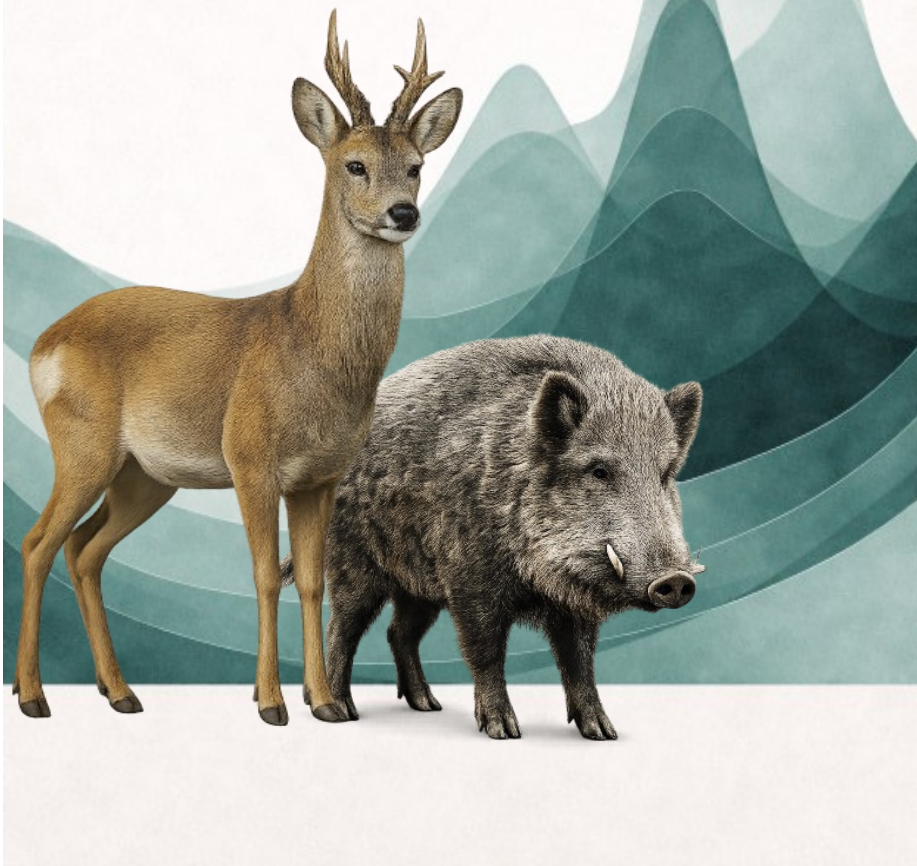


Large-scale Monitoring of Wild Mammal Abundance

Modeling Frameworks for Structured and Unstructured Data

Sonia Illanas
PhD Thesis
2026

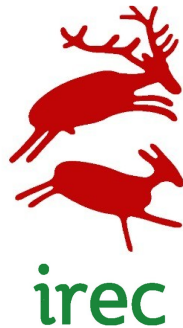


Instituto de Investigación en Recursos Cinegéticos
Programa de Doctorado en Ciencias Agrarias y Ambientales
Universidad de Castilla-La Mancha



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Ciudad Real, 2026

Instituto de Investigación en Recursos Cinegéticos
(CSIC-UCLM-JCCM)

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LARGE-SCALE MONITORING OF WILD MAMMAL ABUNDANCE: MODELING FRAMEWORKS FOR STRUCTURED AND UNSTRUCTURED DATA

Memoria presentada por

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para optar al grado de Doctor con Mención Internacional
por la Universidad de Castilla-La Mancha

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Universidad de Castilla-La Mancha

Where there is a will,

there is a way

—George Herbert

There can be no doubt
that all our knowledge
begins with experience.

—Immanuel Kant

Nature never deceives us;
it is always we who deceive ourselves.

—Jean-Jacques Rousseau

Ideas do not last long.
Something must be done with them.

—Ramón y Cajal

You don't have to win the race.

You just need to **win your race.**

And winning the race **means**
falling in love with the process.

...

Take your mark, and go out there
and **make your mark.**

—Katie Ledecky

*A mis padres, Pablo y Carmen,
a mi hermana Noelia y mis sobrinos Hernán y Darío;
a mis amigos, mis compañeros de la vida:
por estar en cada paso y celebrar cada logro.*

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Abstract / Resumen



Abstract

Large-scale biodiversity conservation and wildlife management increasingly require spatially explicit diagnostics that go beyond species occurrence to patterns of abundance. In Europe, management is typically implemented within administrative units, whereas policy and assessment increasingly operate at supra-national levels, making robust inference on abundance central to decision-making. However, consistent estimation across space and time is challenged by heterogeneous data, uneven observation processes, and aggregation effects from mismatched spatial units. This PhD thesis develops and evaluates a cross-cutting framework to infer abundance patterns of European mammals from complementary monitoring data, and to quantify how data standardization, model selection, and ecological interpretation across spatial scales. It examines how data sources, modeling decisions, and spatial structure shape inference, uncertainty, and transferability of results across scales.

The thesis is structured around four objectives. First, it establishes a reproducible foundation for large-scale inference by compiling and standardizing monitoring data. Chapter 2 mobilizes a decade of hunting-yield records for Spain and addresses a common constraint: fine-resolution count data are often subject to restrictions that limit sharing. To enable open reuse, the hunting records are recast as a public presence-only dataset (presence vs. unknown rather than presence-absence) and released as a harmonized FAIR-aligned product with fully

documented code. This chapter illustrates how unstructured, stakeholder-generated records can be converted into national-scale spatial evidence, while making uncertainty and interpretational limits explicit.

Second, the thesis develops and compares flexible modeling frameworks for large-scale inference on abundance (or relative abundance) from heterogeneous monitoring data. Chapters 3 and 4 demonstrate that “one-size-fits-all” approaches rarely generalize across species because data structure and management context differ (*e.g.*, distribution ranges, reporting completeness, regulation, and the meaning of zeros). Chapter 4 quantifies how preprocessing rules (*e.g.*, imputing zeros vs. treating missingness as unknown) and modeling decisions (*e.g.*, area offset and regionalization) can yield broadly similar-looking maps while substantially shifting predicted magnitudes and uncertainty, demonstrating that these choices are substantive and must be formalized and reported. Chapter 5 then isolates the role of scale and spatial structure in models that explicitly account for spatial dependence by using wild boar data across Europe. It shows that these models can reduce artificial discontinuities at regional borders, but that performance depends on the resolution and homogeneity of observation units when centroids are used to estimate spatial structure. Extreme variation in unit size can destabilize covariance estimation and produce implausible patterns in regions with coarse-data. Finally, Chapter 7 applies a structured national camera-trap design and multispecies N-mixture models to disentangle relative abundance from detectability. The results reveal strong

species-specific differences in detectability and higher uncertainty for low-detectability species.

Third, cross-dataset comparisons indicate only weak agreement between camera-trap-based indices and hunting-yield proxies across scales, underscoring that different observation processes can produce divergent abundance signals and thus should be jointly considered to obtain a more comprehensive assessment of abundance.

Fourth, the thesis extends large-scale inference to interspecific spatial relationships by revisiting bivariate spatial association metrics. Chapter 6 reformulates the global and local L index to incorporate species-specific connectivity. This innovation addresses a key limitation of overlap-based co-location metrics when ecological processes operate beyond observation-unit boundaries. By using species-informed connectivity, the analysis reveals spatial association patterns (*e.g.*, convergence vs. divergence zones) that can differ systematically from interpretations based on uniform-connectivity, with direct implications for multi-species management prioritization.

Overall, this thesis shows that progress in large-scale ecological inference depends on transparent data infrastructures and explicit methodological choices that interact with ecological complexity. By delivering open workflows, evaluating sensitivity to preprocessing and modeling decisions, and developing tools that better represent observation and spatial processes, the PhD thesis provides

practical, policy-relevant evidence for wildlife management, conservation reporting, and animal health risk assessment across Europe.

Resumen

La conservación de la biodiversidad y la gestión de fauna silvestre a gran escala requieren cada vez más diagnósticos espacialmente explícitos que vayan más allá de la mera ocurrencia de las especies y describan patrones de abundancia. En Europa, la gestión se implementa en unidades administrativas, mientras que la política y la evaluación operan cada vez más en niveles supranacionales, lo que sitúa la inferencia sobre la abundancia en el centro de la toma de decisiones. Sin embargo, la estimación consistente en el espacio y en el tiempo se ve dificultada por la heterogeneidad de los datos, la variabilidad de los procesos de observación y los efectos de agregación derivados de unidades espaciales no alineadas. Esta tesis doctoral desarrolla y evalúa un marco conceptual y estadístico transversal para inferir patrones de abundancia a gran escala de mamíferos europeos a partir de datos de monitorización complementarios, y para cuantificar cómo la estandarización de datos, la selección de modelos y la interpretación ecológica cambian con la escala espacial. En particular, analiza cómo distintas fuentes de datos, decisiones de modelización y la estructura espacial condicionan la inferencia, la incertidumbre y la transferibilidad de los resultados.

La tesis se articula en torno a cuatro objetivos. En primer lugar, establece una base reproducible para la inferencia a gran escala mediante la compilación y estandarización de datos de monitorización. El Capítulo 2 moviliza una década de registros de bolsas de caza en España y aborda una limitación frecuente: los recuentos a resolución fina suelen estar sujetos a restricciones en el acceso a los datos. Para facilitar su reutilización en abierto, los registros cinegéticos se transformaron en un conjunto de datos públicos de solo presencia (presencia vs. desconocido, en lugar de presencia-ausencia), y se publicaron como un producto armonizado y alineado con principios FAIR, con código completamente documentado. Este capítulo muestra cómo registros no estructurados generados por actores implicados pueden transformarse en evidencia espacial a escala nacional, explicitando la incertidumbre y los límites de interpretación.

En segundo lugar, la tesis desarrolla y compara marcos de modelización flexibles para la inferencia a gran escala de abundancia (o abundancia relativa) a partir de datos de monitorización heterogéneos. Los Capítulos 3 y 4 muestran que los enfoques únicos rara vez son generalizables entre especies, dado que la estructura de los datos y el contexto de gestión difieren (p. ej., rangos de distribución, grado de cobertura de los datos, regulación y significado de los ceros). El Capítulo 4 cuantifica cómo reglas de preprocesado (p. ej., imputar ceros a valores inciertos frente a descartarlos) y decisiones de modelización (p. ej., el uso del área como offset y la regionalización) pueden producir mapas aparentemente similares, mientras modifican de forma sustancial las magnitudes predichas y la

incertidumbre asociada. Estos resultados evidencian que estas decisiones no son un mero detalle técnico, sino determinantes de la inferencia y deben formalizarse y reportarse como parte del procedimiento analítico. El Capítulo 5 aísla el papel de la escala y la estructura espacial en modelos que incorporan explícitamente la dependencia espacial, utilizando datos de jabalí a escala europea. Los resultados muestran que este tipo de modelos puede reducir discontinuidades artificiales en fronteras regionales, pero su rendimiento depende de la resolución y homogeneidad de las unidades observacionales, especialmente si se emplean sus centroides para la construcción de la dependencia espacial. Una variación extrema en el tamaño de las unidades puede desestabilizar la estimación de la covarianza y generar patrones implausibles en regiones con datos muy agregados. El Capítulo 7 aplica un diseño estructurado de fototrampeo a escala nacional y modelos N-mixture multiespecie para separar abundancia relativa y detectabilidad. Los resultados revelan diferencias marcadas en detectabilidad entre especies y un aumento de la incertidumbre en especies con baja detectabilidad.

En tercer lugar, las comparaciones entre fuentes de datos indican una concordancia débil entre los índices derivados de cámaras trampa y los *proxies* basados en bolsas de caza a distintas escalas, lo que subraya que diferentes procesos de observación pueden generar señales de abundancia divergentes y que, por tanto, considerar conjuntamente ambas fuentes de datos puede dar lugar a una evaluación más robusta de la abundancia.

En cuarto lugar, la tesis amplía la inferencia a gran escala al análisis de relaciones espaciales interespecíficas mediante la revisión de métricas bivariadas de asociación espacial. El Capítulo 6 reformula el índice L global y local para incorporar conectividad específica por especie. Esta innovación aborda una limitación clave de las métricas basadas únicamente en solapamiento espacial cuando los procesos ecológicos operan más allá de los límites de las unidades de observación. Al incorporar la conectividad informada por las especies, el análisis permite identificar patrones de asociación (*p. ej.*, zonas de convergencia frente a zonas de divergencia) que pueden diferir de las interpretaciones basadas en conectividad uniforme, con implicaciones directas para la priorización de la gestión multiespecie.

En conjunto, esta tesis muestra que el progreso en inferencia ecológica a gran escala depende de infraestructuras de datos transparentes y de decisiones metodológicas explícitas que interactúan con la complejidad ecológica. Al proporcionar flujos de trabajo abiertos, evaluar la sensibilidad al preprocesado y a las decisiones de modelización, y desarrollar herramientas que representan mejor los procesos de observación y la estructura espacial, la tesis aporta evidencia práctica y relevante para políticas de gestión de fauna, informes de conservación y evaluación de riesgos sanitarios en Europa.

1. General Introduction



1.1. Why large-scale abundance matters

Biodiversity conservation and wildlife management increasingly depend on spatially explicit diagnostics that move beyond species presence to patterns of abundance (Fletcher et al., 2025). This shift is a cornerstone of the EU Biodiversity Strategy for 2030. While decisions in Europe were historically taken at administrative resolutions (*e.g.*, regional or national), a supra-national ecological perspective is now shaping the trajectory of directives and regulations through a multi-level governance system that integrates policy-making, scientific assessment, data collection, and national implementation.

In this framework, the European Commission (DG Environment) establishes the policy roadmap, including legislation and strategies such as the European Green Deal or the Nature Restoration Law. Meanwhile the European Environment Agency (EEA), through the European Environmental Information and Observation Network (EIONET), provides the technical backbone by coordinating the flow of environmental data and scientific assessment from national experts and institutions to EU decision-makers. Supporting this system are the European Topic Centres (ETCs), specialized thematic centres (*e.g.*, biodiversity, climate change, circular economy) contracted by the EEA to provide technical and scientific expertise. At the national level, National Environmental Protection Agencies (EPAs) and related institutions collect environmental data, implement EU environmental legislation, and manage conservation programs, reporting information back to the EEA through EIONET.

General Introduction

This structure ensures a top-down cascading effects of directives and regulations (**Figure 1.1**), where supra-national goals are transposed into national legislation and, ultimately, translated into regional operational policies. Overall, environmental governance in Europe operates as a coordinated system where data are collected regionally, harmonized and validated nationally, and analyzed and synthesized at the European level, and then used by the European Commission to propose policies and legislation that are implemented again at national level, ensuring that local management aligns with continental ecological needs.

