Tracking the hidden niches: Movement-based insights into northern lapwing intraspecific variation and conservation

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ABSTRACT

Context.

Global monitoring data reveal farmland bird population declines, primarily driven by agricultural intensification, chemical inputs, and climate shifts. The northern lapwing (*Vanellus vanellus*), a ground-nesting wader adapted to lowland agricultural matrices, exemplifies this decline across Europe.

Objectives.

This study quantified intraspecific variation in habitat selection to evaluate the degree of behavioural variance in resource use among individuals and assess its conservation implications. We specifically tested for: (1) inter-individual differences in resource use; (2) repeatability of habitat preferences; and (3) niche components driving selection patterns.

Methods.

Using Movebank high-resolution GPS data from 13 individuals tracked between 2021 and 2023 across Europe, we applied step selection functions (SSFs) incorporating both biotic and abiotic covariates. Repeatability estimates were derived from mixed-effects models to quantify consistent individual-level selection across resource gradients. We also estimated variation of habitat selection across seasons as well as within- and between-individual variation.

Results.

Lapwings most frequently selected grasslands and areas with intermediate cropping intensity. Individual preferences for crop types varied widely, with low repeatability across most types except pulses (R = 0.31) and wheat (R = 0.19). Movement patterns were influenced by abiotic factors, and nocturnal activity increased during full-moon nights. Habitat selection also varied seasonally.

Conclusions.

Conservation strategies should focus on maintaining low-intensity farmland and grasslands, particularly in remote areas. Predator control through culling is ineffective due to rapid recolonization; instead, managing nesting habitats and removing predator perching structures is recommended. Establishing dedicated nesting areas (lapwing plots) can further support the species survival.

Keywords

wader, personality, multifunctional landscape, individualised niches, NDVI, tillage

Introduction

Farmland birds are a group of avian species that are breeding and feeding on or in close proximity to agricultural landscapes. They have adapted to more open landscapes and were favoured by the spread and increase of agriculture in historical times. They promote important ecosystem services such as seed dispersal, biocontrol, nutrient cycling, habitat quality and even cultural services (e.g. recreation). Farmland birds are an indicator of non-avian biodiversity in agricultural landscapes (Kirk et al., 2020).

Multiple long-term monitoring schemes have shown that most farmland bird species undergo significant population declines. Declines of farmland birds have been documented in all continents and in different ecological contexts and scales (from national to global). Country-level declines have been reported e.g. for Germany (Kamp et al., 2021), Denmark (Heldbjerg et al., 2018) and Spain (Traba & Morales, 2019). Meanwhile, BirdLife Australia reported a 56% decline in farmland bird populations since 1970. Similarly, the abundance of farmland birds in North America has declined by 74% from 1966 to 2013. The 2024 report of the PanEuropean Common Bird Monitoring Scheme found a decline of 60% of the Farmland Bird Index since 1980. The main causes of the decrease of farmland birds have been identified as the intensification and modernization of agricultural activities (Reif et al., 2024; Rosin et al., 2016, 2020), the application of pesticides (Fuentes et al., 2023), illegal capture and hunting, urbanization (Tscharntke & Batáry, 2023) and climate change. The European Union, in an attempt to mitigate farmland bird declines, introduced the agri-environment schemes (AES) as a measure within the Common Agricultural Policy (Sharps et al., 2023).

The northern lapwing (*Vanellus vanellus*) is a medium sized bird that feeds and breeds in open agricultural habitats, such as lowland wet meadows, marshes and wet grasslands and open habitats with low vegetation and high water content. Although it is highly popular among the public (NABU, 2024; Sheldon et al., 2004), it is facing severe declines in Europe (PECBMS). The monitoring scheme of common birds has found a 62% decline of northern lapwings across Europe (PECBMS, 2024). The species is characterized as Near Threatened (NT) by the IUCN and it is included in the Annex 2 of the Birds Directive, Annex III of the Berne Convention, and Annex II of the Bonn Convention. At a national scale though its conservation status varies. For example, in Germany it is under the Federal Species Conservation Regulation (BArtSchV), while in France and Greece, despite being protected by EU law, northern lapwing hunting is permitted (Souchay & Schaub, 2016).

Natural communities in human-modified landscapes have been shaped by both agricultural activities and climate shifts (Ellis et al., 2021). European agricultural landscapes have changed significantly in the past decades. Biodiversity has declined and landscape structure has become more homogeneous. The last Common Agricultural Policies (CAP) have introduced the concepts of agro-ecosystems, agri-environment schemes and multifunctional landscapes (Lefebvre et al., 2015; B. M. Taylor & Van Grieken, 2015), which represent practical measures for the promotion of species diversity in agricultural landscapes.

Fine-scale observations are instrumental for the effective design of species conservation measures. Field observations of occupancy rates have shown that, for northern lapwings, the effectiveness of AES for lapwings can be enhanced by the presence of water, which is an integral part of the species ecological niche (Hawkes et al., 2025).

Recent technological advancements in individual tracking devices led to the generation of large datasets of very high spatiotemporal resolution. These data are the core of the field of movement ecology and allow for the investigation of novel research questions in behavioural ecology. For instance, tracking data allow the exploration of individual specialization in space use, also known as spatial personalities (Stuber et al., 2022) which in turn leads to individual differences in resource use, also known as individualized niches (Takola & Schielzeth, 2022). The methodologies that are used to collect movement data can be either through GPS tracking devices or through satellites or (for smaller animals or animals in a limited space) camera tracking or telemetry. These data can then be made available through platforms and web-based interactive maps. The combination of ecological niche theory with technologically advanced individual-level observations represents a new frontier in conservation biology and aligns with recent calls for more broad integration across organizational and spatial scales. The ecological niche of a population can be decomposed to a between-individual and within-individual components (Roughgarden, 1972). Both components are instrumental for the conservation of a species.

The aim of this paper is to quantitatively estimate intraspecific niche variation in northern lapwing in order to inform the conservation of the species. To achieve this, we analyzed the individual resource use by combining biotic (e.g. earthworms, human presence) and abiotic (e.g. weather, soil and vegetation) variables. The research questions of our study were: i) Do northern lapwing individuals differ in their resource use? ii) If yes, how much do they differ? iii) What does intraspecific variation in resource use mean for the conservation of the species? We used step selection functions to quantify how landscape composition structures movement behaviour, offering a mechanistic understanding of resource use and niche expression at the individual level. Subsequently, we used the results of step selection functions to inform the exploration of consistent behavioural differences through repeatability models. Mechanistic approaches of intraspecific variation can shed light into community dynamics and interspecific interactions (Moran et al., 2022). Our study builds upon the recommendation to create new frameworks for cross-scale syntheses and for the integration of individual-level variation in biodiversity conservation (Jeltsch et al., 2025).

