, and the tracking period extended from April 2021 to March 2023. The number of observations per individual ranged from 28 to 1,266 locations.

The environmental variables used to characterize the individualized niches of northern lapwings were temperature, precipitation, wind speed, normalized difference vegetation index (NDVI), crop type, cropping intensity, soil water index, soil organic carbon, soil organic carbon stock, soil nitrogen, pesticide application rates, resource abundance, population density, human footprint, and earthworm abundance. Importantly, earthworm abundance was quantified here as an earthworm abundance factor. The higher the factor value, the lower the earthworm abundance.

Workflow implementation

The mixed-effects resource selection functions for each resource type showed that northern lapwings avoided densely populated areas and frequently cropped fields but showed strong preferences for certain crop types, water, and high earthworm abundance (Fig. 3).

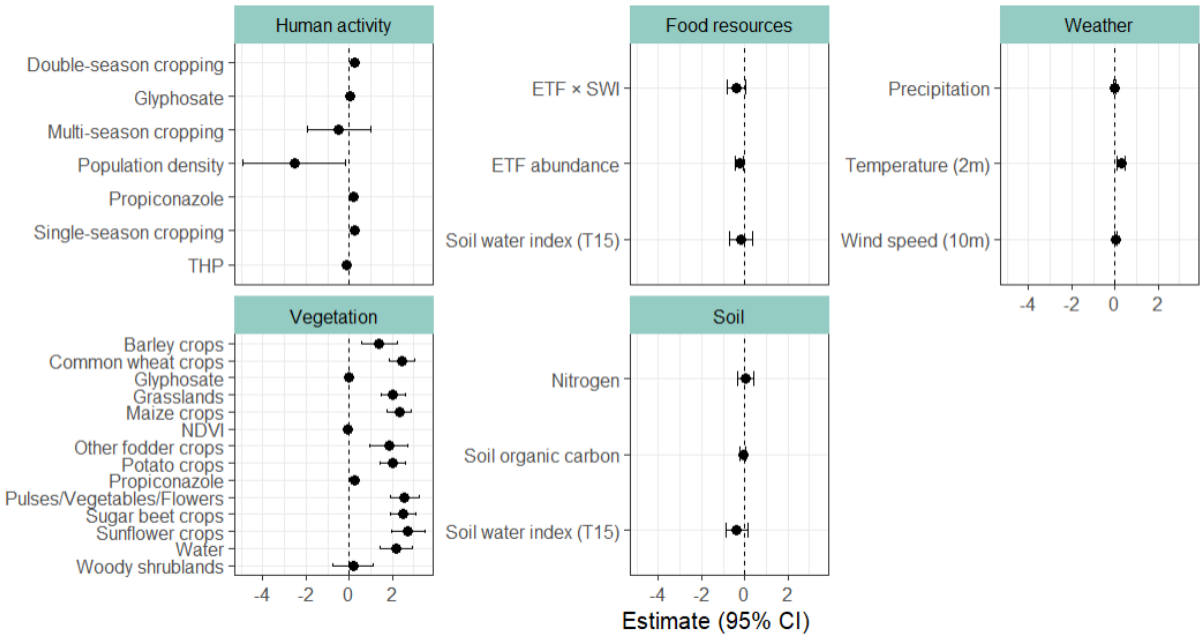

Figure 3. Resource selection function coefficients for each resource type based on the movements of northern lapwings (n = 13). The coefficients represent the population-level averages that describe the strength of selection based on the mixed-effects resource selection functions. The results are based on the entire dataset before filtering.

The resource selection function coefficients (Suppl. material 1: table S1) confirm what is already known about the ecology of the species. To explore individual niche variation in resource selection, it is necessary to incorporate random slopes, also known as reaction norms (Dingemanse et al. 2010), to allow each individual to have a different response to each environmental variable (Fig. 4).

Global individual niche breadth and realized–potential niche overlap were quantified separately for each ecological variable group. For each group, the corresponding group-specific resource selection prediction column was used as an observation-level weight. Thus, food, human disturbance, vegetation, agrochemicals, weather, and soil hypervolumes were weighted by rsp_food, rsp_humans, rsp_veg, rsp_chemicals, rsp_weather, and rsp_soil, respectively.