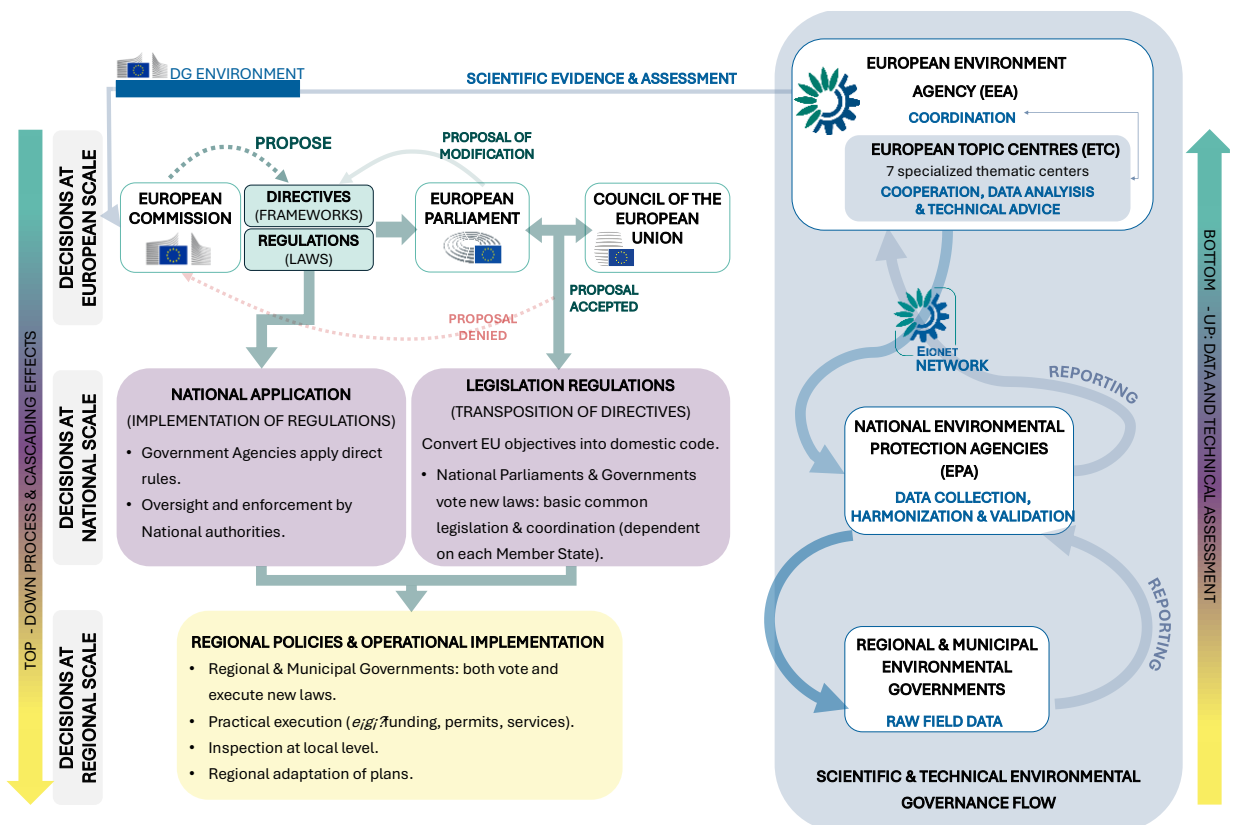
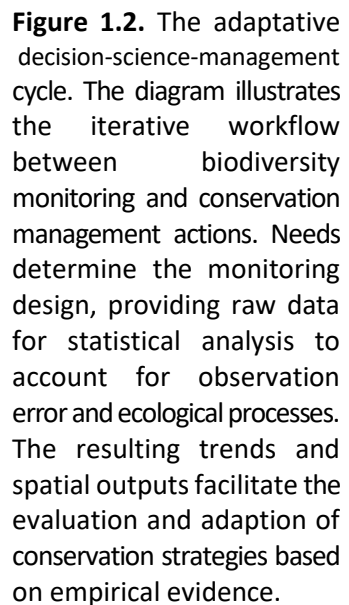


Figure 1.1. Multi-level environmental governance in the European Union. The diagram illustrates the top-down cascading effects of directives and regulations, from supra-national policy to regional and local implementation, alongside the bottom-up data and technical assessment flow.



Wildlife data in Europe are obtained through various sampling methodologies, including direct and indirect methods, under both structured and unstructured designs and by specialized and non-specialized personnel. Notably, a significant portion of these datasets is characterized by a high volume of records collected over time across extensive areas, specifically hunting bags, wildlife-vehicle collisions and citizen science observations. These data are typically recorded without a formal sampling design and are therefore considered unstructured opportunistic datasets (Imperio et al., 2010; Isaac et al., 2014; Kissling et al., 2018; Zipkin et al., 2021). By contrast, structured datasets are developed by specialists following rigorous sampling designs for specific purposes (Nichols & Williams, 2006; Yoccoz et al., 2001). Structured datasets typically came from field work under wildlife population monitoring programs supported science-validated sampling designs and methodologies. However, most of the methodologies such as spotlight counts, listening stations or aerial surveys require intense field work and therefore tend to be locally applied, being mostly unfeasible applied to large spatial scales. More recently, camera trap data have emerged as practical, complementary sources for large-scale inference (*e.g.*, ENETWILD-consortium, Guerrasio, et al., 2024; Rooney et al., 2025; Steenweg et al., 2017; Townsend et al., 2021). They offer wide coverage and multi-species breadth and, under some sampling designs, can be scalable to produce large-scale inference.

Differences in sampling design across data sources lead to variation in detection processes, sampling effort, and spatial structure, which introduce

potential sources of bias. Addressing these sources of bias is essential when integrating opportunistic and structured datasets within adaptive monitoring frameworks, ensuring that their joint use leads to more robust ecological inference and ultimately improves wildlife management and decision-making.

1.2. Abundance as a latent state and why it matters

From an inferential standpoint, abundance is a latent ecological state: it cannot be observed directly and is only inferred through observation processes (Royle & Dorazio, 2008). The observation processes are governed by detectability, sampling effort, and data collection protocols (MacKenzie et al., 2002, 2017). A key challenge is identifiability, as abundance and detection processes can be confounded unless the model is appropriately structured or supported by auxiliary information (*e.g.*, repeated observations, effort data, or independent detection covariates), which help to disentangle ecological and observational processes. A conceptual overview of these components is provided in **Box 1**.

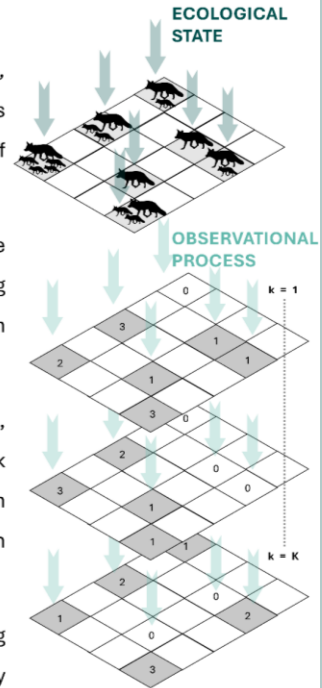
A critical distinction must be made between density (*i.e.*, abundance per unit area), abundance (*i.e.*, counts within a spatial unit), and relative abundance (*i.e.*, an index proportional to abundance or density, *e.g.*, hunting yields) because interpretation, comparability, and management use depend on these distinctions (see **Box 1**).

At local to regional scales, variation in abundance emerges from the interplay of climate and productivity, habitat composition and configuration, land-use intensity,

Box 1 - Glossary

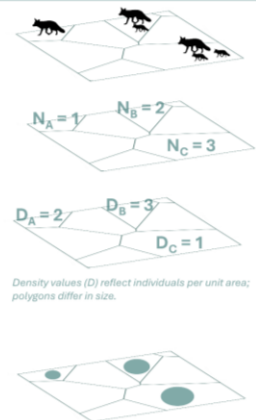
Ecological and Observational processes

- **Latent state** refers to the true underlying ecological state (e.g., abundance, occupancy) that is not directly observed. It represents the actual state of the system (e.g., presence/absence or number of individuals) at a site or across space.
- **Observation process** describes how the latent state give rise to the observed data through imperfect detection. It includes the sampling design and detection process, linking the true ecological state with the data collected.
- **Detection** is the probability of detecting an individual, or a species, given that is present at a surveyed site. When sampling is repeated k times, the cumulative probability of detecting the species, or an individual, at least once is $p^* = 1 - (1 - p)^k$, where p is the detection probability during a single survey occasion.
- **Effort** refers to the sampling intensity (e.g., camera days, hunting effort, transect length, number of occasions) and is typically included as a covariate influencing detection probability and, in some cases, the observed counts.



Population state variables

- **Abundance (N)** is the total number of individuals of a species present within a defined time period in a study area.
- **Density (N/area)** is the number of individuals per unit area (e.g., individuals/km²) within a defined time period, providing a spatially standardized measure of abundance.
- **Relative abundance** is an index proportional to true abundance or density that does not estimate the actual number of individuals, but can be used for temporal, and spatial comparisons. In practice, relative abundance is often quantified using indices derived from raw observational data.



Population quantification

- **Index** is a RAW measure assumed to increase with the underlying ecological state (e.g., abundance), and is therefore useful for temporal, or spatial comparisons. However, it does not explicitly account for effort or detectability and thus cannot be interpreted as an estimate of true population size.
- **Estimator** is the output of a statistical model that explicitly account for components of the observational process, providing an inferred value of population quantity (e.g., abundance, density or relative abundance) along with its associated uncertainty.

species movement and ecological connectivity, interspecific interactions, and management and regulation (*e.g.*, Brown, 1995; Elith & Leathwick, 2009; Hanski, 1999; Turner, 1989; Youngflesh et al., 2025). These drivers often exert nonlinear, spatially structured effects, with thresholds and context dependence that complicate extrapolation across continental bioclimatic gradients (Doser et al., 2025; Rollinson et al., 2021).

1.3. Data sources: hunting yields and camera traps

1.3.1 Hunting yields statistics

Hunting yields (HYs) reflect a composite signal encompassing true abundance (N), hunting effort, hunter strategy, detectability and regulatory constraints, and are therefore interpreted as indices, typically used as proxies for relative abundance (*e.g.*, Imperio et al., 2010). This data source offers several key advantages including extensive spatial coverage, continuity over multiple years, and the ability to provide information on multiple game species (ENETWILD-consortium, Plis, et al., 2024).

Nonetheless, several challenges arise when using HYs, as it is typically reported by non-specialized personnel and do not follow a formal sampling design nor a common protocol, thus constituting an unstructured dataset. Consequently, HYs includes heterogeneity in reporting systems (**Figure 1.3**; Guillemain et al., 2026). This includes potential under or over reported harvest, variability in effort metrics (*e.g.*, number of days, number of hunters, number of dogs, number of

animals seeing, or surface beat), differences in temporal resolution (*e.g.*, annually vs. daily records), and the influence of evolving technologies (*e.g.*, optics). Additional sources of heterogeneity stem from hunters' preferences (*e.g.*, target species, sex, age class, and hunting method), data accessibility (*e.g.*, public administrations, hunting associations, or private managers), variation in willingness or commitment to participate in data recording, and regulatory changes across countries and regions (ENETWILD-consortium et al., 2018; Guillemain et al., 2026; Moreno-Zarate et al., 2021; Ruiz-Rodríguez et al., 2023).

For large-scale inference on abundance, incorporating area size as a proxy for hunting effort may be essential, as it helps standardize units across heterogeneous administrative areas (Lindström & Bergqvist, 2022). When hunting effort data is unavailable, or unreliable, raw counts may need to be reduced to presence-only records, resulting in a loss of quantitative information but providing robust indicators of species occurrence. More generally, appropriate analytical frameworks are required to disentangle the ecological signal from the observation process inherent to HY data (Fernández-López et al., 2025).

1.3.2 Camera traps

Camera traps record the presence of a species moving within the sensor detection zone. As such, detections are governed by animal movement, social and foraging behavior, and patterns of site use, as well as by device configuration and deployment (Burton et al., 2015; Rowcliffe et al., 2008). When camera traps are

deployed by trained personnel under following standardized field protocols and formal sampling design, they constitute structured datasets that can provide information on population abundance.

Their primary advantages include providing a direct, non-invasive monitoring method, scalability to broad spatial extents, the ability to support multi-species inference and increasingly standardized data processing workflows (*e.g.*, DeepFaune v06; **Figure 1.3**; Burton et al., 2015; Rigoudy et al., 2023; Steenweg et al., 2017). Regardless of the formal rigor of sampling designs implemented by specialized personnel, logistical trade-offs during field deployment are common and the final selection of sampling micro-sites often involves a degree of expert subjectivity. Decisions made to ensure equipment safety, to navigate inaccessible terrain (*e.g.*, favoring proximity to trails in areas of high ruggedness or dense forests), or to pursue optimal sensor placement (*e.g.*, ensuring clear visibility of camera trap) may potentially introduce bias in detection probabilities (Cusack et al., 2015; Kolowski & Forrester, 2017). In addition, camera traps sample a small portion of the landscape, making them sensitive to placement decisions and fine-scale habitat heterogeneity (Barton et al., 2025; Fuller et al., 2022; Kolowski et al., 2021). This can limit comparability across species, as detection rates depends strongly on species-specific traits such as sociality (*e.g.*, gregarious vs. non-gregarious), movement ecology (*e.g.*, wide-ranging vs. site-attached species), and foraging strategies (Burton et al., 2015; Caravaggi et al., 2020; Hofmeester et al., 2019).



HUNTING YIELDS

OPPORTUNITIES

Extensive
spatial
coverage

Long-term
time series

Multiple
species
(targeted)

Opportunistic
(low cost)

CHALLENGES

Regional heterogeneity and hunter-driven selectivity

Regulations

Data
accessibility

Spatial
heterogeneity

Hunting
method &
technologies



Hunters
commitment
& motivation



Target
species



Age
class



Sex



CAMERA TRAPS

OPPORTUNITIES

Scalable to
broad spatial
extents

Multiple
years

Multiple
species
(community-level)

Standardized
protocols

Direct ,
non-invasive

CHALLENGES

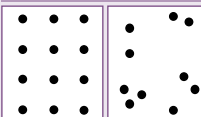
Species site
use



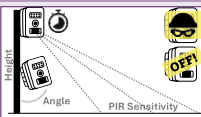
Microhabitat
variation



Sampling
design choices



Camera
performance



Massive
processing



Figure 1.3. Complementary strengths and limitations of hunting yields and camera trap data for large-scale ecological inference.

Furthermore, camera traps are affected by imperfect detection arising from device performance and operational issues, including camera failure, theft, and variation in configuration (*e.g.*, height, angle, sensitivity; DeWitt & Cocksedge, 2023). These factors directly affect the observation process and must be explicitly accounted for in statistical analyses, such as multi-species N-mixture models for repeated counts, with careful treatment of detectability and sampling effort.

1.3.3 Complementarity and integration

Hunting yields provide temporal and spatial continuity in areas where hunting is allowed, whereas camera traps provide higher ecological resolution through structured sampling, particularly when imperfect detection is explicitly accounted for. Species-specific differences in ecological traits influence how they are detected and represented across data sources, as some species are more likely to be captured by structured monitoring approaches such as camera traps, whereas others may be better represented in unstructured data such as hunting yields. Similarly, both methods can inform about the population status in territories under different management schemes; for instance, the list of game species may vary across Europe, such as it is the case with carnivore species, or hunting is prohibited in some areas, such as National Parks in Spain (Carpio et al., 2024; Kurek et al., 2022). As a result, these data sources capture complementary aspects of the ecological state of the community through different observational processes (**Figure 1.4**).

Combining them within a hierarchical, multi-likelihood framework, where each data source is represented by a separate observation submodel linked through a shared latent abundance process, can improve predictions precision, model calibration, and ecological interpretability (Gilbert, Pease, et al., 2021; Yoccoz et al., 2001; Zipkin et al., 2021). Beyond single-species inference, this integration also provides a foundation for analyses that consider multiple species simultaneously, enabling more comprehensive characterization of ecological communities across large spatial scales (*e.g.*, Zipkin et al., 2023). Recent advances in integrated and multi-species modeling frameworks demonstrate that robust inference is feasible even under heterogeneous observation processes (*e.g.*, Doser et al., 2022; Leuenberger et al., 2025). These studies highlight the potential of integrated approaches to overcome limitations of individual data sources and provide more comprehensive insights into ecological systems. However, the success of such integration critically depends on adequately accounting for source-specific biases and differences in sampling processes (Goldstein et al., 2026; Isaac et al., 2020; Zipkin et al., 2021). Failure to do so may propagate systematic errors rather than reduce uncertainty. When properly implemented, integrated models can leverage the strengths of each data type while mitigating their individual limitations, providing a more robust basis for large-scale ecological inference (Gilbert, Pease, et al., 2021; Zipkin et al., 2021).