Methods

Study area and tracking data

We analysed all northern lapwing movement data that are publicly available for Europe through the Movebank database (dataset ID: 1448409403, curator: Jelle Loonstra). The data covered an area across the Netherlands, Belgium, England, France, and Spain (Fig. 1) and the tracking period extended from April 2021 to March 2023. The temporal resolution ranged from 0.08 minutes to 5.6 hours. In order to standardize sampling effort across all individuals, we filtered the points with a sampling rate of 180 minutes, considering ±30 seconds of tolerance. The final dataset contained a total of 40,777 data points from 13 individuals, since one was excluded after resampling. The number of observations per individual ranged from 28 to 1,266 steps.

For each recorded position (used step), we generated a set of 10 random alternative available positions (available steps) that the individual could possibly move towards. Each available random point was at most 10 km away from the used one, as a step length of over 10 km was deemed unrealistic. In the case where the birds appeared to remain in the same location for multiple time intervals (inactive or sleeping), the generation of random steps was not possible; thus, we added jitter (0,001 m) to each repeated point. We removed all points (used or available) that were over the sea (Fig. S1).

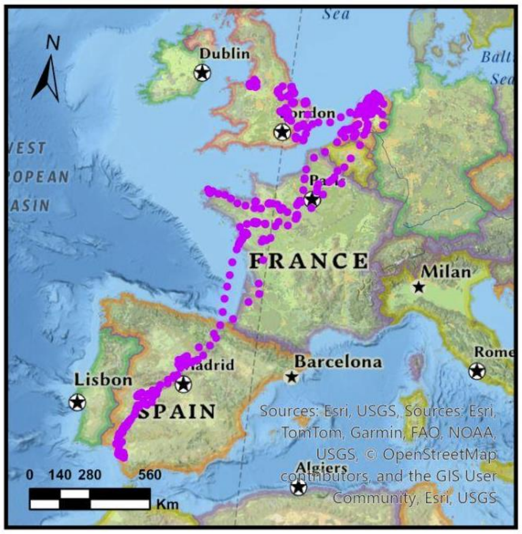

Figure 1. General location of the study area and the GPS recorded positions of overall individuals.

Environmental data cube compilation

We compiled a set of environmental variables hypothesized to influence the movement patterns of northern lapwings and to characterize the ecological niche of the species. These variables included temperature, precipitation, wind speed, distance and phase of the moon, 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 (Table S1).

For each environmental variable, we used the most recent data available, ensuring that temporal alignment was maintained as closely as possible. For example, hourly wind data from ERA5-Land and daily temperature and precipitation data were matched in time. In cases where exact temporal matching was not possible, we incorporated environmental data from the closest year, under the assumption that these variables had changed significantly over time.

We assumed that crop cycles did not change significantly between 2020 and 2023, which justified the use of the GCI30 map from 2020. Similarly, we assumed that pesticide application rates did not change significantly between 2018 and 2021, allowing us to use pesticide usage data from

2018 provided by the EU. We obtained crop type data from the EU Crop Maps for 2018 and 2022, using the 2018 map to fill in gaps not covered by the 2022 map, particularly in the northern part of the study area. We removed all crops that appeared 30 times or less in the dataset.

The time period of tracking data coincides with the COVID-19 pandemic, where human activity was limited. For this reason, we used population density data (for NUTS3 regions) along with the Global 100m Terrestrial Human Footprint dataset, which relies on more permanent and rigid factors, such as infrastructure, and night-time lights, which remain relatively stable over time.

The earthworm abundance variable comprised two distinct components: the earthworm abundance factor and the earthworm abundance and richness factor (Orgiazzi & Panagos, 2018), which were derived from a study on earthworm richness and abundance (Rutgers et al., 2016) and are available upon request from the European Soil Data Centre (JRC, Ispra).

To calculate the distance and phase of the moon for each position, we used the Lunar R package, taking into account the respective timestamp of each observation. NDVI data were extracted for each location from the MODIS Terra Vegetation Indices (250 m) dataset corresponding to the closest available date. Soil carbon and nitrogen content data were derived from 2020 predictions based on the SoilGrids 250 m dataset.

Data analysis

To estimate the intraspecific variation in resource selection among individual northern lapwings, we associated the recorded positions with each environmental variable of the data cube. For each position (used or available) we recorded the corresponding value of every environmental variable. First, we used individual resource utilisation curves (as ridgeline plots and heatmaps) to visualize within- and between-individual variation in each resource variable. We then implemented six step-selection functions with the glmmTMB R package (Brooks et al., 2017) to estimate the importance of each group of variables on the movement of the species. Subsequently, we examined the results of the step selection functions and identified the most important variables (or levels of categorical variables) and estimated the repeatability of usage for each (Stoffel et al., 2017). We also quantified intraspecific variation by extracting the random intercepts for each individual from each step selection function. To determine the seasonal variation of resource use for each predictor, we fitted the six models separately for each season (spring, summer, autumn, winter).

Repeatability is defined as the proportion of population-level variance that can be attributed to the between-individual differences. Repeatability is an indicator of different phenotypes (or personalities) within a population. A repeatability of 0 indicates that a trait is not consistent across observations, whereas a repeatability of 1 indicates that an individual trait remains consistent across measurements. In the context of habitat selection, high repeatability indicates that the individuals' habitat preferences are consistent over time and across contexts (indicating spatial 'personalities') and low repeatability means that individual preferences vary substantially. The repeatability models were applied to the subsets of the crop types that had a significant model estimate in the step selection functions with crop type as the only fixed effect.

We fitted the step selection functions with step ID and individual ID as nested random effects and environmental variables as predictors (Table S2). The response variable in the night-time model was the step length transformed with log+1 and in all the other models (step selection functions and repeatabilities) it was a binary variable indicating whether a step is used or available. Repeatability models included individual ID as a random effect and a crop type as a fixed effect. All glmmTMB models were using nlminb as an optimizer and in the cases where they could not converge, we changed the optimizer from nlminb to BFGS.

We assessed the model fit and performance using the Akaike's Information Criterion (AIC) and the variance explained by random and fixed effects (R^2). To address collinearity among the predictor variables, we calculated correlations for every pair of variables and an auxiliary regression with the numerical variables to estimate the Variance Inflation Factor (VIF) for every variable separately (Fig. S2, Table S3). All analyses were performed in R and all variables were scaled.

Results

Data description

We analysed the movement of 13 northern lapwings, over the course of 3 years (2021-2023) in Europe. We used GPS tracking data to derived used and available steps (n = 40,777 points) and remote sensing techniques to characterize the niche components selected by the individuals.

Movement-habitat relationships of northern lapwings

We fitted six models to describe resource use by northern lapwings in relation to various biotic and abiotic variables (Table S2). Random effects explained from 0.23% to 23% and fixed effects explained from 2.19% to 39.45%.

The step selection functions indicated that temperature, soil nitrogen, soil organic carbon, population density, human presence (population density and terrestrial human footprint), crop intensity (single- and double-season cropping), the presence of certain crop types (wheat, barley, maize, potatoes, sugar beet, sunflower, pulses, vegetables, flowers and fodder crops) and the concentration of propiconazole were significantly associated with the selected locations of northern lapwings (Fig. 2). Overall, the best model based on AIC values (which included NDVI, crop type, glyphosate and propiconazole concentrations) explained almost 40% of the observed variance.