For each ecological group, a group-specific environmental space was first constructed. Available predictors were retained, rows with missing values for the focal predictors were removed, numeric variables were standardized, and categorical variables were converted to dummy variables. Axes with zero variance were excluded. A single bandwidth vector was estimated from the full group-specific environmental matrix and then applied consistently to all individual hypervolumes within that group. This ensured that differences among individuals and niche components were not caused by changes in kernel bandwidth.

For every individual and ecological group, observations were split into potential and realized niche components using the used–available classification.

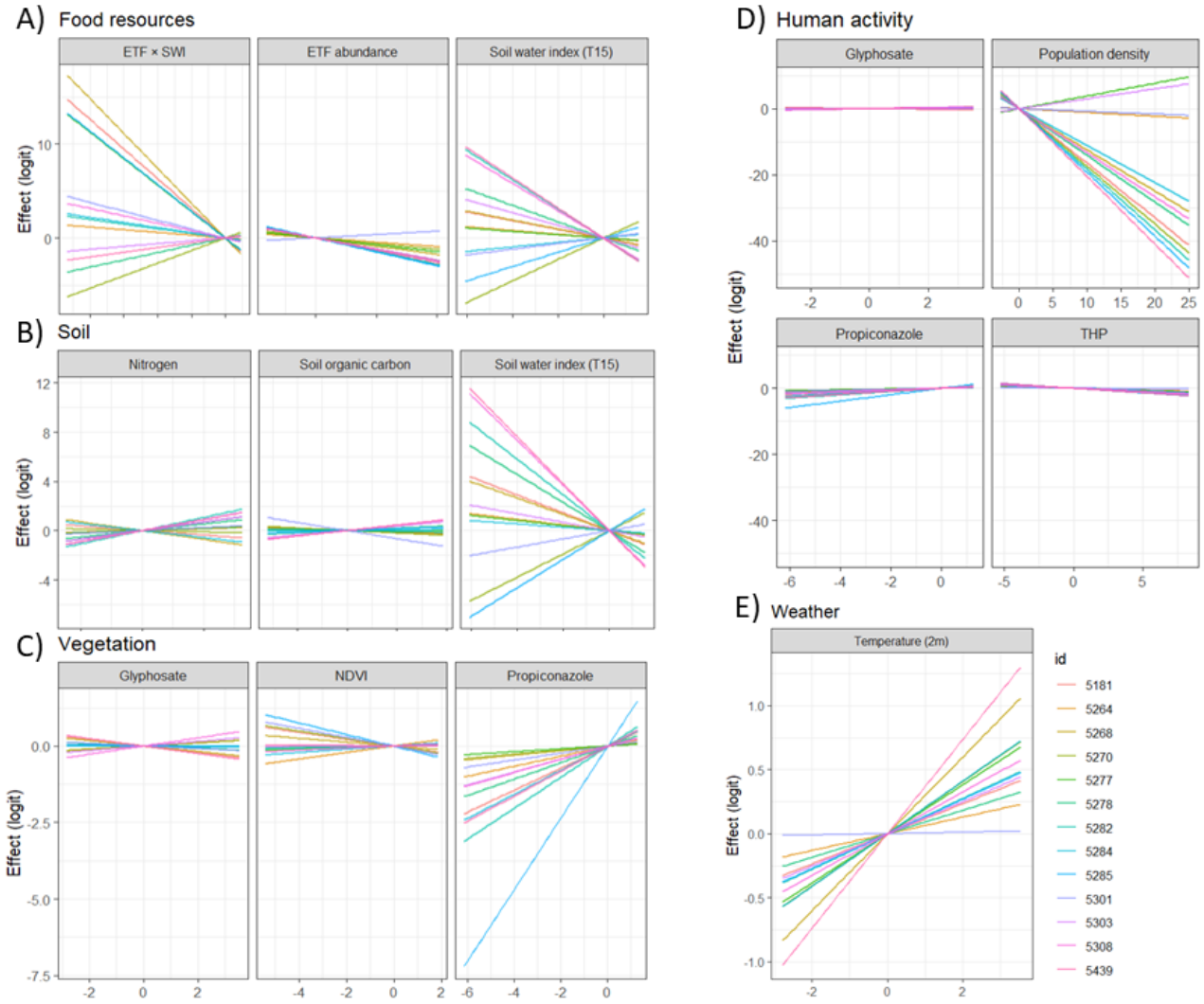

Figure 4. Random slopes (reaction norms) of each northern lapwing (n = 13) and model predictor (facets). The random slopes were calculated using mixed-effects resource selection functions. The results are based on the entire dataset before filtering.

Potential niches corresponded to available observations, whereas realized niches corresponded to used observations. One potential and one realized hypervolume were then estimated per individual using Gaussian kernel density estimation in the full transformed environmental space. Hypervolumes were weighted by the corresponding resource selection