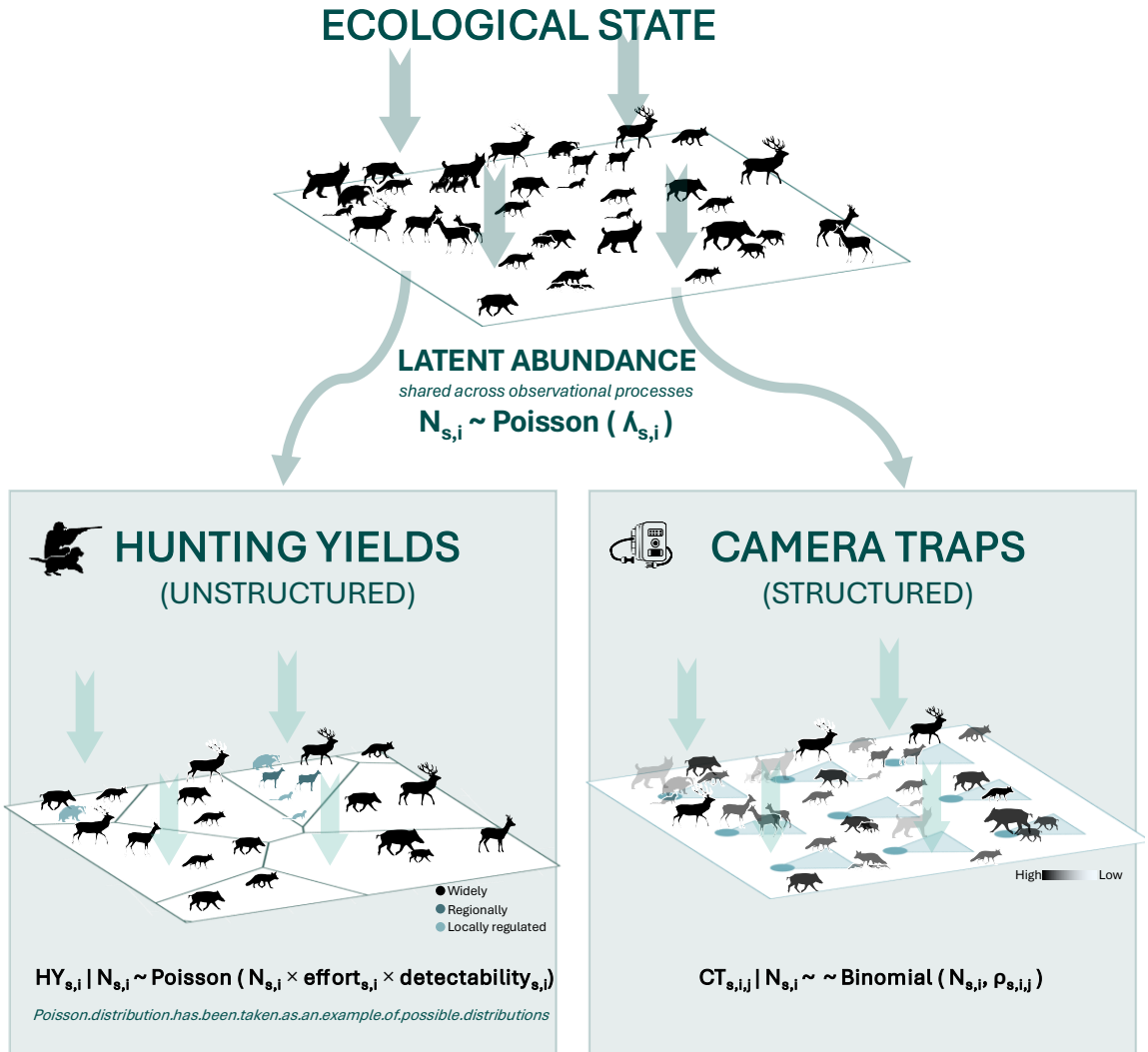


Figure 1.4. Conceptual representation of a shared latent ecological state and its observation through two distinct processes: unstructured hunting yield data and structured camera trap data. Each observation process provides a partial and biased view of species abundance, driven by species distribution, selectivity and regulatory constraints (hunting yields) or imperfect detection (camera traps).

1.4. Challenges of estimating abundance at large spatial scales

Estimating abundance at large scales is inherently challenging due to multiple interacting sources of uncertainty arising from data collection, observation processes and model-based inference (Guisan & Thuiller, 2005). These challenges affect the reliability, comparability and transferability of ecological inference.

i) **Detectability, effort and sampling biases.** Observation processes are shaped by variability in detectability and sampling effort. Detectability varies across species, habitats, behaviors, seasons, observation methods, and in some cases may itself depend on abundance (Kéry & Schmidt, 2008). Technological advances can simultaneously affect detectability and introduce heterogeneity in observation processes when unevenly adopted across space or time (Hughes et al., 2026; Kułaga & Budka, 2019; Schmidt et al., 2023). Sampling effort (*e.g.*, hunting area, hunting days, number of hunters, dog teams, number of cameras) is highly heterogeneous in space and time and is often incompletely recorded (ENETWILD-consortium, Vicente, et al., 2019). In addition, many ecological datasets are affected by sampling and reporting biases, including preferential sampling, where observations are more likely to occur (high-activity locations) or easy to access (Diggle et al., 2010). Together, these factors introduce systematic distortions in the observation process and can lead to biased or non-comparable estimates if not explicitly accounted for.

ii) **Spatial heterogeneity, dependence, and scaling effects.** European administrative borders vary widely in area, shape, and ecological

representativeness, which has implications for the estimation of abundance at broad spatial scales. Furthermore, spatial ecological data are inherently structured across multiple scales, and estimates of abundance are sensitive to the spatial units over which data are aggregated. Aggregating spatial ecological data to arbitrary spatial units, such as administrative boundaries, gives rise to the Modifiable Area Unit Problem (MAUP; Openshaw, 1983; see **Box 2**) and related change-of-support issues (Gotway & Young, 2002). At the same time, ecological processes such as movement, dispersal, and resource use operate independently of these boundaries, inducing spatial dependence by creating correlations in abundance across neighboring locations (Legendre, 1993). Failing to account for these spatial structures can result in biased inference, particularly when aggregating or comparing studies conducted at different spatial resolutions (Mäkinen et al., 2022; Paciorek, 2010).

iii) **Collinearity, confounding and transferability.** Environmental and anthropogenic drivers (*e.g.*, climate, productivity, habitat, human footprint) often covary, leading to collinearity and confounding that can obscure ecological relationships (Dormann et al., 2013). In particular, correlated predictors can make it difficult to disentangle their individual effects, resulting in unstable parameter estimates and ambiguous ecological interpretation. In addition, confounding arises when relevant drivers are omitted or imperfectly represented, leading to misleading attribution of ecological effects (Gelman & Hill, 2007). Without appropriate modeling strategies these issues can propagate into biased inference and unreliable

ecological conclusions. Furthermore, models calibrated under specific environmental conditions may fail when transferred to new context due to covariate shift and domain mismatch (Elith et al., 2010). Particularly, while confounding may still allow accurate predictions within the range of observed conditions, it can severely limit model transferability when relationships among predictors change across space or time (Mäkinen et al., 2022; Werkowska et al., 2016). Distinguishing interpolation from extrapolation —*i.e.*, whether predictions are made within the sampled geographical domain or projected into new geographical areas, even when environmental conditions are represented in the data— identifying regions of reliable prediction, and explicitly quantifying uncertainty are therefore essential for robust and transferable large-scale inference (Elith et al., 2010; Waldock et al., 2022; Yates et al., 2018).

1.5. A transversal conceptual and statistical framework

Building on a long-standing tradition of studying the relationships between species and the environment, from early naturalists to the field of modern quantitative ecology, the increased availability of biodiversity data and advances in computational methods have made it possible to take a more formal approach to linking ecological processes with environmental and anthropogenic gradients since the late 20th century (Gilbert et al., 2024). These developments are particularly relevant in the context of large-scale biodiversity monitoring, where heterogeneous data sources and complex ecological processes must be jointly considered (Goldstein et al., 2026; Zipkin et al., 2023).

As described in [section 1.3](#), different data sources provide partial and potentially biased representations of ecological systems (**Figure 1.3**), as observations

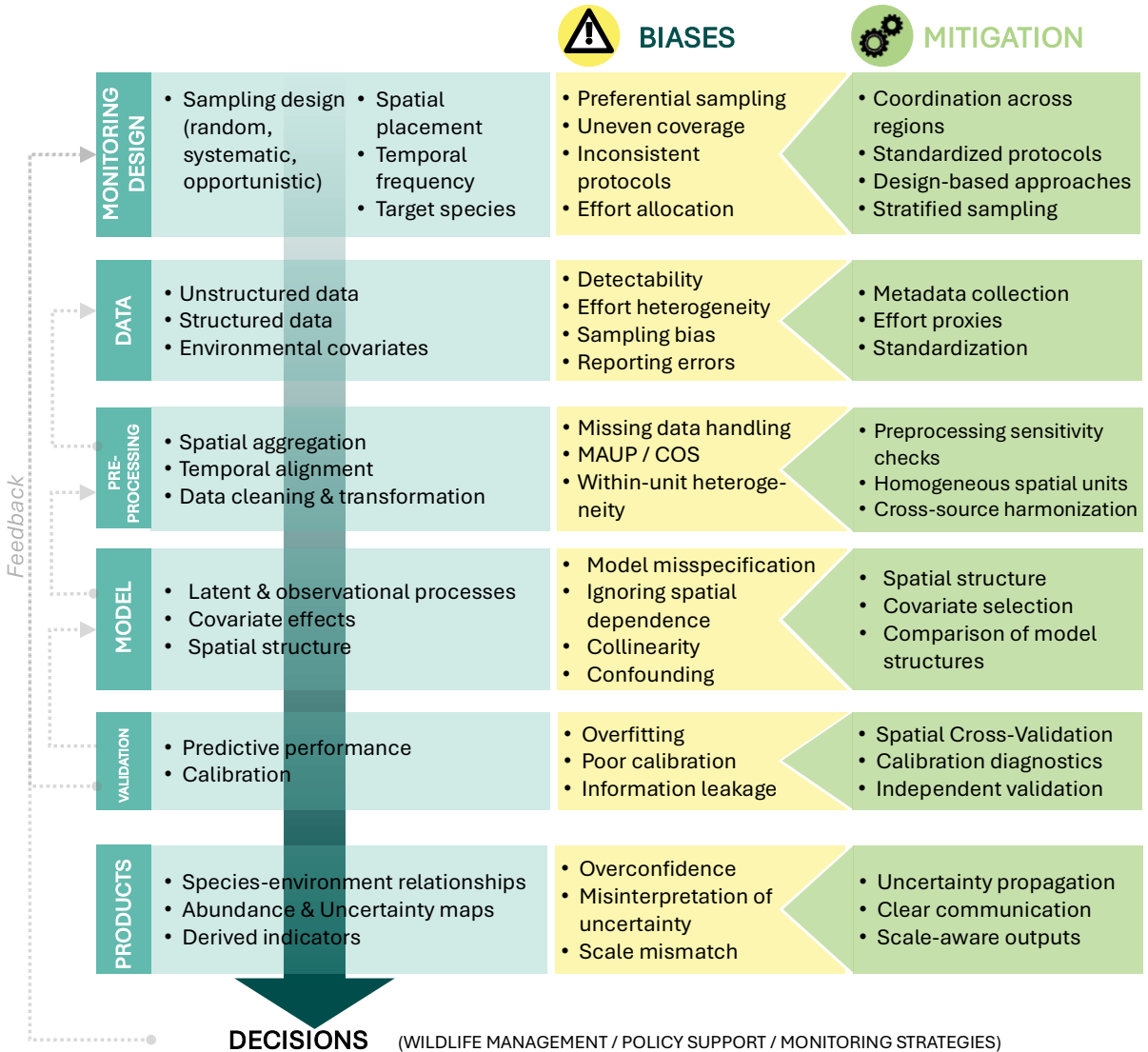


Figure 1.5. Conceptual pipeline for ecological modeling. The diagram illustrates the main stages from data collection to decision-making, highlighting where biases arise (yellow) and how they can be mitigated (green). Feedback loops between stages reflect adaptive monitoring and model refinement processes.

Box 2 – The Modifiable Areal Unit Problem (MAUP)

Biodiversity patterns across space can be conceptualized as arising from an **Inhomogeneous Point Process (IPP)**, in which the intensity of occurrence is governed by continuous environmental, biotic and dispersal-related drivers. However, ecological data are rarely observed at infinitesimal resolution and are typically aggregated into discrete spatial units for analysis. This aggregation step can introduce systematic distortions in the observed patterns.

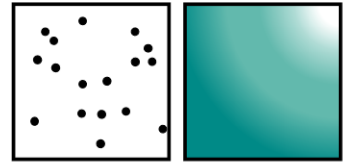
The **modifiable areal unit problem** (MAUP; Openshaw, 1983) occurs because statistical summaries depend on the spatial partition used. It comprises two components: the **scale effect**, whereby results vary in the size (or resolution) of spatial units, and the **zoning effect**, whereby results vary with the configuration or boundaries of units at a fixed scale. Aggregating fine-scale biological data into coarser units alters the internal structure of variability, typically reducing local heterogeneity and modifying distributional properties, which can subsequently affect statistical inference.

MAUP also influences spatial dependence. Because spatial autocorrelation is inherently scale-dependent, changes in the size or configuration of aggregation units can alter both the apparent strength and range of spatial autocorrelation. This, in turn, affects model fit and uncertainty quantification.

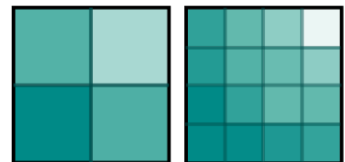
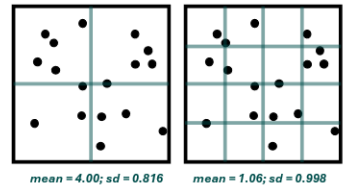
A further implication is that aggregation affects not only the response variable but also the spatial resolution of covariates. As resolution decreases, covariates tend to become more homogeneous, potentially obscuring fine-scale variation that is ecologically relevant. This can generate scale mismatches between ecological processes and their representation in the data, complicating interpretation and limiting comparability across studies conducted at different spatial resolutions.

Finally, the size and configuration of the prediction units may also affect the transferability of model estimates. When there is a mismatch between the spatial support of observations and of predictions, inferred relationships may not generalize. This issue is closely related to the **change of support problem** (COS), which formally addresses how statistical properties of spatial variables change when the spatial support is modified. Consequently, caution is required when extrapolating results across spatial scales or zoning schemes.

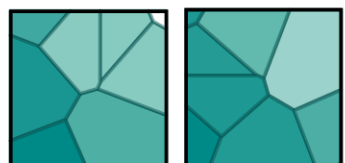
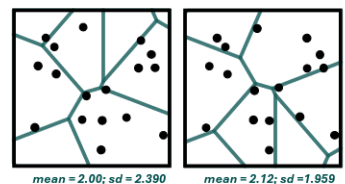
BIODIVERSITY & COVARIATE PATTERN



SCALE EFFECT



ZONING EFFECT



are shaped by the processes through which data are collected (**Figure 1.4**). Data alone do not provide direct or unbiased description of ecological patterns, and statistical models are required to relate observed data to environmental drivers and to support inference across spatial and temporal scales (Royle & Dorazio, 2008; Yoccoz et al., 2001). Models provide a formal framework to integrate heterogeneous data sources and infer underlying ecological processes. Importantly, modeling approaches also enable more efficient use of available data, allowing robust inference over large spatial domains without the need for exhaustive sampling that become unfeasible at large spatial scales (national or continental). By leveraging spatial and environmental structure, models can generalize information from sampled locations to unsampled areas, thereby supporting scalable monitoring strategies (Acevedo, González-Quirós, et al., 2014; Elith & Leathwick, 2009; Guisan & Thuiller, 2005).