Northern lapwings tended to move more during full-moon nights compared to new-moon nights (Fig. S3). Earth-moon distance was positively correlated with step length (estimate = 0.31, S.E. = 0.08), indicating that northern lapwings tend to be more active when the moon is less bright and step length was positively correlated with the full moon phase (estimate = 0.83, S.E. = 0.22).

Although earthworm abundance was not a significant predictor in the step selection function, northern lapwing movement was positively correlated with soil moisture and nitrogen-rich soils, possibly due to high abundances of other invertebrates.

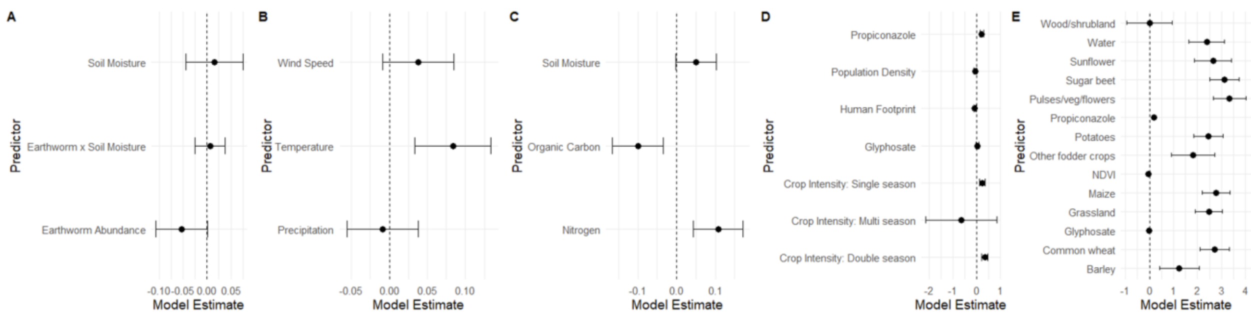

Figure 2. Model estimates for the resource model.

We also detected seasonal variation for all models (Fig. S4). Northern lapwing preferences varied across seasons for each crop type, while earthworm abundance and soil water index both had negative coefficients for winter and spring, but positive for summer and autumn (earthworm glmmTMB model estimates with S.E. for spring: -0.350±0.05, summer: 0.01±0.058, autumn: 0.07±0.063, winter: -0.17±0.24).

Individual variation in resource use

We detected both between-individual and within-individual variation in resource use, through a visual inspection of individual resource utilisation curves and heatmaps (Fig. S5, S6). The random intercepts of the step selection functions showed that individuals differ in their average responses (Fig. S7). Although grasslands were not the land use type with the highest positive model estimates in the step selection functions, it was the most frequently selected land use type among the used steps. However, the removal of grasslands from the plot revealed the patterns of between- and within-individual variation (Fig. 3). Similarly, individuals showed different patterns in their exposure to herbicides (glyphosates) and human population density (Fig. 4).

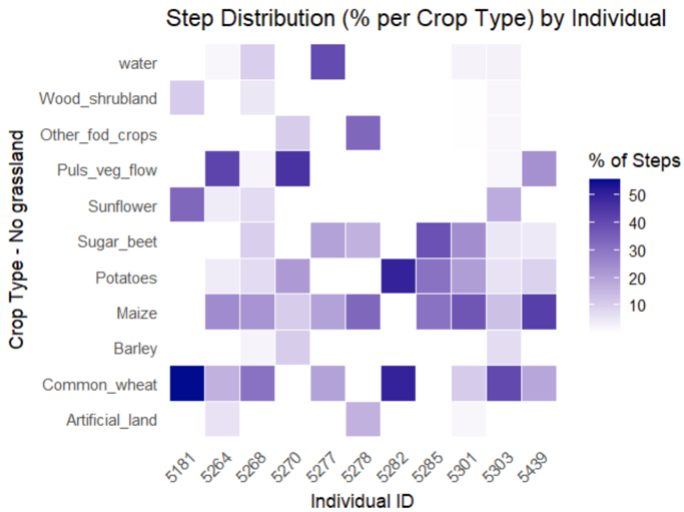

Figure 3. Within-individual variation in crop types (left).

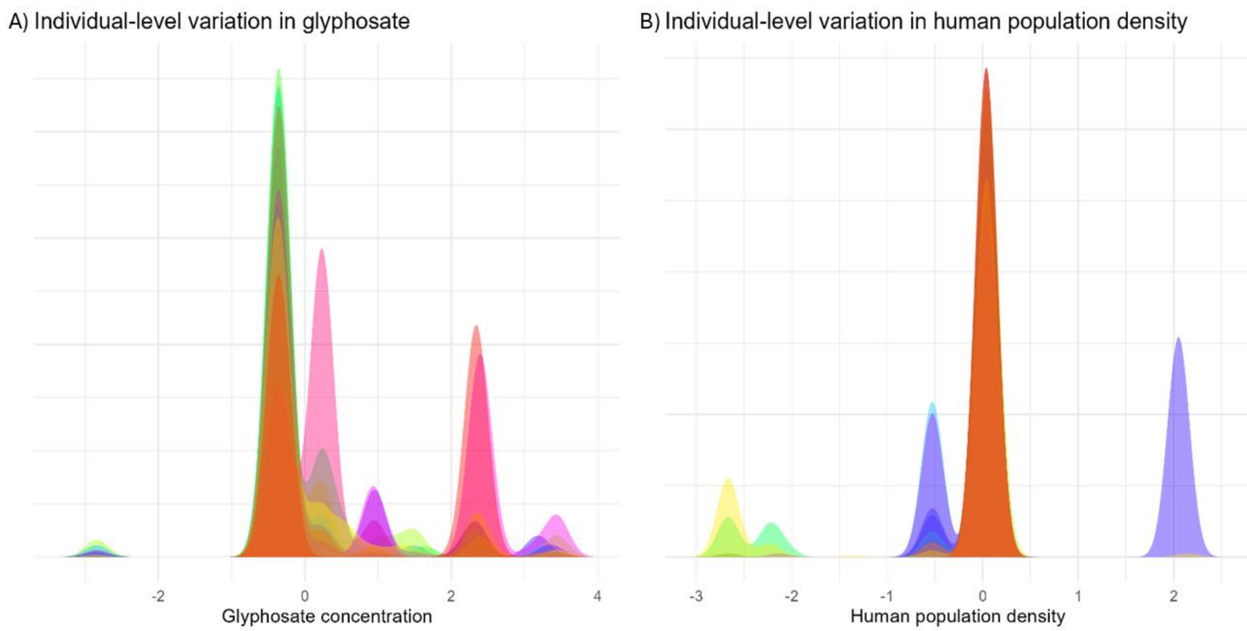

Figure 4. Individual resource utilisation curves for glyphosate (A) and human population density (B).