prediction values after cleaning and normalization. Nonfinite and negative weights were set to zero, and valid weights were rescaled to sum to one. Hypervolumes were estimated using 100 random samples per observation and thresholded at the 95% probability contour. Hypervolumes were not estimated when fewer than 20 observations or fewer than five observations per hypervolume axis were available.

Individual niche breadth was quantified as the volume of each fitted hypervolume. Breadth was calculated separately for potential and realized niches for every individual and ecological group. Realized–potential overlap within each individual was quantified by comparing the realized hypervolume with the corresponding potential hypervolume. Overlap was summarized using Jaccard similarity, Sørensen similarity, and the fractions of hypervolume space unique to the realized and potential components. These metrics describe, respectively, the proportional overlap between realized and potential environmental space

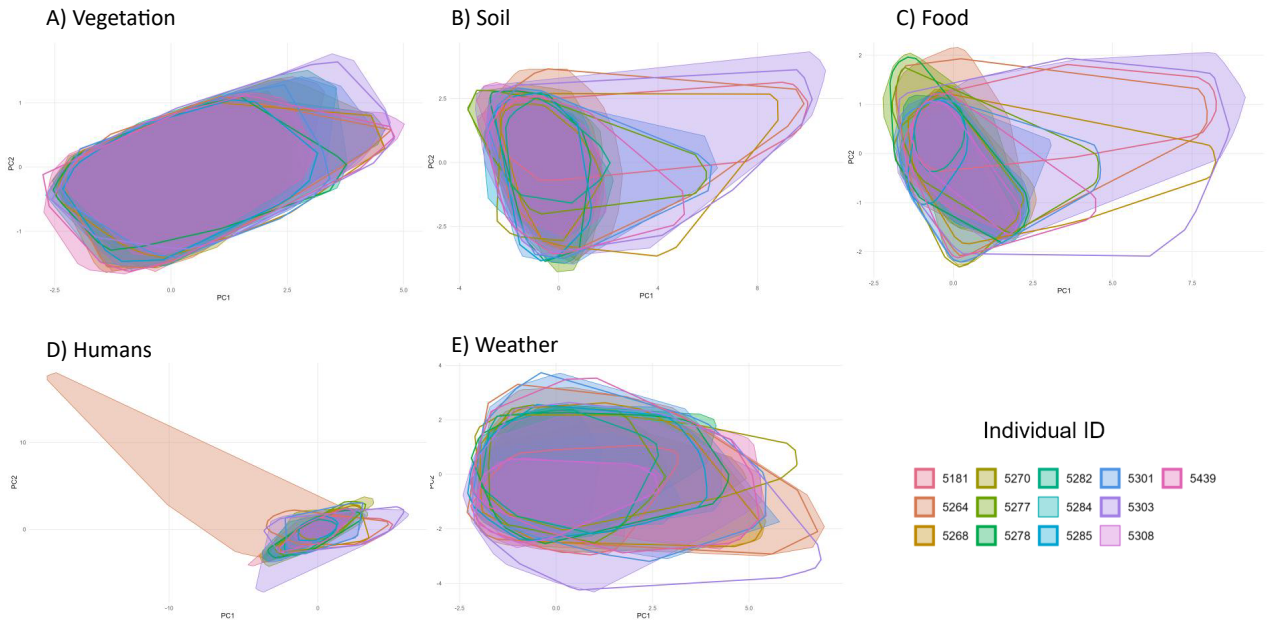

Figure 5. Individualized niche hypervolumes produced as convex hulls. Potential hypervolumes are plotted as semitransparent filled polygons, and realized hypervolumes are plotted as outlines. Each individual is represented by a different color.

and the degree to which each niche component occupies nonshared regions of the group-specific environmental space.