To address these challenges, this thesis has adopted a conceptual modeling framework in which ecological systems are understood as the result of the interaction between an underlying ecological process and the observation processes that generate the data (MacKenzie et al., 2002). Although not all models implemented in this thesis explicitly separate these components, all data sources considered arise from their interaction. Distinguishing between ecological and observation processes provides a unifying perspective to interpret model outputs and to assess their limitations across different analytical approaches, including both unstructured data such as hunting yields and structured data such as camera traps.

Within this framework, species abundance, density, or relative abundance is treated as an underlying ecological state that varies across space as a function of environmental and anthropogenic drivers, including climate, land use and land-cover, human footprint, and management practices and regulations. These effects may be nonlinear and species-specific and may exhibit spatial structure due to unmeasured processes and neighborhood dependence. Accounting for spatial dependence is therefore essential when modeling ecological patterns at large spatial scales (Cressie, 1993; Legendre, 1993).

A central theme of the thesis is that modeling decisions, from data preprocessing to model specification and predictions, have first-order effects on ecological inference. While statistical models provide the primary tools for linking data to ecological processes, these decisions shape how models are implemented and how their outputs should be interpreted, influencing model performance, transferability, and uncertainty (Guillera-Arroita et al., 2015). These include the representation of spatial structure, the choice of spatial resolution and aggregation units, the treatment of effort and detectability or the interpolation and extrapolation. Such decisions influence not only model performance, but also interpretation, transferability and uncertainty of the resulting estimates. This conceptual perspective is operationalized through a workflow that links data sources, preprocessing decisions, modeling approaches, and validation steps (**Figure 1.5**). To ensure robust inference, models are evaluated through comparisons across alternative specifications and assessed using calibration plots and sensitivity

to data preprocessing decisions. This allows understanding the impact of modeling decisions across species and spatial context, as well as the extent to which inference depends on modeling decisions, which is essential for their use in ecological understanding and wildlife management.

1.6. Study area, scales and focal species

Large-scale ecological inference requires a clear definition of both the spatial and temporal domains from which the underlying processes emerge and where management decisions are enacted. This thesis covers multiple spatial domains across Europe. It includes continental-scale analyses and national-scale case studies in Spain. Across these domains the combination of pronounced bioclimatic gradients, heterogeneous administrative units, and diverse monitoring systems provides an ideal setting for evaluating how spatial structure and environmental non-stationarity affects abundance inference derived from both structured and unstructured data.

1.6.1. Spatial domain: Europe and Spain

Europe encompasses five major bioclimatic regions: Atlantic, Mediterranean, Continental, Alpine, Boreal and Subtropical, which collectively shape species distribution, abundance and ecological strategies (**Figure 1.6**; Kriticos et al., 2012; Metzger et al., 2013). Within this continental context, Spain constitutes a biodiversity hotspot characterized by the convergence of Atlantic, Mediterranean, and Alpine climatic regimes, steep altitudinal ranges, and highly diverse land-cover

General Introduction

mosaics (Myers et al., 2000). This variability generates sharp ecological transitions over relatively short geographic distances. In addition, long-term anthropogenic pressures, including agriculture, forestry, hunting, and urbanization, introduce additional spatial structure to wildlife abundance patterns. Together, these gradients, both at continental and national level, introduced marked environmental heterogeneity and potential non-stationarity in species-environment relationships, a major challenge in macroecological modeling (Beale et al., 2010; Dormann et al., 2007).

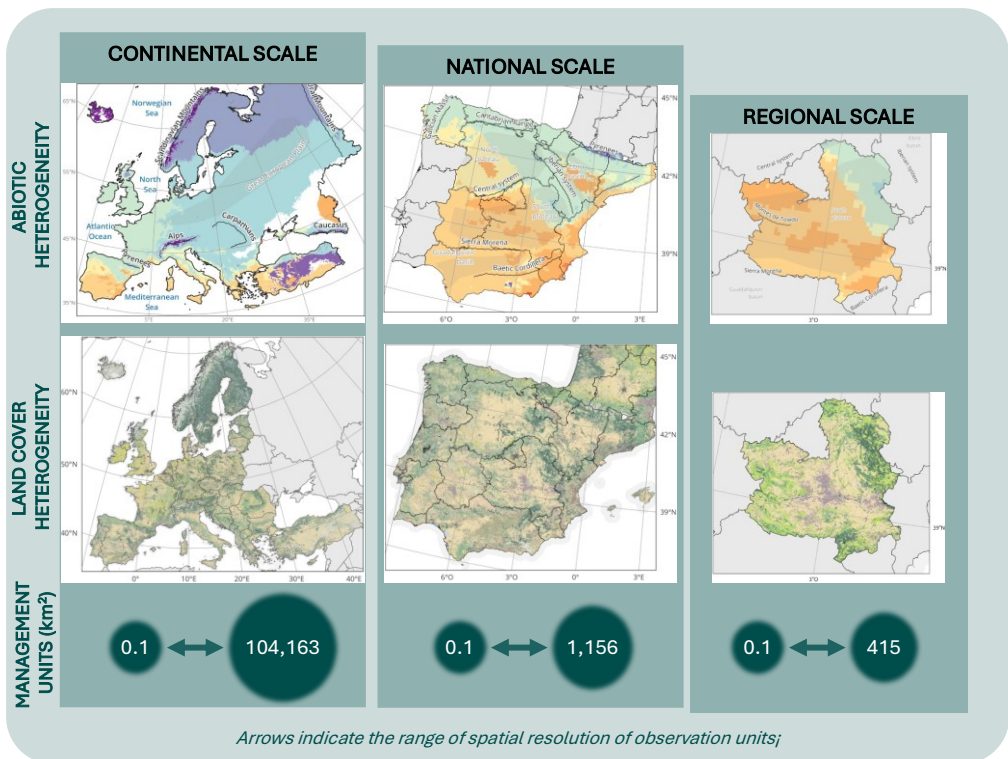


Figure 1.6. Multi-scale heterogeneity in ecological systems. The upper panel illustrates broad-scale environmental gradients across continental, national and regional scales, while the lower panel highlights variation in the size and resolution of management units. Sources: abiotic heterogeneity based on Kriticos et al. (2012) and land cover data from CORINE Land Cover (2018). *Generated using Copernicus Land Monitoring Service information 2018.*

1.6.2. Administrative units and the scale of management

Wildlife data, particularly hunting yields, are typically aggregated within administrative boundaries, which define the operational scale for management. However, these units vary significantly in size, shape and internal heterogeneity across European countries, reflecting differences in governance and reporting systems (**Figure 1.6**; ENETWILD-consortium, 2025). Because boundaries rarely align with ecological units, their use can introduce scaling artefacts (see [Section 1.4](#) and **Box 2**), potentially affecting both estimated abundance and spatial patterns. This thesis explicitly examines how variation in unit size influences abundance estimates and the resulting spatial patterns.

1.6.3. Temporal domain

Interpreting long-term patterns in hunting yield data requires accounting for multi-annual dynamics and changes in hunting regulations that affects populations. In the absence of high-resolution temporal data at continental or national scales, this thesis utilizes the maximum observed values within each administrative unit for the 2014-2023 period as a pragmatic proxy for potential upper levels of hunting yield. While these maxima do not directly represent ecological baselines or true carrying capacity, they may approximate periods of favorable conditions for both species population and data reporting, given that hunting yields are often used as a proxy of abundance (*e.g.*, Imperio et al., 2010). This approach implicitly assumes that, at broad spatial scales, populations may

intermittently approach states constrained by environmental limits, although not necessarily remaining in equilibrium (Rapacciuolo et al., 2019). In addition, by focusing on these peaks, in this thesis, we aim to reduce the influence of transient perturbations, such as disease outbreaks (*e.g.*, African swine fever; Schulz et al., 2019), administrative reporting delays, or punctual changes in hunting regulation that can depress annual records. Overall, this strategy prioritizes comparability across species and regions.

In addition, the temporal structure of camera trap data requires explicit consideration of the sampling window relative to population dynamics. Unlike HYs, which integrate information over annual cycles, camera trap surveys in this thesis provide snapshots of local populations over relatively short periods. The sampling design allows a temporal window of approximately two months. Within this timeframe, the analysis assumes that local abundance remains effectively constant, *i.e.*, it assumes demographic closure: no births, deaths, immigration or emigration. While strict demographic closure is rarely met in wild populations, the relatively constrained movement of the focal mammal species (see [Section 1.6.4](#)), together with the temporal resolution of sampling design, suggests that demographic processes affecting local population size are minimized. Instead, short-term movement are incorporated into the detection process, where the probability of an individual being available for detection captures the animal activity at the micro-site level. Consequently, repeated detections are interpreted as a variation in detectability rather than true changes in population size within the sampling period.

1.6.4. Focal mammal species and ecological traits

This thesis focuses on medium-sized and large mammal species widely distributed across Europe (Croft et al., 2025; Linnell et al., 2020), including:

- **Ungulates:** *Alces alces*, *Ammotragus lervia*, *Capra ibex*, *Capra pyrenaica*, *Capreolus capreolus*, *Cervus elaphus*, *Cervus nippon*, *Dama dama*, *Ovis aries*, *Rangifer tarandus*, *Rupicapra rupicapra*, *Rupicapra pyrenaica*, and *Sus scrofa*.
- **Carnivores:** *Meles meles* and *Vulpes vulpes*.
- **Lagomorphs:** *Lepus granatensis* and *Oryctolagus cuniculus*.

These species encompass a wide range of ecological strategies, solitary to gregarious behavior, life histories, contrasting detectability and movement patterns, that directly influence both observation processes and abundance inference (**Figure 1.7**; Apollonio et al., 2010; Burton et al., 2015; Hofmeester et al., 2019). Their broad distribution across bioclimatic zones provide a unique opportunity to examine non-stationarity, habitat heterogeneity and anthropogenic gradients (Doser, Kéry, et al., 2024).

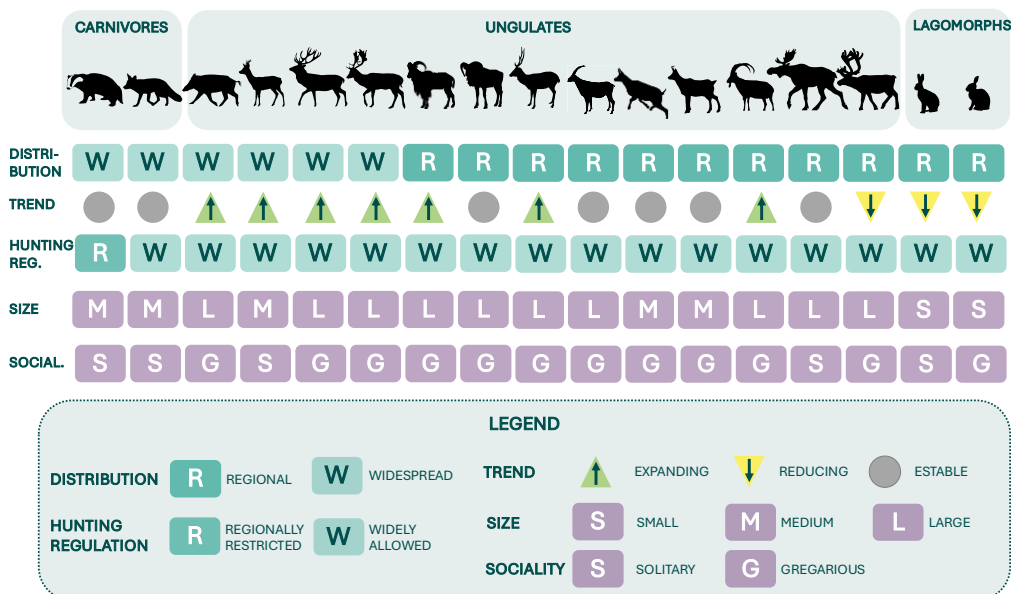


Figure 1.7. Overview of the focal species illustrating variation in distribution, population trends, hunting regulation, body size, and sociality. Species are grouped taxonomically (carnivores, ungulates, and lagomorphs) to highlight differences in key ecological traits relevant to data representation and subsequent modeling.

1.7. General, specific objectives and hypotheses

The main objective of this thesis is to develop and evaluate a large-scale inference of abundance patterns for a set of European mammals from both unstructured (hunting yields) and structured (camera traps) wildlife monitoring data and to quantify how modeling and preprocessing decisions influence ecological inference and model transferability. To achieve this goal, the thesis addresses the following specific objectives:

- O1. To compile and standardize large-scale wildlife monitoring data for mammal species, providing a consistent and reproducible basis for ecological spatial inference.
- O2. To develop and apply flexible modeling frameworks to estimate mammal species abundance and ecological responses at large spatial scales, while evaluating how data characteristics and modeling choices influence model performance and ecological inference.
- O3. To evaluate the agreement to which mammal abundance estimates derived from camera traps datasets are consistent to observed raw measures from unstructured datasets.
- O4. To assess how spatial relationships between species change when species-specific connectivity inform the spatial association.

These objectives lead to the formulation of the following hypotheses:

- H1. Large-scale unstructured datasets, such as hunting yields, can be transformed into standardized and reproducible occurrence data suitable for large-scale biodiversity monitoring.
- H2. Estimates of mammal abundance and ecological responses are sensitive to modeling and preprocessing decisions, including data transformation, spatial resolution, effort representation, and model specification.

- H3. Abundance-environment relationships are species-specific and vary across large spatial extents, reflecting differences in species ecology and spatial context.
- H4. Accounting for spatial dependence yields more coherent spatial patterns than approaches that ignore spatial structure, particularly when observation units are highly heterogeneous.
- H5. The size and heterogeneity of spatial units influence abundance estimates and spatial patterns, leading to differences in ecological inference across aggregation scales.
- H6. Abundance estimates derived from structured data are positively associated with independent indices from unstructured data. The strength of this association varies among species and spatial contexts.
- H7. Species-specific connectivity metrics yield more ecologically realistic interspecific spatial associations than approaches based on uniform spatial connectivity assumptions.

1.8. Overview of chapters

This thesis develops and evaluates frameworks for inferring large-scale mammal abundance from heterogeneous data, explicitly addressing the challenges posed by data standardization, model selection, and ecological interpretation across spatial scales. It examines how different data sources, modeling choices, and representations of spatial processes influence ecological inference, uncertainty, and transferability. The thesis is structured around the progression of the specific objectives.

Addressing Objective 1 (O1), [Chapter 2](#) compiles and standardizes large-scale wildlife monitoring data, presenting a presence-only dataset derived from hunting yield data for all ungulate and carnivore species legally hunted in Spain over a ten-

year period. By transforming raw count data into a harmonized and flexible format, this chapter establishes a consistent and reproducible basis for large-scale ecological inference.

Chapters 3, 4, 5, and 7 address Objective 2 (O2) by developing and evaluating flexible modeling frameworks to estimate mammal species abundance and ecological responses across large spatial scales using both unstructured and structured data. Chapter 3 applies alternative modeling approaches to estimate spatial patterns of relative abundance for multiple mammal species, highlighting how species distribution and uneven, management-driven data availability shape model formulation. Chapter 4 evaluates how preprocessing decisions and model specifications affect model performance, estimates of species abundance and spatial patterns. Chapter 5 examines the role of spatial structure, assessing its influence on inference under highly heterogeneous spatial units and its implications for spatial continuity. Adopting a modeling framework specifically tailored to structured monitoring data, Chapter 7 applies a multi-species N-mixture approach to camera trap data to estimate relative abundance and species environment relationships. This chapter also addresses Objective 3 (O3) by evaluating the consistency of these estimates with independent, unstructured data sources used in wildlife management.

Addressing Objective 4 (O4), Chapter 6 analyzes spatial relationships between species using bivariate spatial association indices, explicitly incorporating species-specific connectivity to provide a more ecologically meaningful representation of interspecific patterns across landscapes.

The [Chapter 7](#), synthesizes the main findings and presents the general conclusions of the dissertation, highlighting their implications for large-scale ecological inference and wildlife monitoring.