To quantify between-individual variation in the selection of different niche components, we fitted individual ID as a random effect in the six step selection functions. The between-individual variation for each model ranged from -1.3 to 2.13.

Repeatability of resource use

We used a step selection function to identify the important crop types across all data. The step selection function had significant effects for the following crop types: barley, maize, potato crops, sugar beet, common wheat and pulse-vegetable-flower crops. We then fitted a repeatability model for each of these crops (Fig. S8). The highest repeatability was observed in the dry pulses, vegetables, and flowers category (R=0.31, 95% CI: 0.00–0.61), followed by common wheat (R=0.19, 95% CI: 0.01–0.33), and sugar beet (R=0.10, 95% CI: 0.00–0.26). All other crop types, including maize, barley, potatoes, grassland, and water, showed negligible repeatability estimates (R<0.03) with confidence intervals overlapping zero. Repeatability for grasslands and water was also negligible.

Discussion

In this study we analysed over 40,000 GPS locations of 13 northern lapwing individuals from 2021 to 2023. We used step selection functions and repeatability models to associate lapwing movement with abiotic and biotic variables and estimate intraspecific niche variation. Overall, northern lapwings selected area with high soil moisture and high abundance in earthworms, warmer areas, with high nitrogen concentration, low human presence and more wind. In addition, they were actively choosing single and double season cropped fields and higher concentrations of herbicides (glyphosate, propiconazole). Regarding land cover types, lapwing used steps were positively and significantly associated with the presence of water bodies (lakes and rivers), sunflower fields, sugar beet fields, pulses, vegetables and flowers, potato fields, maize fields, grasslands, common wheat and barley fields. The strength of selection differed among individuals. Although northern lapwings appeared to select crop types such as wheat, barley and potatoes, the repeatability for these crop types was negligible. This is ought to an underlying within-individual variation in the usage of the different crop types. The between-individual and within-individual variation varied largely across abiotic and biotic variables, and the level of variation was higher in the abiotic variables rather than the biotic variables, indicating the presence of distinct behavioural phenotypes. In the case of fitness-related variables (individualized niche axes), such as the exposure to herbicides such as glyphosates and propiconazole, we observed very high between-individual variation and low within-individual variation.

The main biotic variables that we tested were earthworm abundance and human presence. Although earthworms are an important component of the northern lapwing diet (Sheldon et al., 2004), we did not find a relationship between earthworm abundance and used steps. This result can be ought to the homogeneous distribution of earthworm abundances between used and available steps. However, a recent study analysed dietary habits of northern lapwings in the Netherlands and Germany using metabarcoding techniques and found that earthworms were not a major part of the species' trophic niche (Lagendijk et al., 2025). Previous studies have found, similar to ours, that lapwings show low tolerance to the presence of humans (Roche et al., 2016). However, the individual resource utilisation curves revealed that one individual actually preferred human presence very strongly.

The main abiotic variables that we tested, beyond crop types, earthworms and pesticides, were related to wetland and water occurrence, crop intensity, soil composition, climate and night visibility. The presence of wetlands was not a strong predictor in our study, a finding that is in accordance with previous findings on nesting site selection (McCallum et al., 2018). However, the presence of water (rivers, lakes) had a positive and significant effect on northern lapwing selection.

Regarding diurnal activity, our results show that northern lapwings do not always remain inactive during the night. On the contrary, we have shown that northern lapwings tend to be more active (longer steps) in nights with full moon, confirming previous observations (Milsom et al., 1990), but their activity was negatively correlated with moon luminosity (measured as the distance between

Earth and Moon), likely due to higher predation risk in bright nights. The moon model showed a positive significant relationship between full moon and step length, but with a high standard error. In addition, a large amount of the model's variance was explained by between-individual variation, indicating that activity during night hours differs significantly among individuals. The highest variance explained by among-individual differences was in the moon model, which, in combination with the wide confidence interval of activity during full moon, indicates that not all individuals are equally active at night.

Agri-environment schemes have proved to be beneficial for northern lapwings, since AES provide foraging and breeding sites (Chamberlain et al., 2009; O'Brien & Wilson, 2011). However, when designing conservation interventions, it is important to take into account that northern lapwings show preference for an intermediate level of crop management, such as planting or rolling (Fraixedas et al., 2020; McCallum et al., 2018). In other words, they tend to avoid non-managed and natural areas (even with low vegetation), while, in the present study, they also avoid areas where there is multi-seasonal planting. Interestingly, our results confirm previous findings that lapwings select for medium cropping intensity or tilled areas (Düttmann et al., 2018; Horvat & Denac, 2019; McCallum et al., 2018) and improved grasslands (Düttmann et al., 2018), but see (Taylor & Grant, 2004), although this result is not confirmed in the case of restored meadows (Berg et al., 2002). In addition, nesting site selection is not always driven by a perceived breeding success, implying that there might be more complex and intrinsic factors for breeding habitat selection (Berg et al., 2002).

Although northern lapwings are a well-studied species, there are still key gaps in our understanding of the underlying mechanisms of their population declines. Moreover, lapwings seem to be well studied in Europe, but not throughout the range of their distribution (Phoswa & Downs, 2025). Future research can focus on linking fine-scale movement and habitat use with fitness outcomes across countries and continents. In other words, future studies can adopt the principle 'think globally, measure locally'. To this day, there are two main bodies of studies on northern lapwings: habitat selection and breeding success. The relationship between these two, across ecological contexts and scales, is the missing link.

Conservation recommendations

Based on the results of our study and the literature search, we suggest the following conservation measures for the protection of the northern lapwing:

1. Habitat management

- Northern lapwings avoid humans (densely populated areas) and human infrastructure, thus conservation measures should target habitat in remote areas (present study).
- The presence of even small (e.g. size of 10x10 meters) water bodies (rivers, lakes) is a very important resource for northern lapwings (present study).
- Spring tillage benefits northern lapwings, but they tend to avoid autumn tillage (Milsom, 2005; Sheldon et al., 2004).
- Plant spring crops when doing crop rotations particularly roots and cereals (Sheldon et al., 2004).
- Fewer machinery operations during breeding season (Schekkerman et al., 2009)
- Habitat management interventions supported by expert advice (Hunt et al., 2023). Lapwing conservation requires an active involvement of the land managers (McCallum et al., 2018).
- Liming is likely beneficial for northern lapwing breeding (McCallum et al., 2018).
- Northern lapwings select for fields with single- or double-season cropping intensity (present study).

2. Predation

- Culling is a sub-optimal solution because predators like foxes can be replaced very fast from neighboring populations (Porteus et al., 2024). Eliminating one predator does not decrease predation overall (Teunissen et al., 2008).

- Northern lapwings are active also during nights with intermediate moon light (present study).