Uncertainty in hypervolume breadth was estimated by bootstrap resampling. For each individual, ecological group, and niche component, 50 bootstrap hypervolumes were generated using the same sample size as the original hypervolume. When valid weights were available, weighted bootstrap resampling was used; otherwise, the procedure reverted to ordinary bootstrap resampling. Empirical 95% confidence intervals for niche breadth were calculated from the 2.5% and 97.5% quantiles of the bootstrapped hypervolume volumes. Confidence intervals for realized–potential overlap were calculated from the corresponding bootstrap hypervolume sets.

For visualization, fitted hypervolumes were projected onto the first two axes of a principal component analysis (PCA) fitted to the full group-specific environmental matrix. These PCA projections were used only for plotting; all hypervolume estimation, volume calculation, and overlap analyses were performed in the full multidimensional environmental space.

The R package hypervolume (Blonder et al. 2013) was used to quantify the niche breadth of each individual.

Quantifying individualized niches: overlap and breadth

Niche breadth was quantified as the hypervolume shown in Fig. 5 in Step 3 (Suppl. material 1: table S2). Here, niche breadth can be considered equivalent to the within-individual variance of the individualized niche. In many cases, for example, in the selection of soil and human-presence variables, realized niche breadth was smaller than potential niche breadth, providing evidence of stronger individual specialization (Fig. 6).

Regarding pairwise overlap among individuals (Fig. 7), high overlap among potential individualized niches was observed for soil variables, which can be inter-