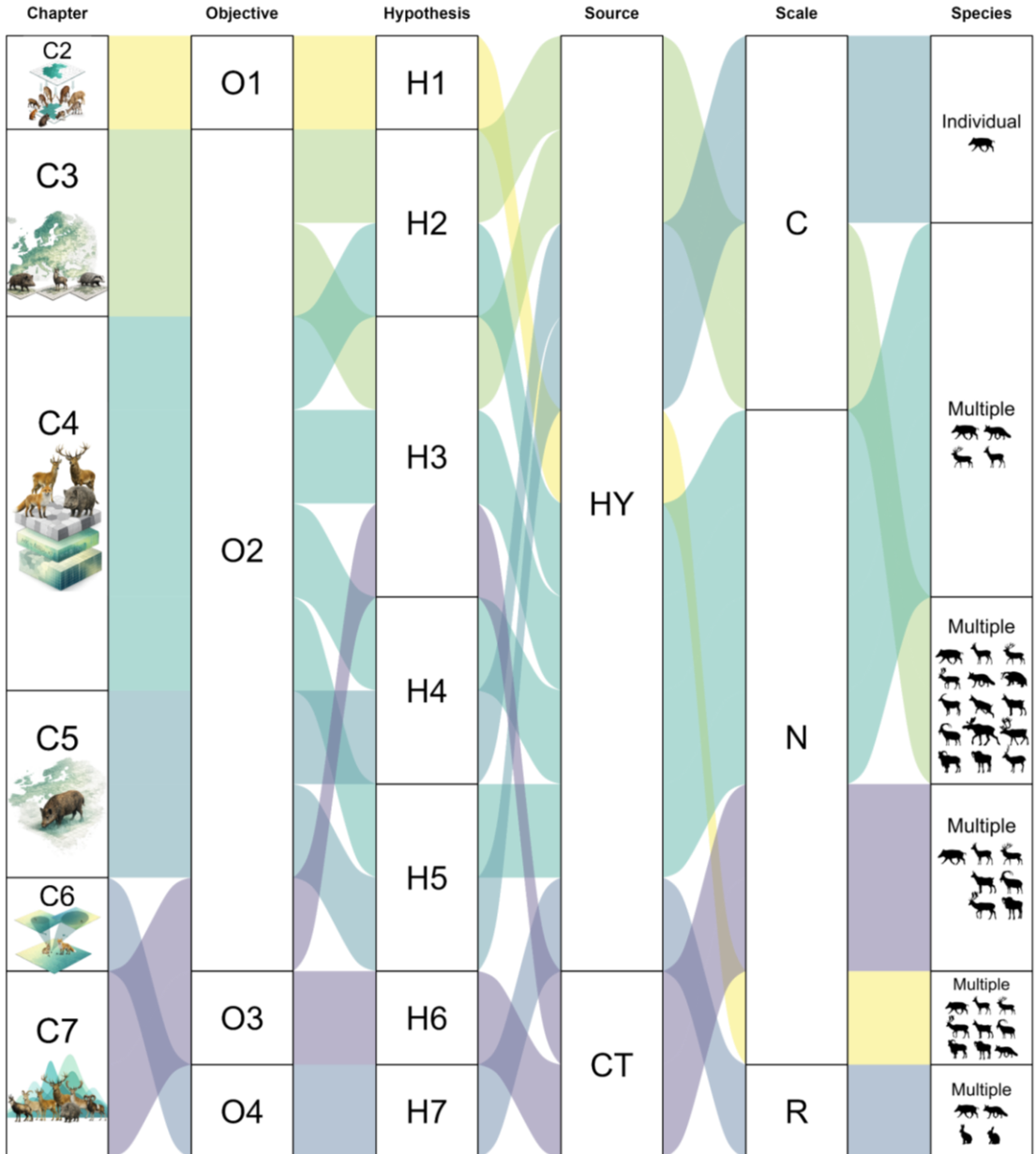
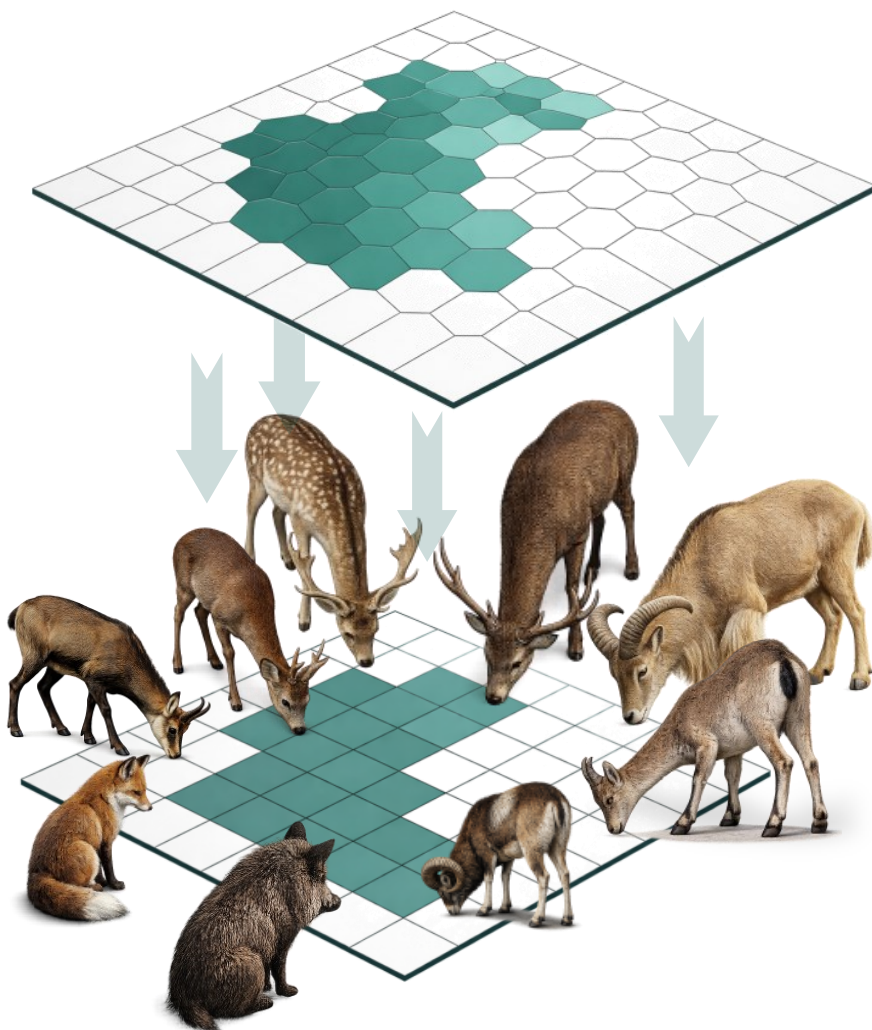


Figure 1.8. Conceptual map of the thesis. Visual representation of the research flow, illustrating the connection between chapters, objectives, hypothesis, data sources (HY: hunting yields & CT: camera traps), spatial scales of inference (C: continental, N: national, R: regional), and the species involved in the analysis. The different colors correspond to each chapter.

2. Presence-only Data for Wild Ungulates and Red Fox in Spain based on Hunting Yields over a 10-year period



Illanas. S., Fernández-López, J., Vicente, J. Ruiz-Rodríguez, C., López-Padilla, S., Sebastián-Pardo, M., Preite, L., Gómez-Molina, A., Acevedo, P., Blanco-Aguilar, J.A. (2025). Presence-only data for wild ungulates and red fox in Spain based on hunting yields over a 10-year period. *Sci Data* 12, 236 <https://doi.org/10.1038/s41597-025-04574-z>

Abstract

The data sets provide long-term information (2013–2022) of the presence-only of eight wild ungulates and red fox derived from harvest data in a grid of 5×5 km of Spain (21,836 cells). The collected data has been processed and reported yearly, as well as in two monitoring periods in accordance with Habitats Directive from the European Union to facilitate data reporting about the State of nature, and the sum of the whole period. Data sets are structured following the Darwin Core biological standard. The data set was published in the Spanish node of the Global Biodiversity Information Facility (GBIF), which are the most updated publicly available information for these species' presence in Spain.

Resumen

Los conjuntos de datos proporcionan información de solo presencia sobre un periodo temporal largo (2013–2022) para ocho ungulados silvestres y el zorro rojo derivados de estadísticos cinegéticos en una malla de 5 × 5 km en España (21,836 celdas). Los datos recopilados se han procesado y reportado anualmente, así como en dos periodos de seguimiento de acuerdo con la Directiva Hábitats de la Unión Europea para facilitar la comunicación de información sobre el estado de la naturaleza, así como la suma de todo el periodo. Los datos se han estructurado siguiendo los estándares biológicos de Darwin Core y se ha publicado en el nodo español del *Global Biodiversity Information Facility* (GBIF), constituyendo la información pública más actualizada disponible sobre la presencia de estas especies en España.

2.1. Background and summary

Member States of the European Union (hereafter EU) have the duty of reporting the Conservation Status of Habitats and Species every six years since the approval of Habitats Directive 92/43/ECC and Bird Directive 2009/147/CE were approved. In Spain, there is not yet a national mammal monitoring program to assess the status (distribution and abundance) of species of no Community interest, nor to report the presence of species at coarse resolution.

Different data sources have been proposed to feed the sexennial reports. On the one hand, collaborative citizen science (Fraisl et al., 2022; Shirk et al., 2012) is a useful collaborative model for wildlife monitoring at large scales, particularly for taxa such as birds and butterflies (Sullivan et al., 2009; Van Swaay et al., 2008). Its application to mammals presents additional challenges due to their nocturnal behavior, lower detectability and the need for species-specific observation techniques. Therefore, opportunistic observations of mammals through citizen science are less frequent (Battersby & Greenwood, 2004). Nonetheless, citizen science initiatives employing camera-trapping are used to detect mammal species and to increase the number of opportunistic observations in areas where mammal sightings are limited (Casaer et al., 2019; Hsing et al., 2022; Lasky et al., 2021).

On the other hand, another important source of data on species distribution and abundance is hunting yields of game species since: i) they are

yearly updated, as hunting is an activity taken every year (Ruiz-Rodríguez et al., 2023), ii) they are spatially referenced (Ruiz-Rodríguez et al., 2023) and cover most countries' territory, excluding some protected areas such as national parks and security areas around urban areas and roads (Carpio et al., 2024), and iii) hunting managers may have the duty to report harvested animals to the administration (*e.g.*, hunting managers in Spain are required to report this data to their respective Autonomous Communities, as outline in Decree 506/1971, of 25th March, which approves the Regulation for the execution of the Hunting Law of 4th April, 1970). In fact, hunting yields are often considered a proxy of abundance (Fernández-López et al., 2025; Imperio et al., 2010) and they are frequently used in a wide variety of studies (Baz-Flores et al., 2024; Delibes-Mateos et al., 2009; ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023). Therefore, hunting yields could be considered the most widespread information for reporting distribution and relative abundance of game species at national and European levels.

The National Wildlife Research Institute (IREC; CSIC-UCLM-JCCM) gathered and merged hunting yield data in Spain for wild ungulate and red fox for the period 2013 - 2022. The data set comprised hunting yields for 8 different ungulate species: barbary sheep (*Ammotragus lervia*), Southern chamois (*Rupicapra pyrenaica*), fallow deer (*Dama dama*), Iberian wild goat (*Capra pyrenaica*), European mouflon (*Ovis aries*), red deer (*Cervus elaphus*), roe deer

(*Capreolus capreolus*), and wild boar (*Sus scrofa*) and a carnivore species: the red fox (*Vulpes vulpes*; Figure 2.1).

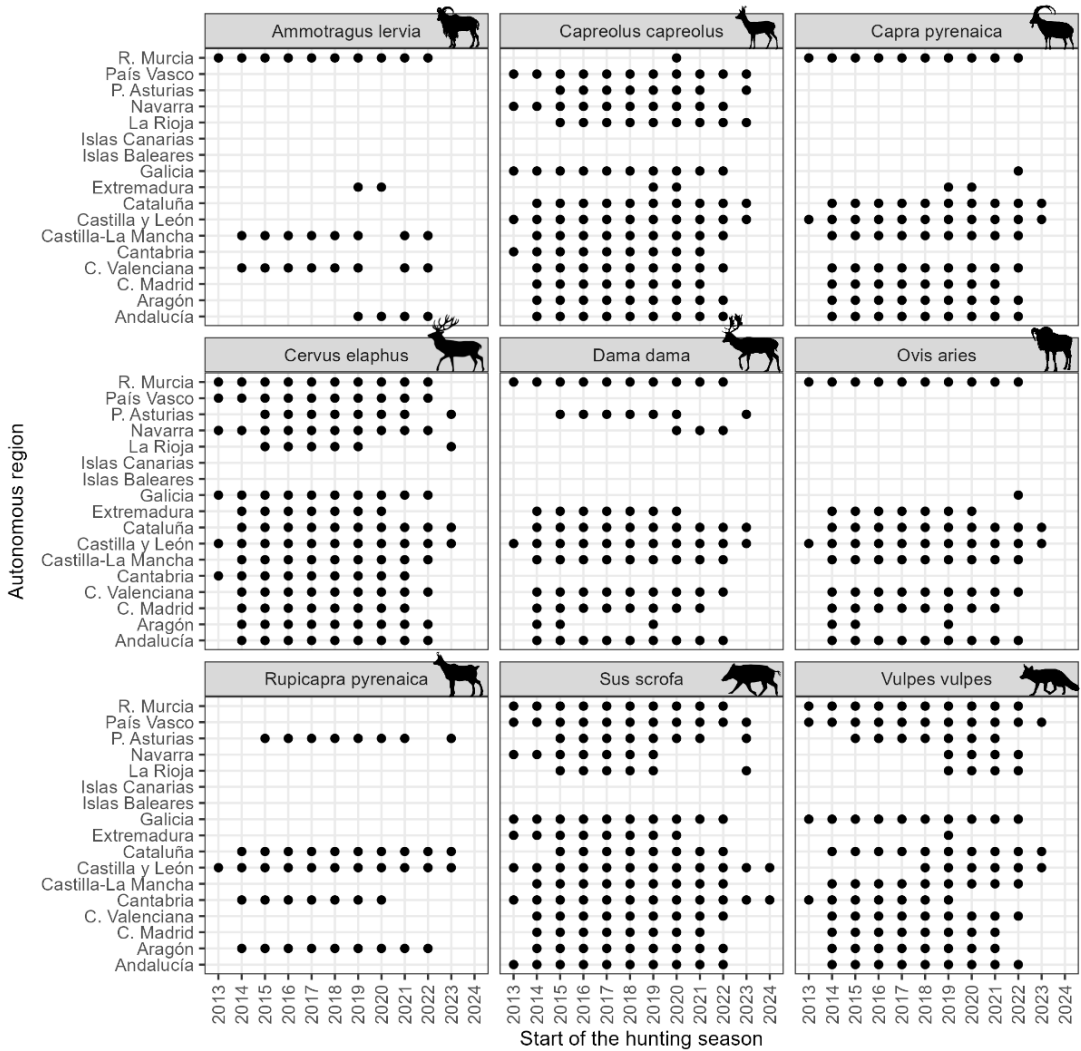


Figure 2.1. Autonomous Communities (Spain administrative regions) that reported data of hunting yield for each game species.