3. Supporting breeding success

- Avoiding mowing and grass harvesting reduces chick mortality (Schekkerman et al., 2009).
- Ground nests are more threatened by horses rather than cattle (Mandema et al., 2013).
- Set aside areas for lapwing nesting (aka lapwing plots) (Chamberlain et al., 2009).
- Provision of nesting sites should be coupled with limited nest destruction and establishment of cropland-grassland mosaics (Milsom, 2005).
- Lapwings choose to nest away from potential predator perching spots (e.g. hedges) (McCallum et al., 2018), thus the removal of vegetation (such as shrubs) can reduce predation (Hunt et al., 2023).

Statements & Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

CRediT statement: JE: Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing, ET: Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, AGS: Writing - Original Draft, Writing - Review & Editing, MF: Writing - Original Draft, Writing - Review & Editing

Data Availability

All data and code generated during and/or analysed during the current study are available in OSF (https://osf.io/rcqd2/files/osfstorage) and GitHub (https://github.com/ETakola/NorthernLapwing_CurrentFutureMovements/tree/main/EsguerraJ-HabitatSelection/Publication).

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Supplement

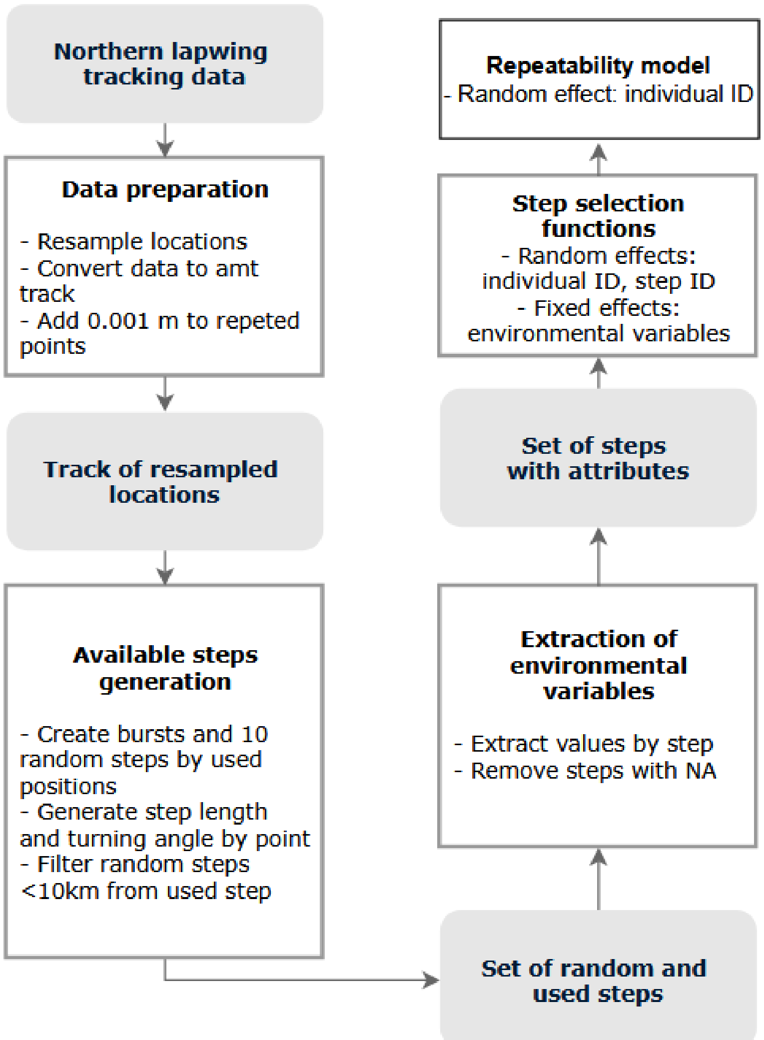


Figure S1. Workflow diagram for modelling habitat selection of the northern lapwing.

Table S1. Environmental variables used for the movement models.

Name dataset	Description	Frame time	Spatial resolution	Source
Northern lapwing tracking data	Set of recorded positions from GPS-tagged individuals.	04.2021 - 03.2023	Point-level	Movebank: Study Lapwing NFW Vanellus Vanellus Link: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1448409403
Earthworm abundance and richness factor	Maps of factors derived from the abundance and richness of earthworms.	2018 (Baseline: 1963 - 2014)	500 m	Study: Soil biodiversity and soil erosion: It is time to get married (Orgiazzi & Panagos, 2018) Host: European Soil Data Centre (JRC, Ispra) Link: https://esdac.jrc.ec.europa.eu/content/biodiversity-factor-soil-erosion
Soil Water Index (SWI)	Raster of moisture condition at various depths in the soil	2015 - present	1 Km	Host: Copernicus Land Monitoring Service (CLMS) Link: https://land.copernicus.eu/en/products/soil-moisture/daily-soil-water-index-europe-1km#download

SoilGrids	Predictions of soil properties: Carbon and nitrogen content	2020	250 m	Host: ISRIC–World Soil Information Link: https://www.arcgis.com/home/item.html?id=73aefa635a644c548fd57814a4e18114
MOD13Q1.061 Terra Vegetation Indices 16-Day Global	Data of normalized difference vegetation index (photosynthetic activity)	2000 - 2025 (May) Every 16 days	250 m	Provider: NASA LP DAAC at the USGS EROS Center (Kamel Didan. 2021) Link: https://developers.google.com/earth-engine/datasets/catalog/MODIS_061_MOD13Q1
Pesticides application rate maps in the European Union	Map of estimated average annual rate of pesticide application for active ingredients: Glyphosate and propiconazole.	2018	250 m	Study: Pesticides application rate maps in the European Union at a 250 m spatial resolution (Porta et al., 2025) Link: https://figshare.com/articles/dataset/Pesticides_application_rate_maps_in_the_European_Union_at_high_spatial_resolution/27743286
ERA5-Land Hourly - ECMWF	Data of atmospheric variables: Wind speed, temperature	Time point-level	~ 9 Km	Provider: Climate Data Store Copernicus. (Muñoz Sabater J., 2019) Link: https://developers.google.com/earth-

Climate Reanalysis	and precipitation.			engine/datasets/catalog/ECMWF_ERA5_LAND_HOURLY
Population density	Data on the population density, calculated as the number of people living within a NUTS 3 region divided by its area.	2021	NUTS 3 - level	Provider: Eurostat Link:https://ec.europa.eu/eurostat/databrowser/product/page/DEMO_R_D3DENS
Global 30-m cropping intensity	Map presenting the estimated annual frequency of cultivation for the same land area.	2020	30 m	Study: GCI30: a global dataset of 30 m cropping intensity using multisource remote sensing imagery (Zhang et al., 2021) Google Earth Engine Catalog: projects/sat-io/open-datasets/GCI30
EU Crop Map	Dataset of crop types at the agricultural parcel level for all EU member states.	2018 and 2022	10 m	Host: Joint Research Centre Data Catalogue (European Commission) Link EU crop map 2018: https://jeodpp.jrc.ec.europa.eu/ftp/jrc-opendata/EUCROPMAP/2018/ Link EU crop map 2022:

					https://data.jrc.ec.europa.eu/dataset/555e5d1d-1aae-4320-a716-2e6d18aa1e7c

Table S2. A list of the models used in this study, their structure and their technical characteristics.