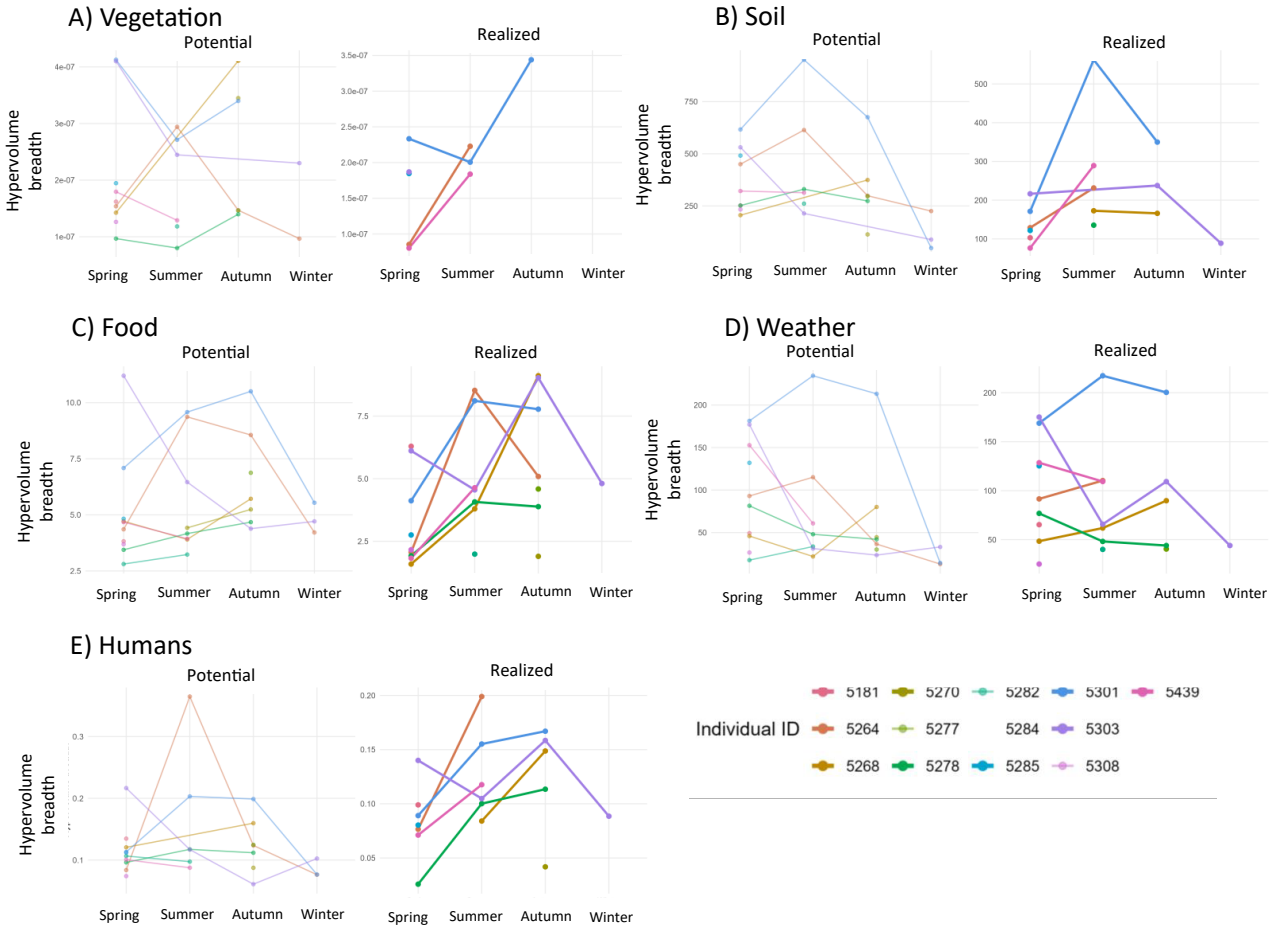

Figure 6. Niche breadth of the potential and realized individualized niches of northern lapwings (n = 13) for each season. Each facet corresponds to a niche type (variable group).

preted as limited potential for individual differentiation and likely a highly suitable environment. High overlap among realized individualized niches was observed for food resources (soil water index, earthworm abundance, and their interaction), which, in practice, means that individuals tended to use the same resources.

Repeatability of individual resource use

This step accounts for resource availability, which can strongly influence individual variation in resource use. Repeatability of the realized niche indicates whether individuals consistently use different parts of an environmental axis, whereas repeatability of the potential niche indicates whether they consistently differ in the conditions available to them because of spatial segregation, differences in home ranges or study sites, or sampling design. Repeatability was therefore calculated separately for the environmental conditions used by individuals and those available to them. Comparing these values indicates whether consistent differences in realized use are accompanied by similar differences in environmental opportunity; it does not test whether selection strength changes with availability. Realized repeatability exceeding potential repeatability is consistent with individuals differing in use beyond what would be expected from their opportunity sets, supporting an interpretation of individualized selection or specialization. Similar realized and potential repeatability suggests that differences