The different administrative Autonomous Communities reported heterogeneous data sets, requiring data harmonization into a common structure (Palomo et al., 2007; Ruiz-Rodríguez et al., 2023). The Autonomous Community is the primary political and administrative division below the national level, to which environmental policies, such as hunting and wildlife monitoring, are delegated. They may have varying priorities, resources and methodologies, which could potentially complicate national assessments on wildlife. A structured database following the Darwin Core standards was used (ENETWILD consortium et al., 2020) for data harmonization purpose. However, there may be constraints on making public these data, which prevents raw data from being shared publicly at game management unit. They contain information of hunting yields, which is considered sensitive in some Autonomous Communities, such as the number, sex and age of hunted individuals, the number of individuals seen (alive) on a hunting day, the number of hunters, beaters and dogs, as well as the hunting method (Ruiz-Rodríguez et al., 2023). Hunting is an activity that constitutes an important economic resource in some Spanish regions and involves diverse stakeholders (Kupren & Hakuc-Błazowska, 2021; Martínez-Jauregui et al., 2014; Middleton, 2014; Sánchez-García et al., 2021). For this reason, we reached data-share agreements with each administrative Autonomous Communities, limiting the information that can be shared, maintaining the privacy of raw hunting yield data at the finest spatial scale (**Figure 2.2a**). Nonetheless, if hunting yields are

transformed at coarser spatial resolution and simplified to presence-only, the information could be made publicly available.

Consequently, a 5 x 5 km grid resolution was used for transferring hunting yield information into presence-only data. The transformed data sets include presence-only records for these wild species in Spain over the last decade. These valuable data are the most updated and complete known available distribution of the nine species in Spain, as the national-scale public information for mammals dates back to 2007 (Palomo et al., 2007). These data can be used in multiple studies concerning species management, spread of diseases, species distribution models, *etc.* in the future (ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023; Fernández-López et al., 2023).

2.2. Methods

We received the data after holding meetings with the game services of each Autonomous Community in Spain (*i.e.*, 17 administrative regions). We reached a data-sharing agreement with each of them, which restricted the publication of data: raw data cannot be shared publicly at finest resolution provided; however, they can be transformed or aggregated into derived information products. The received data included hunting yields at hunting ground level from 2013/2014 to 2022/2023 hunting seasons (**Figure 2.1** and **Figure 2.2a**).

Since each Autonomous Community has its own (different) system/data set structure, we transformed and standardized the data received following the Wildlife Data Model template (WLDM; Body, Mousset, et al., 2020) developed by the *ENETWILD* consortium under EFSA (<https://enetwild.com>; ENETWILD consortium et al., 2020), which follows the Darwin Core Criteria. Once we had harmonized a data set and joined with its spatial data (hunting ground perimeters), we validated the structure of each harmonized data source using ShinyIVT (ENETWILD-consortium, López-Padilla, et al., 2023). We use tidyverse 2.0.0 (Wickham et al., 2019) and sf 1.0-16 (Pebesma, 2018) packages of R 4.3.3 software (R Core Team, 2025) for data management.

To update the distribution of presence of wild ungulates and red fox in Spain, it was decided to present the information in the 5 x 5 km squared grid of the European Environment Agency (European Environment Agency, 2024) masked with Spain. Nonetheless, to facilitate comparisons with the latest publicly available information on mammals' occurrence (Palomo et al., 2007), which has a grid resolution of 10 x 10 km, an additional field is included (`verbatimCoordinates`) to allow conversion from the 5 x 5 km grid to the 10 x 10 km grid.

After that, we transferred presence-only records of each species to the grid separately for each hunting season, and for the total period. We considered that a species was presence for a hunting season only if at least one individual

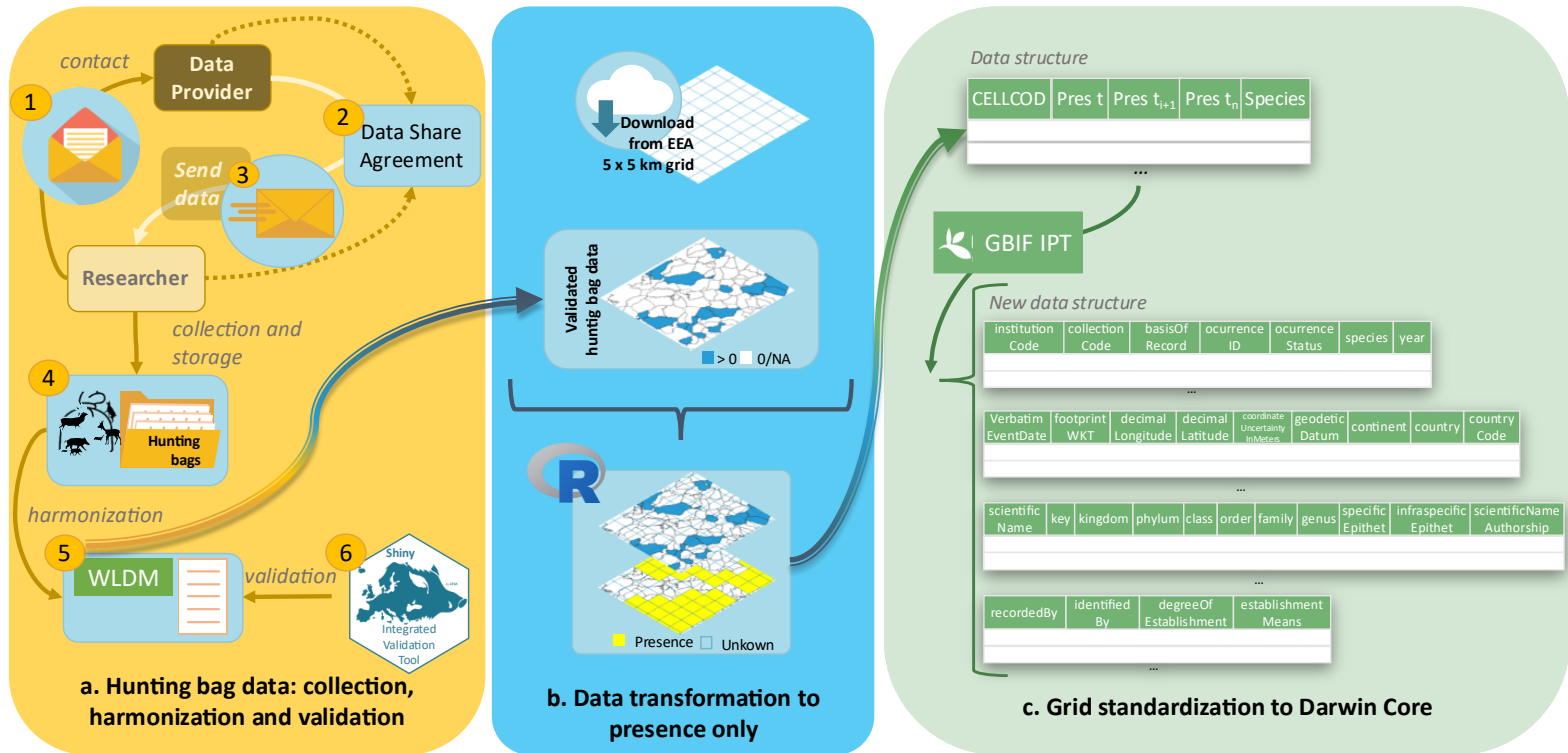


Figure 2.2. Stages of hunting yields transformation developed: from collection to publicly availability in GBIF repository.

has been hunted in an overlapping hunting estate, by using the function *gridPresence* (**Figure 2.2b**, see code [section 2.7](#)). Otherwise, the cell remained as unknown presence. It must be remarked that the later does not mean the species is absent in that cell, it just informs that it has not been hunted or reported, but no further inferences could be made about the absence of the species' record.

An important consideration regarding data sets is that hunting yields are reported in relation to a hunting season which generally spans from September to March of the following year. Therefore, it is not feasible to assign a hunting yield to a specific natural year. The criteria for determining presence- only for each year was to take the first year that comprises the hunting season as presence since animals are mostly hunted between September and December (Datta-Roy, 2022; Milner et al., 2006). For example, for the 2013/2014 hunting season presence- only would be referred to the year 2013.

In addition, we arranged the data in two monitoring time periods (2013-2018 and 2019-2022) which match reporting periods of the Habitat Directives from the EU. We grouped presence cell records and determined as "present" if in any year the species was present in that cell or "unknown presence" if it was not registered as present in any of the years that encompass each of the monitoring periods. We followed the same criterion for determining presence or unknown presence for the whole decade (2013-2022; **Figure 2.4**).

2.3. Standardization

We formatted and published the data set, standardized to the Darwin Core structure (**Figure 2.2c**; Wieczorek et al., 2012), in the Spanish node of the Global Biodiversity Information Facility ([GBIF](#)) through the Integrated Publishing Toolkit (IPT v3.0.4; Robertson et al., 2014). Other countries could easily format and publish their data sets in GBIF following our procedure, as hunting yields from (almost) all European countries adhere to the same harmonization procedure (ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023). Hunting yields are transformed into the WLDM template, joined with their hunting ground perimeters, and validated using ShinyIVT (ENETWILD-consortium, López-Padilla, et al., 2023). However, a significant challenge to consider is the varying spatial resolution at which each country reports their hunting yields, ranging from fine-scale resolutions (*e.g.*, hunting grounds) to coarse-scale resolutions (*e.g.*, NUTS2 level). Therefore, making our approach available may contribute to addressing the need of up-to-date information on species and habitat state not only at national but also at European level.

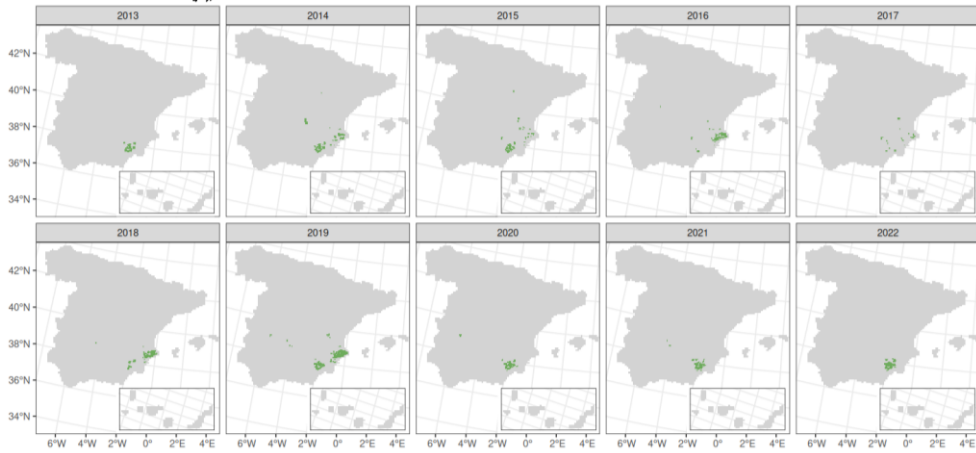
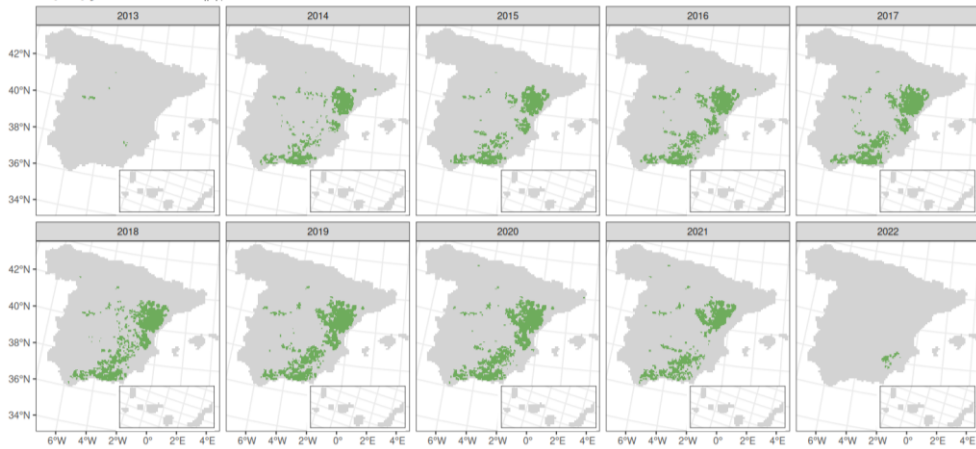
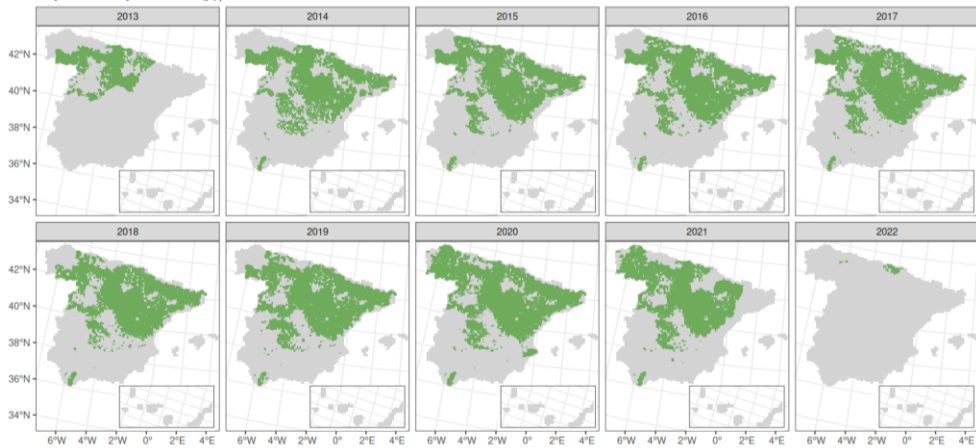
The main bottleneck in current biodiversity data flows is data integration and data accessibility. Only if different monitoring programs are harmonized, and particularly the spatial components of data merged, subsequent data streams will be possible to derive essential biodiversity variables (Liquete et al., 2024),

such as those proposed by EuropaBON for a European Biodiversity Observation and Coordination (EBOCC). Our data sets, presented spatially in a grid, align with the requirements of the Habitat Directive and provide sufficient resolution to evaluate temporal changes, analyze spatial patterns, and investigate drivers of change. They are also available for inclusion in the derivation of the aforementioned biodiversity variables.

2.4. Data Records

The data set is available at GBIF (Illanas et al., 2024) as a Darwin Core Archive (DwC-A) under a Creative Commons Attribution 4.0 International License (CC BY 4.0). The data sets presented here correspond to version 1.4, which is the most up-to-date compilation of presence-only records available for wild ungulates and red fox in Spain, derived from hunting yield data sets (**Figure 2.3**).

Be aware that data sets do not contain complete information for all years, depending on the species and Autonomous Communities (**Figure 2.1**). Despite the former, hunting yields from which data sets were derived from, are reported to public administrations on a mandatory and annual basis. Therefore, even if there are some current limitations in these data sets for certain species, hunting yields are continuously reviewed and updated, making them a valuable data source with extensive spatial and temporal coverage.