model	Response variable	Fixed effects	Random effects	AIC	R2 fixed	R2 random	Data
food	Step selection	etf_abundance_r*swi_t1	id/step_id_	12010	0.33	0	All data
weather	Step selection	temp_2m + t_precipitation + wind_speed_10m	id/step_id_	12003	0.33	0	All data
soil	Step selection	swi_t1 + nitrog + org_carbon	id/step_id_	12003	0.33	0	All data
humans	Step selection	pop_dens + thp + crop_intens + p_glyphosate + p_propico	id/step_id_	11882	0.35	0.002	All data

		nazole					
vegetation	Step selection	NDVI + crop_type + p_glyphosate + p_propiconazole	id/step_id_	11613	0.39	0.002	All data
moon	Step length	moon_phase + moon_dist	id	3950	0.02	0.233	Only active at night (subset “night”)

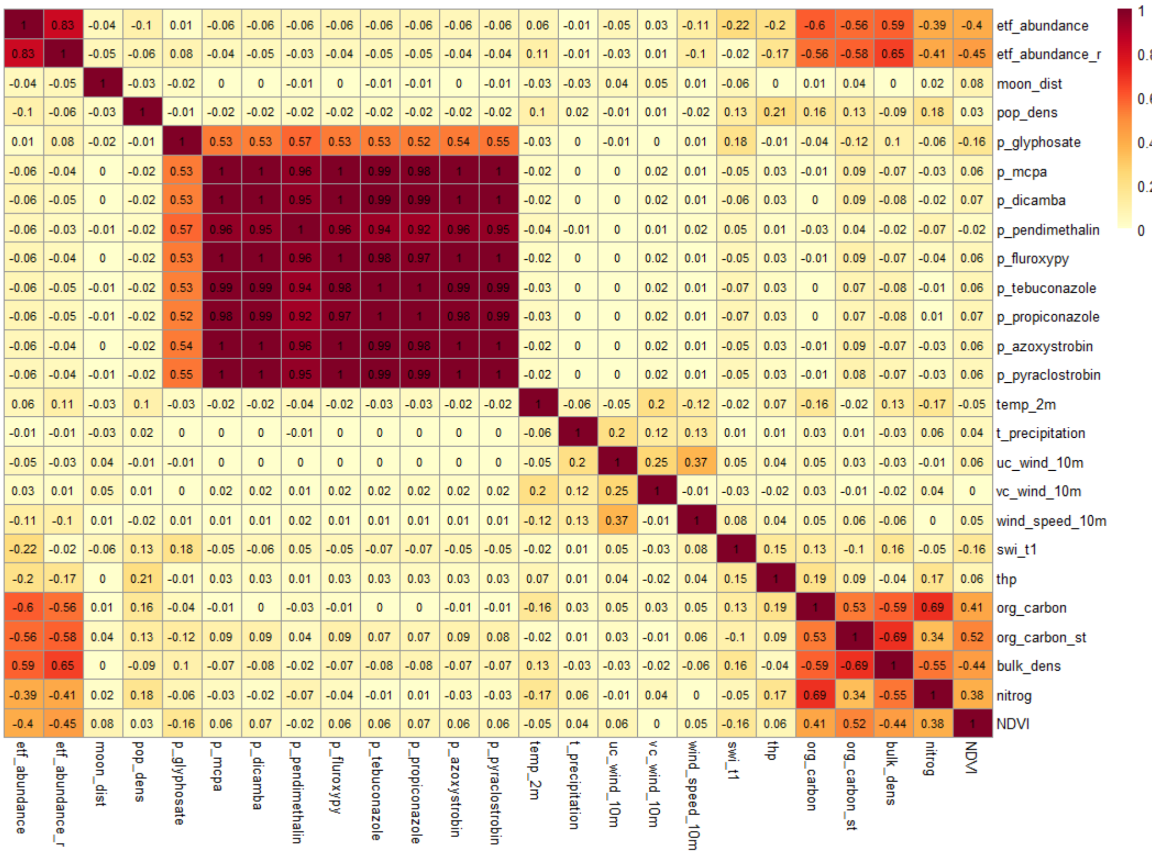


Figure S2. Calculated correlation coefficients

Table S3. Variance Inflation Factor (VIF)

Variable	VIF
etf_abundance_r	2.12
moon_dist	1.02
pop_dens	1.12
p_glyphosate	1.56
p_propiconazole	1.5
temp_2m	1.16
wind_speed_10m	1.2
swi_t1	1.28
thp	1.15
org_carbon	2.82
nitrog	2.38
NDVI	1.59