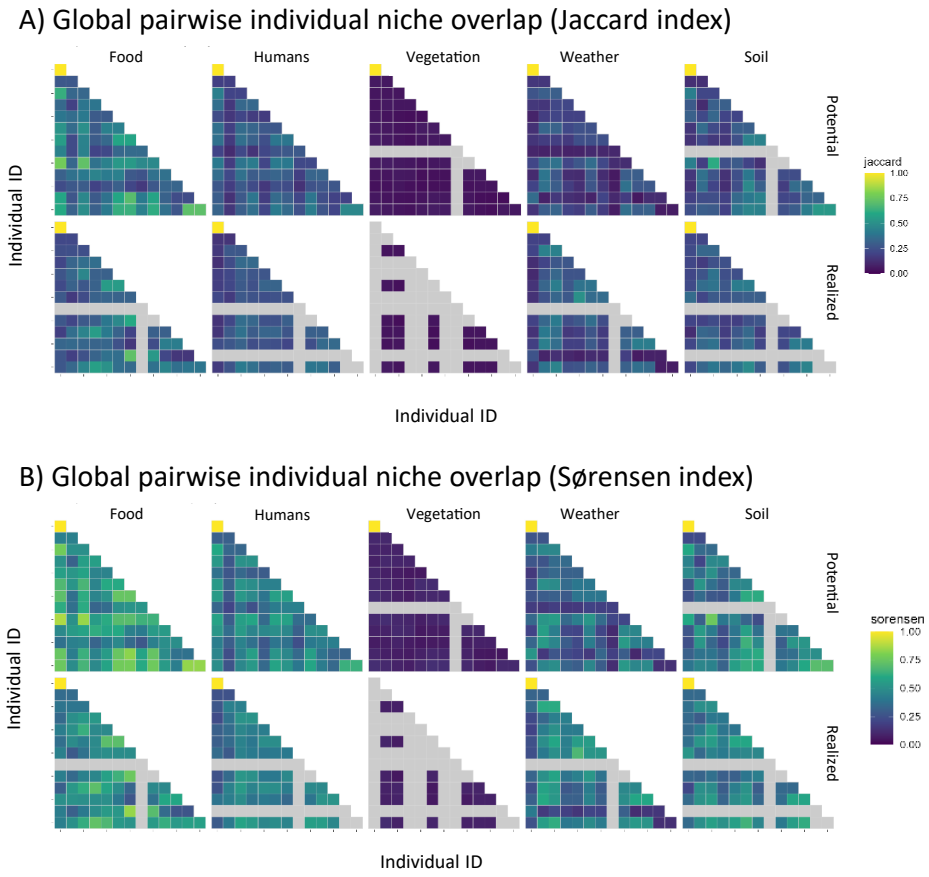

Figure 7. Pairwise overlap among 13 individual northern lapwings calculated using the Jaccard index (top) and Sørensen index (bottom) in a two-dimensional PCA space.

in use largely reflect differences in availability, whereas higher potential repeatability indicates greater differentiation in environmental opportunity than in realized use, potentially because of spatial or home-range segregation.

Repeatability of potential and realized individualized niches in northern lapwings did not differ significantly, and the relationship between them differed among predictors (Suppl. material 1: table S3), with repeatability values ranging from 0 to 0.55 for potential niches and from 0 to 0.83 for realized niches (Fig. 8). In most cases, repeatability of the realized niche was higher than that of the potential niche, which is consistent with the hypothesis that northern lapwings exhibit “individual variation in space use.”

Discussion

This study proposes a workflow to quantify among-individual differences in resource use and produce metrics and indices that can be used for further analyses. It is a synthesis of existing tools and concepts commonly used in movement ecology, behavioral ecology, and remote sensing. Furthermore, it is a response to calls over the last decade for the incorporation of individual-level variation into ecology and conservation (Réale et al. 2007; Panzacchi et al. 2015; Merrick and Koprowski 2017; Matthiopoulos 2022; Jeltsch et al. 2025).

The repeatability of potential and realized individualized niches is proposed here as an approach to addressing the problem of availability. In many cases, habitat-selection studies compare individual patterns without accounting for