Ammotragus lervia ***Capra pyrenaica*** ***Capreolus capreolus*** 

Presence-only data for wild ungulates and red fox In Spain based on hunting yields over a 10-year period

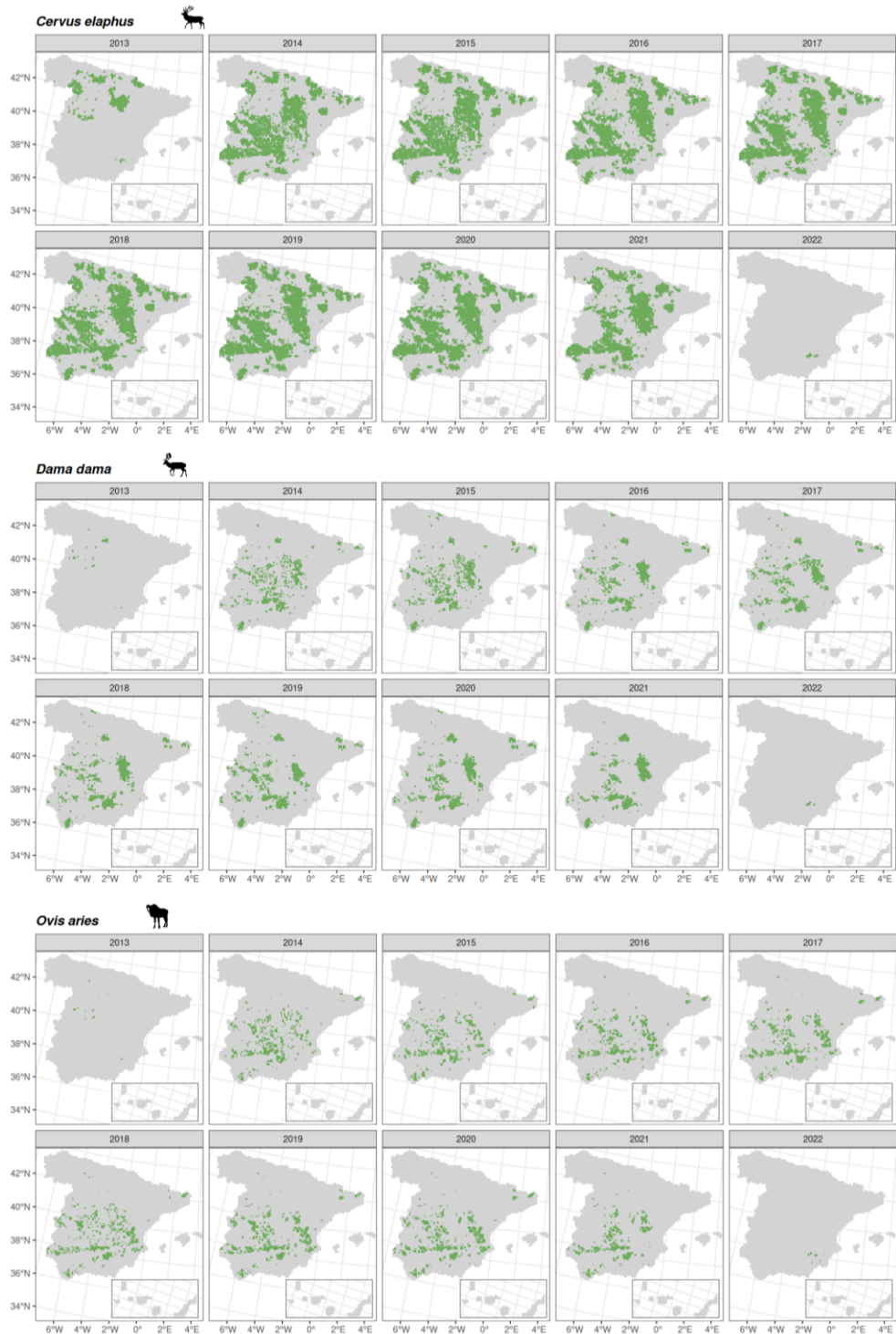




Figure 2.3. Reported presence-only (green) and unknown presence (grey) of each species per year in Spain based on hunting yields at projected 5 x 5 km grid.

The current data set will be continuously updated as new data collections from providers are received and harmonized. The DwC-A contains 1818198 records. Remarks of the Darwin Core Archive available at GBIF are provided below:

- basisOfRecord: (<http://rs.tdwg.org/dwc/terms/basisOfRecord>) Occurrence.
- occurrenceID: (<http://rs.tdwg.org/dwc/terms/occurrenceID>) unique ID code for each record.
- occurrenceStatus: (<http://rs.tdwg.org/dwc/terms/occurrenceStatus>) it is reported as presence when at least one individual has been registered as hunted in that squared grid.
- year: (<http://rs.tdwg.org/dwc/terms/year>) natural year that belongs to the year that the hunting season begins.
- verbatimEventDate: (<http://rs.tdwg.org/dwc/terms/verbatimEventDate>) hunting season.
- footprintWKT: (<http://rs.tdwg.org/dwc/terms/footprintWKT>) corresponds to the vertexes of the 5 x 5 km squared grid to which each record belongs.
- decimalLongitude and decimalLatitude: correspond to the centroid coordinates of the 5 x 5 km squared grid (<http://rs.tdwg.org/dwc/terms/decimalLongitude>, <http://rs.tdwg.org/dwc/terms/decimalLatitude>).
- coordinateUncertaintyInMeters: (<http://rs.tdwg.org/dwc/terms/coordinateUncertaintyInMeters>) it is recorded as 5km, but that is the squared resolution, which corresponds to an error of 3535 meters.

- geodeticDatum: (<http://rs.tdwg.org/dwc/terms/coordinateUncertaintyInMeters>) coordinate reference system that the coordinates are given using "WGS84".
- recordedBy: (<http://rs.tdwg.org/dwc/iri/recordedBy>) mainly performed by hunters, game managers and veterinary services.
- identifiedBy: (<http://rs.tdwg.org/dwc/iri/identifiedBy>) administrative regional services that shared the information and cross-checked with veterinary and forestry services.
- degreeOfEstablishment: (<http://rs.tdwg.org/dwc/doc/doe/>) degree to which an organism survives, reproduces, and expands its range at the given place and time.
- establishmentMeans: (<http://rs.tdwg.org/dwc/doc/em/>) information about whether an organism or organisms have been introduced to a given place and time through the direct or indirect activity of modern humans.
- verbatimCoordinateSystem: (<http://rs.tdwg.org/dwc/doc/em/>) the coordinate format for the verbatim Coordinates of each location.
- verbatimcoordinates: (https://dwc.tdwg.org/list/#dwc_verbatimCoordinates) the verbatim original spatial coordinates of each location.

On the other hand, we generate a simulated count data set for three years in a GeoPackage file, which can be accessed on Zenodo (Illanas, 2025), as we cannot share the collected hunting yields due to data confidentiality agreements. We created random polygons in Spain and used a random Poisson distribution where the lambda parameter was set under a random normal

distribution (mean=50, sd=10) to simulate count data for each of the years. Moreover, we selected a 25% of the polygons each year to change their count value to 0, to simulate unknown presences. The simulated count data is to demonstrate the transformation process from count data to presence-only data.

2.5. Technical Validation

Data sets are difficult to validate since the most updated information available dates to 2007 (Palomo et al., 2007). Nonetheless:

- a) Data sets contain information of wild ungulate species and red fox. Public administrations collect this information mainly through different departments: agriculture and wildlife services, as well animal health departments, the later aimed at disease surveillance. The information sent to agriculture and environmental departments is normally collected by hunting managers, whereas the one sent to health departments is responsibility of veterinarians carrying out big game meat inspection in some regions. Therefore, the collected information can be double-checked. However, while this double-checking process is available for big game species, it is not feasible for small game species. Nevertheless, holding different hunts on different days and the multiple participation of hunters mitigates the risk of errors in species identification.
- b) Reporting hunting yields to public administrations is mandatory in Spain. Hunting estates that violate the law by not sending their annual activity reports may face penalties, such as hunting bans in subsequent season/s. However, these sanctions are not always applied, leading to potential data gaps for certain years and hunting grounds.
- c) Hunting or population control for conflict management (e.g., to prevent damage to crops, even in areas that administratively are not considered

hunting estates, national parks, peri-urban) may not always be reported or included to hunting yield databases in some Autonomous Communities. This may result in gaps in data, especially in areas where regular hunting activities are not allowed (*e.g.*, some blank cells in our maps, such as for wild boar).

- d) Data set with full hunting yields by region (RAW data) was harmonized and checked before being transformed into a presence-only grid. Data harmonization was performed by the same team which followed the same manual procedure to ensure consistency. After data was harmonized, the team monitored the quality of the data product: i) ensuring no missing values by summing the total number of individuals hunted per species and hunting season and comparing the result to the RAW data total, ii) avoiding overcounting by identifying duplicate hunting yields per species and hunting season, and iii) verifying that counts correspond to their respective hunting grounds by randomly selecting 30 rows per along the terciles of harmonized data set and cross-checking the hunting ground and counts with the RAW data. Data validation was made under the Integrated Validation Tool (IVT) developed by ENETWILD (ENETWILD-consortium, López-Padilla, et al., 2023).
- e) In addition, a simulated data set is provided as well as the code used to generate presence-only data, which ensures reproducibility of the whole process.

2.6. Usage Notes

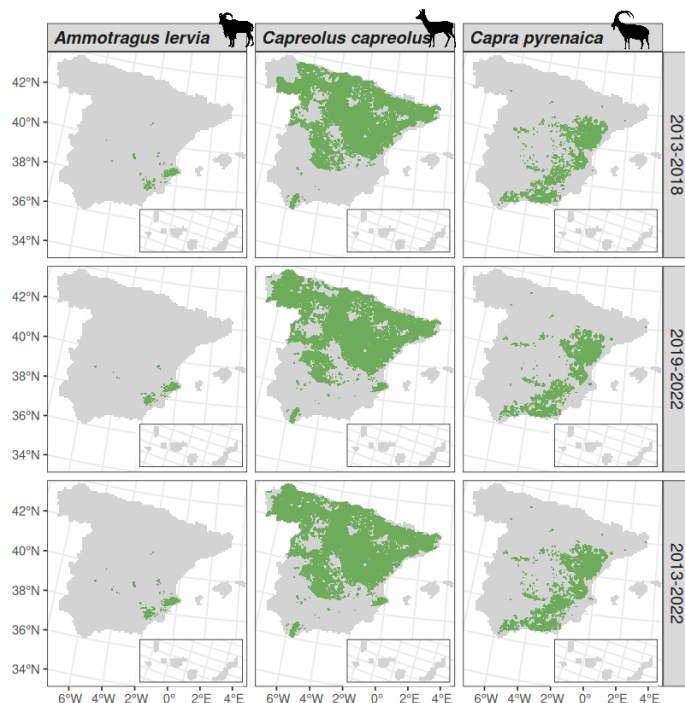
Monitoring programs developed for mammal species of Community interest are, mainly, those for which conservation status was reserved and are carried out at small-scale (Blanco et al., 2020; Croose et al., 2023; Gisbert & García-Perea, 2014; Palazón, 2023; Rodríguez & Calzada, 2015). On the contrary,

widespread, and abundant mammals, which in their majority are considered game species, have lacked monitoring programs to assess either their presence or abundance (ENETWILD-consortium, Acevedo, et al., 2023). There are only few proposals for monitoring those species that have started to cause economic damages to agriculture, livestock or through car crashes (European Climate, 2024; Fernández-López et al., 2022; Schwartz et al., 2020; SECCEM, 2021). Therefore, hunting yields have become the most commonly used source of information for knowing their distribution and abundance at national or European scale. The data set provided, which update the presence-only of several game species per year, could inform about changes in their distribution range. They can be used also to evaluate environmental-species relationships by modelling or provide important information to data-integration models (Fernández-López et al., 2023). Moreover, the methodology proposed here could be extended to other game species, as lagomorphs, bird game and fishing species.

The presence-only records provided in the data set (**Figure 2.3**), correspond to all data received (**Figure 2.2**). Not all Autonomous Communities reported the same hunting seasons and/or species, as that also depends on species distribution. For example, Southern chamois is only distributed on Cantabrian and Pyrenean mountain range, but not in Southern Spain; contrarily, European mouflon is distributed in the mid-term Southern Spain, but not in the

Northern. Future updates will incorporate new data obtained from providers. European and Spanish authorities are increasingly involved into the development of wildlife monitoring programs (ENETWILD-consortium, Guerrasio, et al., 2023). In accordance, there are funding projects with that aim at European (ENETWILD and EOW project) and National scale (HAWIPO, AGROBOAR, FAUNET). These projects are going to give the opportunity of maintaining an updated presence-only data set for these game species. For that reason, we encourage readers to look for updated versions on the GBIF repository after this publication.

The function developed for transforming the data (*gridPresence*, see code availability) could also be used for other types of counting data transformation into presence-only data.



Presence-only data for wild ungulates and red fox In Spain based on hunting yields over a 10-year period

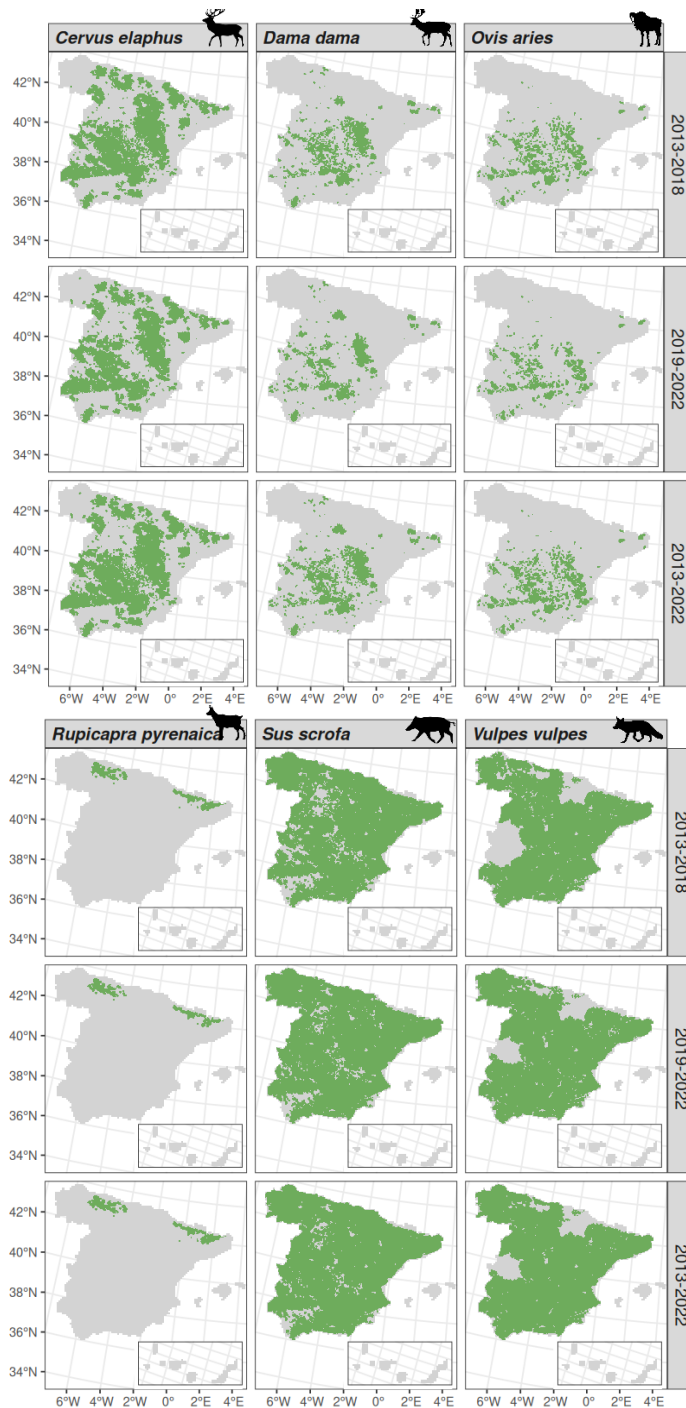


Figure 2.4. Presence-only of species (green) and unknown presence (grey) based on hunting yields for two monitoring periods and the whole period projected at 5 x 5 km grid.

2.7. Code Availability

Due to data confidentiality agreements, collected hunting yields cannot be shared. However, a simulated count dataset for several years is provided in a GeoPackage file, along with the masked 5 x 5 km grid from the EEA, to show the transformation process from count data set to presence-only data.

We make the simulated count data set by generating random polygons within the surface of Spain (lines 31-46). For each random polygon, we generated three count surveys data sets (e. g., year) based on a random Poisson distribution, where the lambda parameter followed a random normal distribution (mean =50, sd=10; lines 31-46). To simulate unknown presences, 25% of the polygons in each survey were randomly assigned a count of 0 (lines 60-62). We exported the information as a vectorial layer in a Geopackage (lines 82-89). The simulated count data set represents the simplest data structure that researchers may encounter in their RAW or harmonized data sets. The R script example file is prepared for transforming three years counts to 5 x 5 km grid (line 24), as well as 10 x 10 km grid. The transformation of the 5 x 5 km grid to the 10 x 10 km grid can be found at line 28. The function used for transforming hunting yields data to presence-only (*gridPresence*) is also provided (lines 46-93). An example of how to run the function for more than a year and for both grid resolutions is given as well (lines 97-105). Both results are given and plotted (lines 109-128). The R script files has been written in R 4.3.3 computing language and utilized the packages

tidyverse 2.0.0 (Wickham et al., 2019), sf 1.0-16 (Pebesma, 2018), terra 1.8-15 (Hijmans, 2025), dismo 1.3-16 (Hijmans et al., 2024), and deldir 2.0-4 (R. Turner, 2024).