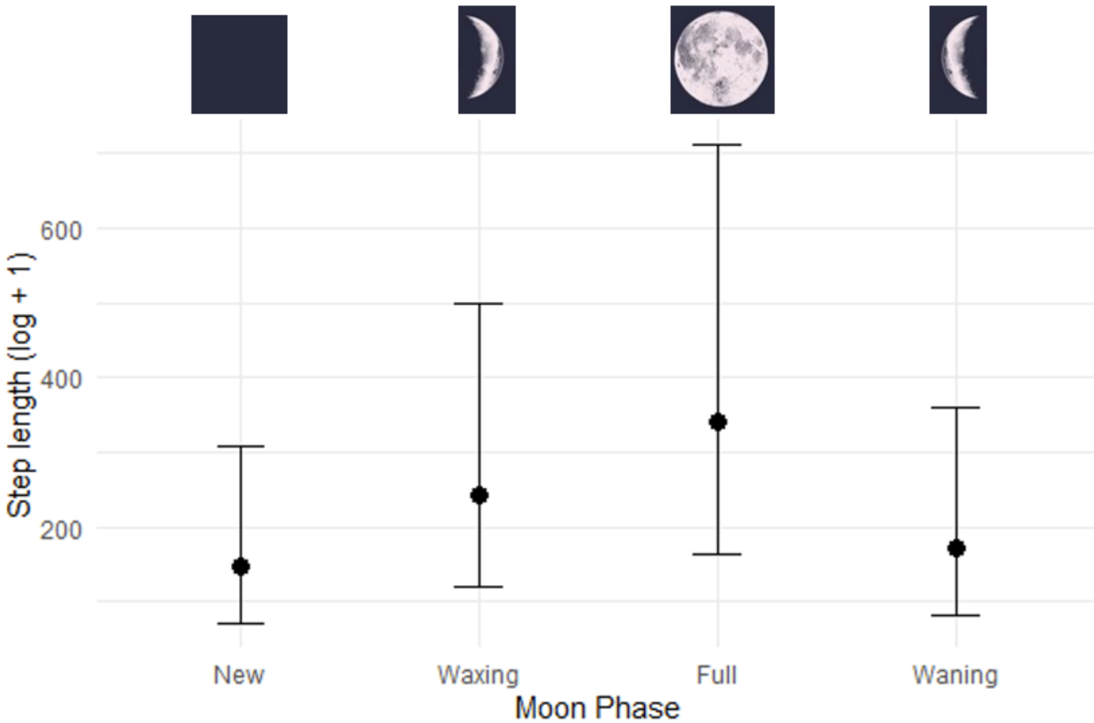
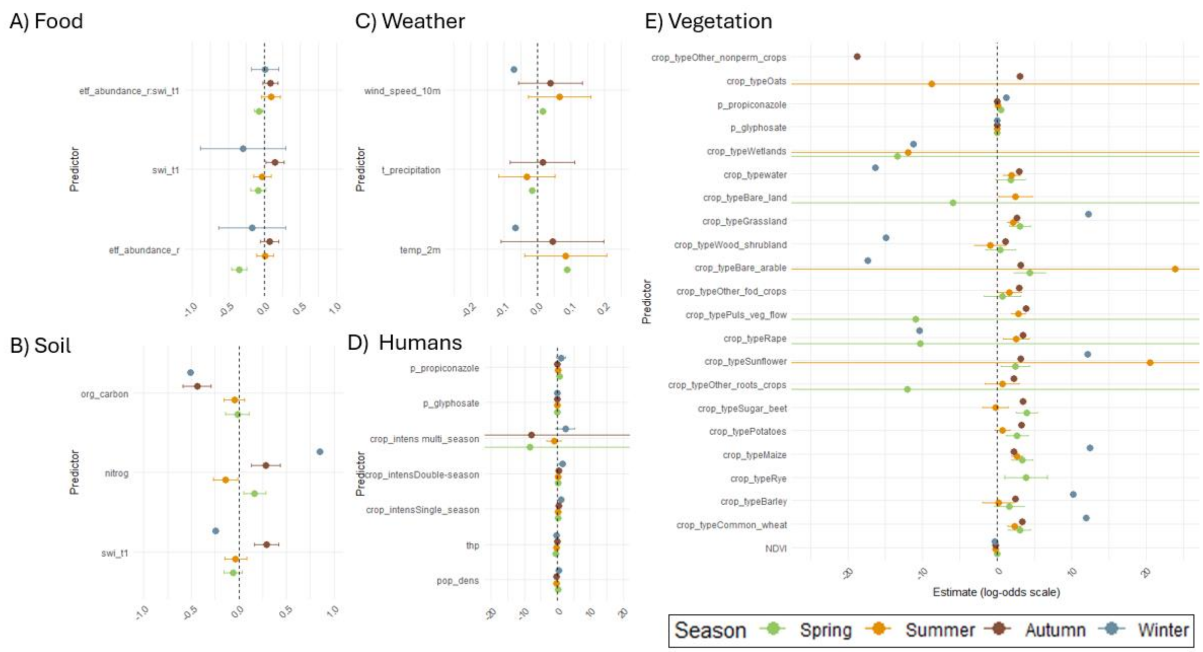


Figure S3. Model estimates for log-transformed step length during the different moon phases.



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549 Figure S4. Seasonal variation for each model.
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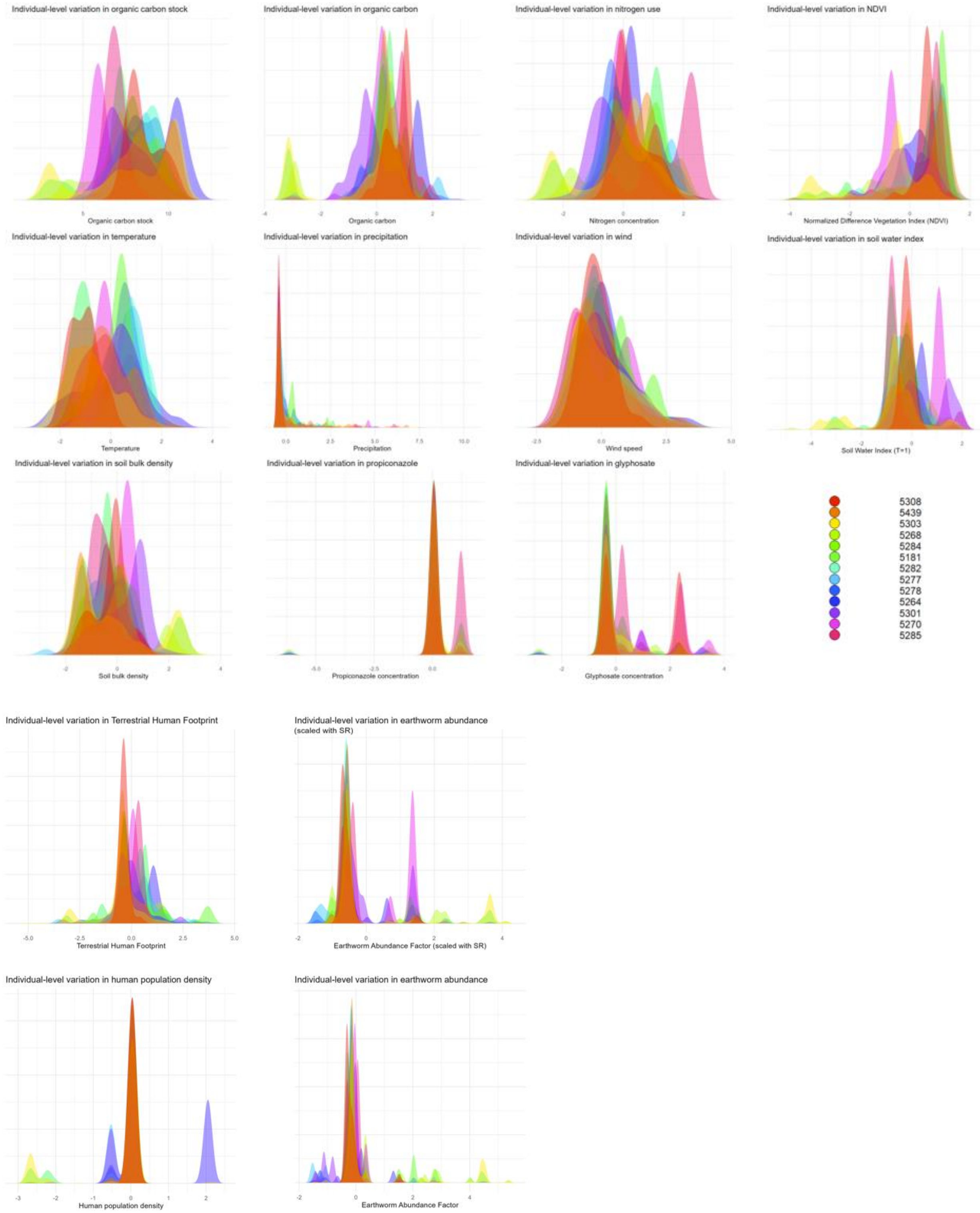
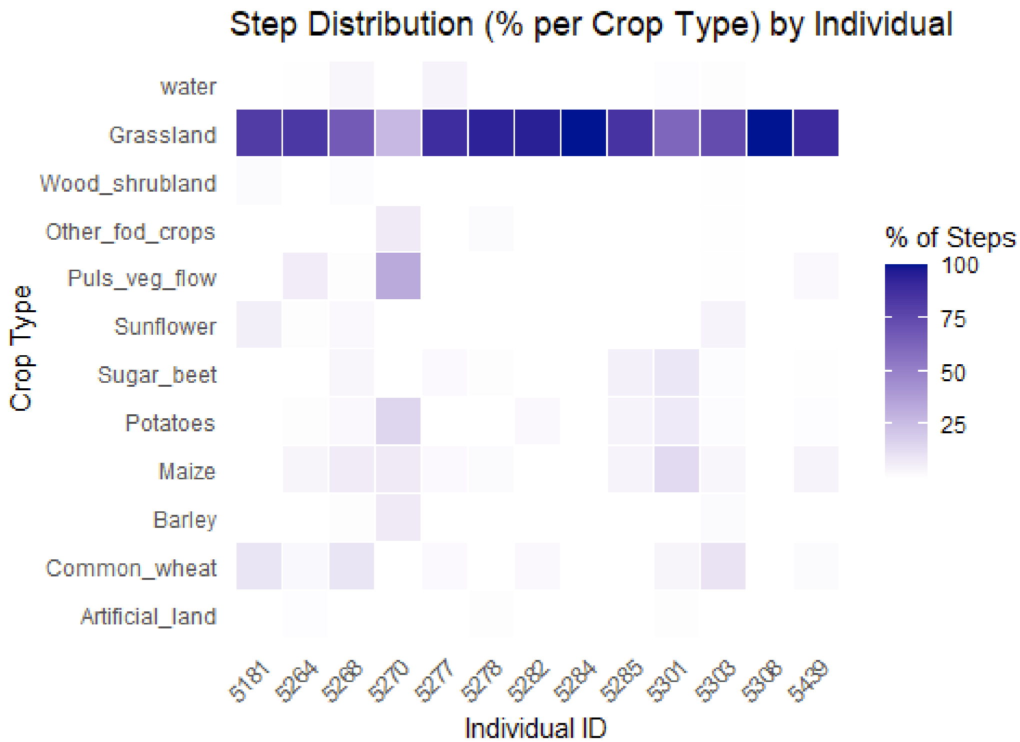