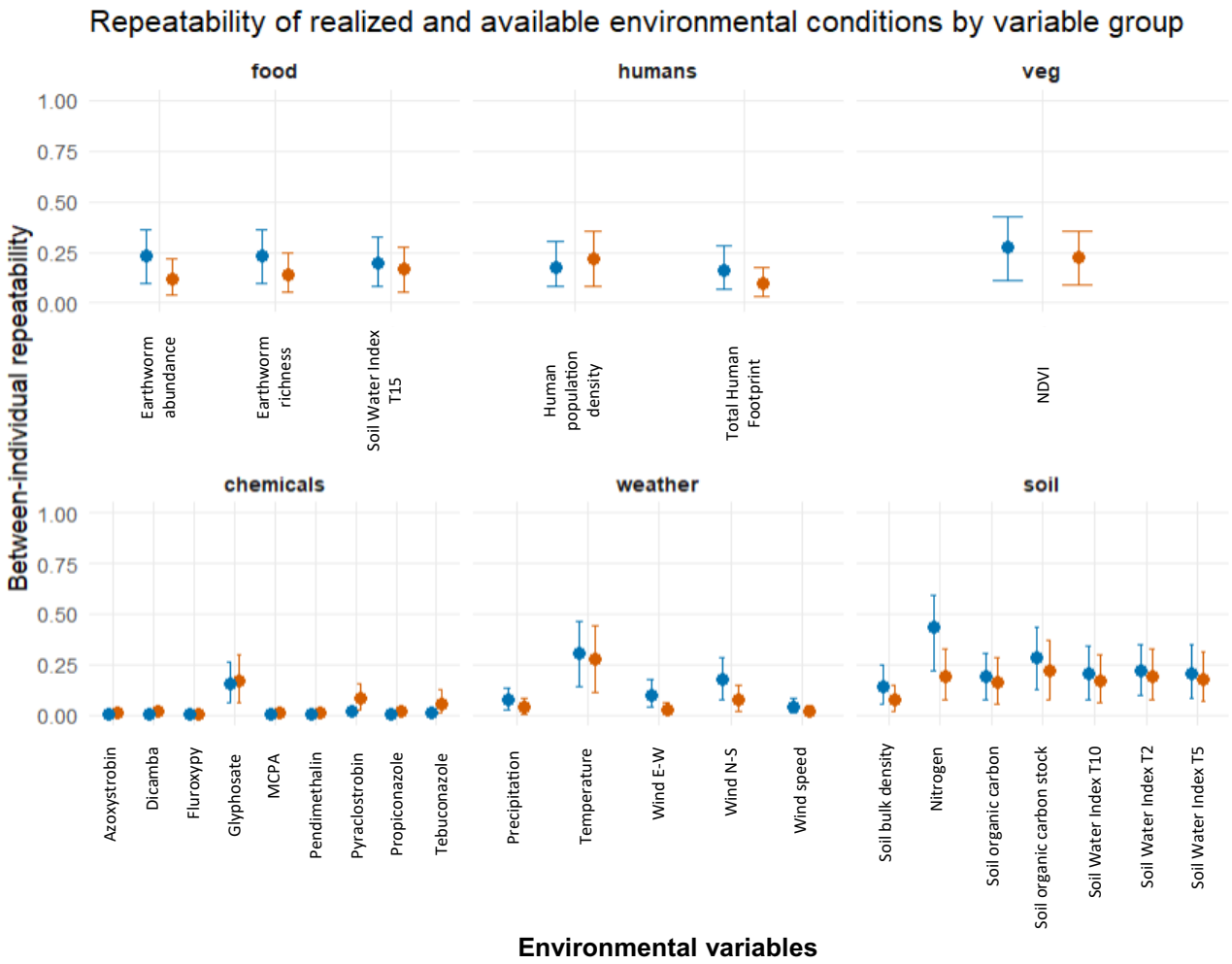

Figure 8. Repeatability of potential and realized niches across all predictors for northern lapwings (*n* = 13).

availability. Based on the workflow of the present study, resource availability is taken into consideration through the comparison of the repeatability values of potential and realized niches.

The individualized niche is a useful conceptual tool with multiple implications for conservation. The development of individual-based models that incorporate energy costs, demographic trends, habitat-selection patterns, and life-history traits holds promise for a more accurate and mechanistic representation of wild population dynamics (Van Benthem and Wittmann 2020; Zurell et al. 2024; Bluhm et al. 2025) and their future trajectories (Braschler et al. 2020).

An important distinction between the potential and fundamental individualized niches is that the former takes the conspecific context into consideration, whereas the latter does not. The fundamental niche and its individualized expression (Takola and Schielzeth 2022) are two theoretical concepts that were introduced as thought experiments to present the counterfactuals of realized niches. In practice, the fundamental niche of species has shown a mismatch with the realized (observed) niche, which has revived the debate about the usefulness of the niche concept (McInerny and Etienne 2012; Angilletta et al. 2019; Matthiopoulos 2022; Musters and De Snoo 2025). Overall, the observed mismatch between the fundamental and realized niches (Rosado et al. 2016; Jiménez et al. 2019), in combination with behavioral syndromes, stress

tolerance (Lian et al. 2022), and phenotypic plasticity (Angilletta et al. 2019), might explain the smaller breadth of the potential individualized niche compared with the realized individualized niche breadth in some cases.