Figure S5. Individual resource utilisation curves



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557 Figure S6. Within-individual variation in crop type use.

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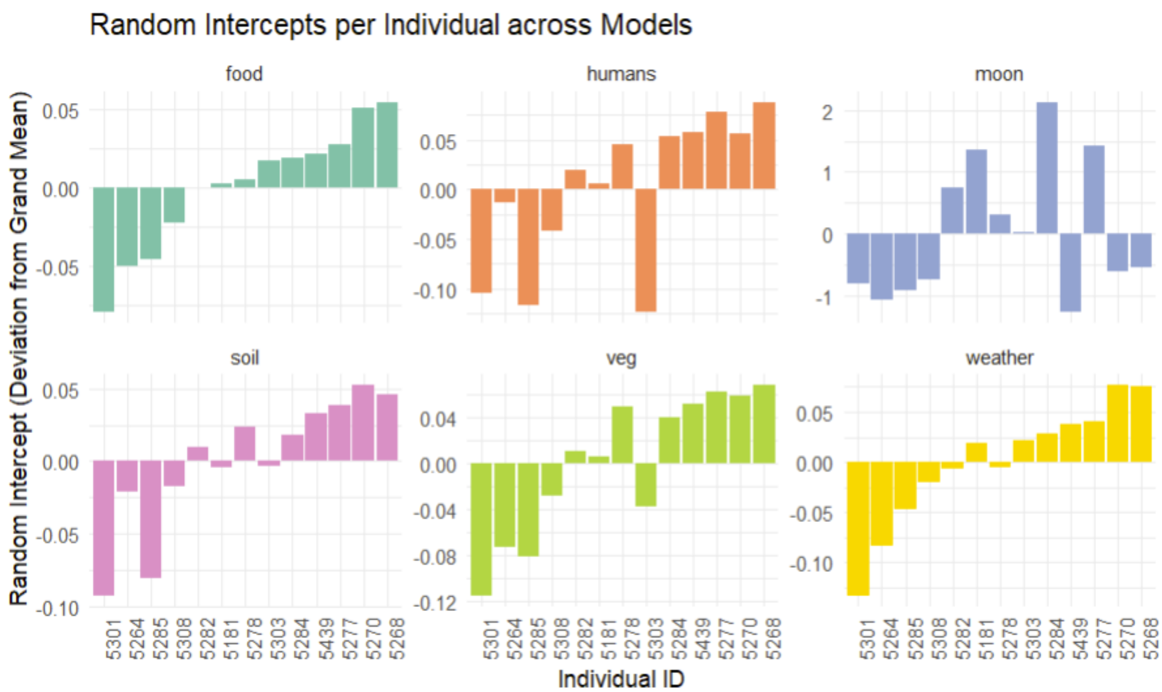

Figure S7. Random intercepts of all step selection function models.

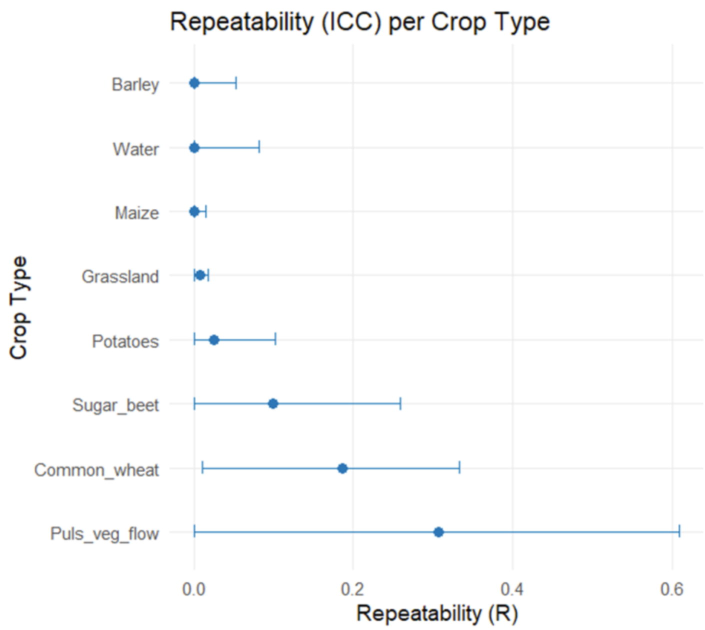

Figure S8. Repeatability estimates for each crop type with 95% confidence interval.