Future research can focus on identifying the link between individualized niches and population growth rates. Previous studies have established a link between intraspecific variation and both intra- and interspecific competition (Moran et al. 2022; Enne et al. 2026). Furthermore, multiple attempts have been made over several decades to establish conceptual links between habitat selection and population dynamics (Holt 1987; Pulliam and Danielson 1991; Rosenzweig 1991; Morris 1996; Kristan III 2003; Matthiopoulos et al. 2015; Boyce et al. 2016), as well as to find empirical evidence of the mechanisms underlying this link (Weimerskirch 2018; Smith et al. 2023). However, none of these attempts has occurred within the individualized niche framework. The difficulty in identifying this link may lie either in the perspective adopted (top-down rather than bottom-up) or in the strong methodological traditions of habitat-selection studies, which focus on correlational models (Boyce and McDonald 1999; Gehring and Swihart 2003; Fieberg et al. 2010).

Nevertheless, the intersection of behavioral and landscape ecology is one of the areas of ecology in which methods have evolved faster than concepts. As a result, particularly over the last decade, ecology has developed stronger analytical pathways but retains relatively weak inference and limited cross-pollination with philosophy (Heger et al. 2025). The philosophy of science is central to the development, clarification, and critical evaluation of ecological concepts. From this perspective, the concept of individualized niches can provide the conceptual "epoxy" needed to connect analytical advances with stronger ecological inference.

Environmental niche modeling has been useful for predicting invasions (De Andrade et al. 2019), and incorporating fitness and eco-evolutionary variation could strengthen these predictions by linking individual responses to population persistence and broader macroecological patterns (Lancaster 2022; Grinder and Wiens 2023). Individualized niche breadth may also facilitate the inclusion of intraspecific trait variation in global-change studies (Carscadden et al. 2020). Accounting for this variation may improve forecasts of persistence and redistribution by revealing whether populations contain individuals with contrasting environmental tolerances. Indeed, climatic niche breadth predicts recent range shifts across moths, butterflies, and birds, demonstrating its value for anticipating species responses to climate change (Hällfors et al. 2024).

Outlook

This framework provides a practical step toward scaling up individual-level movement behavior and facilitating population-level inference. It achieves this by quantifying individual niche variation, filtering for areas with high selection probability, and aggregating resource-use data into meaningful indices of intraspecific variation. The workflow requires the compilation of a dataset containing recorded locations and the corresponding environmental variables. It is designed to be transparent, reproducible, and compatible with common movement-ecology data structures and tools. Future work can further examine links among movement patterns, resource use, and fitness outcomes. As the individualized niche concept becomes established in ecology, there is an increasing

need to draw population-level inferences from individual-level data. Quantifying individualized niches is therefore an essential tool for behavioral ecologists.

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The author accepts full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: GPT
Used for: Language, style and writing, Other, De-bugging code.

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Data availability

The data and code underpinning the analysis reported in this paper are deposited at https://github.com/ETakola/individualised_niches/tree/main/Takola2026_IBE.

Supplementary material 1

Supplementary tables S1–S3 and figures S1–S3

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Explanation note: **table S1.** Model coefficients for the mixed-effects resource selection functions. **table S2.** Realized and potential individualized niche breadth per individual. **table S3.** Variance decomposition of the repeatability of realized and potential niches per model and predictor. **figure S1.** Seasonal individualized niche hypervolumes of northern lapwings by variable group: A) weather, B) food, C) vegetation, D) humans, and E) soil. **figure S2.** Seasonal hypervolume overlap for potential and realized niches based on the Jaccard index. **figure S3.** Seasonal hypervolume overlap for potential and realized niches based on the Sørensen index.
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