We released version 1.6.0 of the transformation process (code and data set files) in Zenodo (Illanas, 2025). There are also available at [github](#).

Acknowledgements

The investment of time for making the data set available was supported by the Spanish Ministry of Science and Innovation thanks to the 2020 PhD contract (PRE2020-095091) associated to I+D+i HAWIPO Project (PID2019-111699RB-I00), the I+D+I AGROBOAR Project (PID2022-142919OB-I00), funded by MCIU/AEI/10.13039/501100011033/y – FEDER – EU. The Spanish Ministry of Agriculture, Fisheries and Food thanks to the FAUNET Management Order (https://www.boe.es/diario_boe/txt.php?id=BOE-A-2023-17249) and the support of the Subdirector General for Livestock and Hunting Productions. The Margarita Salas from the European Union – NextGenerationEU through the Complutense University of Madrid. Talent Return and Retention Project SBPLY/23/180225/000176 – and researcher contract for scientific excellence from the UCLM co-financed by the European Social Fund Plus.

All data providers: Diputación Foral de Álava, Diputación Foral de Bizkaia, Diputación Foral de Gipuzkoa, Generalitat de Catalunya, Generalitat Valenciana, Gobierno de Aragón, Gobierno de Cantabria, Gobierno de la Comunidad de

Madrid, Gobierno de la Región de Murcia, Gobierno de La Rioja, Gobierno del Principado de Asturias, Gobierno de Navarra, Junta de Andalucía, Junta de Castilla y León, Junta de Comunidades de Castilla-La Mancha, Junta de Extremadura, Junta de Galicia. Katia Cezón and Francisco Pando kindly provided support to incorporate IREC into GBIF as data provider and helped to properly format the database to meet GBIF requirements.

Author contributions

SI: contacted data providers, collected, stored, harmonized, and transformed data information, uploaded information to the GBIF repository, wrote the article and prepared the figures. JAB-A: contacted data providers, collected and stored data information. Helped with Darwin Core transformation and uploaded it to the GBIF repository. CR-R: contacted data providers, collected, stored and harmonized data information. SL-P: harmonized and validated data information. AG-M: contacted data providers, collected, stored, harmonized and validated data information. Made the data share agreement with data providers. LP, MS-P: harmonized and validated data information. JF-L: had the idea of the data paper and helped to draft the manuscript. PA: acquired financial support and helped to draft the manuscript. JV: acquired financial support and helped to draft the manuscript.

Competing interests

The authors declare no competing interests.

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3. Modeling Frameworks for Abundance Patterns of European Wild Mammals



Based on the reports:

ENETWILD-consortium, **Illanas. S.**, Croft, S., Smith, G. C., López-Padilla, S., Vicente, J., Blanco-Aguilar, J.A., Scandura, M., Apollonio, M., Ferroglio, E., Zanet, S., Vada, R., Keuling, O., Plis, K., Podgorski, T., Brivio, F., Fernández-López, J., Ruiz, C., Soriguer, R.C., Acevedo, P. (2022). New models for wild ungulates occurrence and hunting yield abundance at European scale. *EFSA Supporting Publication*. 19(10): EN-7631. 43 pp. doi: [10.2903/sp.efsa.2022.EN-7631](https://doi.org/10.2903/sp.efsa.2022.EN-7631)

ENETWILD-consortium, **Illanas. S.**, Croft, S., Smith, G. C., Vicente, J., Blanco-Aguilar, J.A., Scandura, M., Apollonio, M., Ferroglio, E., Keuling, O., Plis, K., Gómez-Molina, A., Preite, L., Ruiz-Rodríguez, C., López-Padilla, S., Zanet, S., Vada, R., Podgorski, T., Brivio, F., Fernández-López, J., Soriguer, R.C., Acevedo, P. (2023). Wild carnivore occurrence and models of hunting yield abundance at European scale: first models for red fox and badger. *EFSA Supporting Publication*. 20(2): EN-7894. 377 pp. doi: [10.2903/sp.efsa.2023.EN-7894](https://doi.org/10.2903/sp.efsa.2023.EN-7894)

Abstract

Reliable large-scale estimates of wildlife abundance are scarce, limiting the capacity to manage and conserve wildlife. Across Europe, hunting yield statistics constitute one of the few continent-wide data sources available for common game mammals, yet their heterogeneous structure has limited their consistent use for abundance modeling. Here, we present four flexible, species-tailored frameworks based on hunting densities (HDs) to infer spatial patterns of relative abundance for 15 common mammal species with wide and restricted distribution ranges across Europe. These frameworks include global, regional, country-level and zero-inflated approaches tailored to species distribution and management regimes. Within each framework, we modeled relative abundance as a function of climatic, land-cover, anthropogenic, and spatial predictors, evaluated model performance using independent data and generated spatial predictions across species' distribution ranges.

Data availability and the prevalence of zero values differed markedly between widespread and constrained species, strongly influencing model formulation and performance. For widespread species, excluding zero values yielded well-calibrated predictions, suggesting that zero hunting yields often reflect reporting limitations or management constraints rather than true zeros. In contrast, zero values for constrained species carried relevant ecological information on distribution limits and local absence, requiring explicit treatment in abundance models. Across all species, strong overdispersion supported the

use of negative binomial distributions, while spatial predictors consistently captured residual variation beyond environmental predictors.

Spatial predictions revealed pronounced species-specific gradients and hotspots of relative abundance across Europe for the selected species, with generally higher predicted abundances in central and southern regions and lower values toward northern latitudes. Mountain-associated species exhibited spatially restricted high-abundance areas aligned with known ecological limits. Our results demonstrate that hunting yield data, when coupled with species-tailored preprocessing and modeling strategies, can robustly capture continental-scale patterns of relative abundance. These findings highlight the necessity of flexible ecology-informed modeling frameworks for large-scale wildlife management and monitoring.

Resumen

Las estimaciones fiables de abundancia de fauna silvestre a gran escala son escasas, lo cual limita las capacidades de gestión y conservación. En Europa, las estadísticas de capturas cinegéticas constituyen una de las pocas fuentes de datos disponibles a escala continental para mamíferos cinegéticos comunes; sin embargo, su estructura es heterogénea y esto ha limitado su uso para la modelización de la abundancia. En este estudio presentamos cuatro marcos de trabajo flexibles para inferir patrones espaciales de abundancia relativa de 15 especies de mamíferos comunes con rangos de distribución tanto amplios como restringidos en Europa. Estos marcos incluyen enfoques globales, regionales, a escala de país y con inflación de ceros, y están adaptados según la distribución de las especies y sus regímenes de gestión. Dentro de cada marco, modelizamos la densidad de animales cazados (abundancia relativa) en función de predictores climáticos, de cobertura del suelo, antropogénicos y espaciales; evaluamos el rendimiento de los modelos mediante datos independientes y generamos predicciones espaciales a lo largo de los rangos de distribución de las especies.

La disponibilidad de datos y la prevalencia de ceros difirieron notablemente entre especies de amplia distribución y especies de distribución restringida, influyendo de forma decisiva en el marco analítico a aplicar en cada una de ellas. Para las especies ampliamente distribuidas, la exclusión de ceros dio lugar a predicciones bien calibradas, lo que sugiere que los ceros en las capturas cinegéticas de estas especies suelen reflejar limitaciones en la notificación o restricciones de gestión más

que esfuerzos de captura de la especie sin éxito. Por el contrario, cuando se modelizan especies de distribución restringida los ceros aportaron información ecológica relevante sobre los límites de distribución y las ausencias locales, señalando que para ellas se requiere un tratamiento de esta información explícito en los modelos. En todas las especies se detectó una fuerte sobredispersión, lo que respalda el uso de distribuciones binomiales negativas, mientras que los predictores espaciales capturaron de forma consistente la variación residual más allá de los predictores ambientales.

Las predicciones espaciales revelaron gradientes y zonas de elevada abundancia relativa marcadamente específicas de cada especie en Europa, con abundancias generalmente más altas en regiones centrales y meridionales, y valores más bajos hacia latitudes septentrionales. Las especies asociadas a sistemas montañosos mostraron áreas de alta abundancia espacialmente restringidas y alineadas con límites ecológicos conocidos. Nuestros resultados demuestran que los datos de capturas cinegéticas, cuando se combinan con estrategias estadísticas adaptadas a cada especie, pueden captar de forma robusta patrones de abundancia relativa a escala continental. Estos hallazgos ponen de relieve la necesidad de marcos de modelización flexibles e informados por la ecología para la gestión de la fauna silvestre a gran escala.

3.1. Introduction

The assessment of how many species exist, where they occur, and how abundant they are is a critical aspect for environmental science, particularly for policymakers. Management decisions should encompass scenarios ranging from evaluating the status of populations (*e.g.*, endangered, overabundant, invasive; Atwood et al., 2020; Dirzo et al., 2014; Häkkinen et al., 2023) to health-socio-economic considerations (*e.g.*, disease outbreaks and spread, vehicle collisions, assessment of hunting quotas; Apollonio et al., 2017; Carpio et al., 2021; Fa et al., 2002; Ripple et al., 2017). In addition, it is essential to have available wildlife information at the same scale at which management decisions are made. However, obtaining such information on a continental scale is particularly challenging for common species with extensive distribution ranges, making accurate population monitoring unfeasible (Moersberger et al., 2024; Yoccoz et al., 2001).

Wildlife information can be obtained through different sampling methodologies commonly classified as either direct or indirect, which are implemented using structured or unstructured monitoring designs by both specialized and non-specialized observers (ENETWILD-consortium, Acevedo, et al., 2021; Melo et al., 2021). Direct monitoring methods (*e.g.*, spotlight counts, listening stations, aerial surveys) require direct contact between an individual and a surveyor through visual or acoustic encounters. In contrast, indirect monitoring approaches (*e.g.*, pellet counts, eDNA, harvest statistics) rely on

evidence of an individual's presence by detecting traces in a location, without requiring direct contact between individuals and surveyors. Nonetheless, the evasive and nocturnal behavior of many wildlife species limits the efficiency of some direct sampling methods. Techniques such as spotlights, total counts or capture-mark-recapture often require substantial effort whereas methods based on camera traps or acoustic devices are generally more efficient (Battersby & Greenwood, 2004; Bell & Malerba, 2025; Burivalova et al., 2018; Garland et al., 2020; Hsing et al., 2022; Leempoel et al., 2020; Wearn & Glover-Kapfer, 2019).

Comprehensive and harmonized data on common wild mammals at continental scales remain scarce, limiting the ability to implement evidence-based management actions (Nichols & Williams, 2006). Consequently, the short-term approach for obtaining information on common wild mammals involves harmonizing monitoring data across different administrations and stakeholders. To address this challenge at pan-European scale, since 2017 the European Food Safety Authority (EFSA) funds the ENETWILD project (www.enetwild.com). Its main objective has been to improve European capacities to monitor wildlife population, develop standards for the collection of information regarding the geographical distribution and abundance of wild ungulates and carnivores throughout Europe to subsequently create geospatial tools to be used in further risk assessment of human-wildlife conflicts. These conflicts, especially relevant for humans, encompass shared diseases, not only because the possible emergence of zoonotic diseases (*e.g.*, highly pathogenic avian influenza, West

Nile virus, tick borne encephalitis, Crimean Congo Haemorrhagic Fever; ENETWILD-consortium et al., 2023) but related to the wildlife-livestock interface (e.g., African swine fever, tuberculosis), as well as management and conservation of species (Acevedo et al., 2023).

The collection of wildlife information at European scale includes presence and abundance data (ENETWILD-consortium, Plis, et al., 2024). Presence data provides information about the detection or, when systematically collected, non-detection of an individual, or a species, at a given location. At broad geographic scales, this type of data is often derived from opportunistic records, ranging from historical museum specimens to collaborative citizen science, such as GBIF, iNaturalist, eBird, eMammal, iMammalia (Fraisl et al., 2022; Shirk et al., 2012), or, from systematic data collection frameworks. These data have been widely used to develop species distribution models (SDMs; Elith et al., 2020; Feldman et al., 2021). In parallel, current initiatives, such as the European Observatory of Wildlife (EOW) or Snapshot USA, provide structured and harmonized data on mammal densities through the deployment of camera traps in many locations, following standardized sampling protocols. These approaches represent important advances for large-scale mammal monitoring. However, despite their methodological strengths, they are currently unable to achieve full continental coverage. This limitation is especially relevant for mammals, which have relatively scarce opportunistic occurrence records from citizen science (see [S3-1](#); Battersby & Greenwood, 2004). Harvest reports, which provide basic counts

of animals killed, are often opportunistic because they depend on hunter effort, chance, and shifting regulations rather than a fixed scientific design. Nevertheless, a well-designed hunting data collection framework may follow a pre-defined, standardized protocol to ensure data is representative and comparable over time (Guillemain et al., 2026). Consequently, one of the “opportunistic” datasets available for game mammals at the continental scale is hunting yields statistics (*i.e.*, number of individuals harvested in a defined territorial unit; HYs), which serve as a source of relative abundance data, and have been widely used for modeling spatial abundance and population trends (Acevedo et al., 2014; Fernández-López et al., 2025; Moreno-Zárate et al., 2021; Ruiz-Rodríguez et al., 2023). While HYs enable generally wide coverage within the species distribution range, their integration with structured datasets may offer more accurate wildlife abundance estimates (Gilbert, Pease, et al., 2021; Twining et al., 2024). To do so, it is essential to know how to address specific methodological challenges associated with each data source and with the ecological characteristics of the species being modeled.

Modelers should take advantage of the knowledge of species’ ecological strategies, as well as consider known species management practices and the objectives of the study, to make informed decisions throughout the modeling process, since these decisions will ultimately influence the predictions obtained (Muscatello et al., 2021). The modeling process encompasses primary decisions (Escobar & Craft, 2016) regarding:

- How to handle the information contained in a dataset (the response variable), which environmental predictors to include (*e.g.*, climatic, land cover);
- The modeling choices themselves (*e.g.*, selection of the mathematical distribution: Poisson, Negative Binomial, Zero-Inflated, *etc.*, the specification of linear or polynomial relationships between the response and the environmental variables, and the choice of model algorithm: GLM, GLMM, GAM, RF, BRT, Maxent, *etc.*);
- Where predictions will be made (*i.e.*, interpolation vs. extrapolation).

These decisions should be aligned with the main goal of the model as they determine the capabilities of the model to make inferences about a determined ecological process. In other words, at the end the inferences that can be made with a model are determined by the decisions that are mainly conditioned to data availability.

The global, regional or restricted distribution range of common wildlife species (**Figure 3.1**) is largely influenced by their life-history (*e.g.*, age at maturity, reproductive rate, dispersal ability) and their ecological functional traits (*i.e.*, specialist vs. generalist). Their distribution ranges determine data availability (*e.g.*, large datasets for regional widespread species), as well as to the reliability of uncertain records (NA/0; *e.g.*, true absences outside the distribution range of restricted species). For species whose hunting is permitted throughout their entire range, HYS may be available across all distribution areas, regardless of

whether they span the entire European continent or only specific regions. In contrast, some regionally widespread species may present spatial HYs gaps within their distribution range because hunting regulations for the same species may vary from permitted to prohibited depending on the country, as occurs for the European badger, *Meles meles* (Kurek et al., 2022). These artificial patchy availabilities are a consequence of species management and not a result of ecological processes. Moreover, this pattern may not only be characteristic of regionally widespread species, but also of certain exotic species that have been introduced in some countries for hunting purposes, such as the European mouflon, *Ovis aries*, while remaining absent from other ecologically suitable areas where

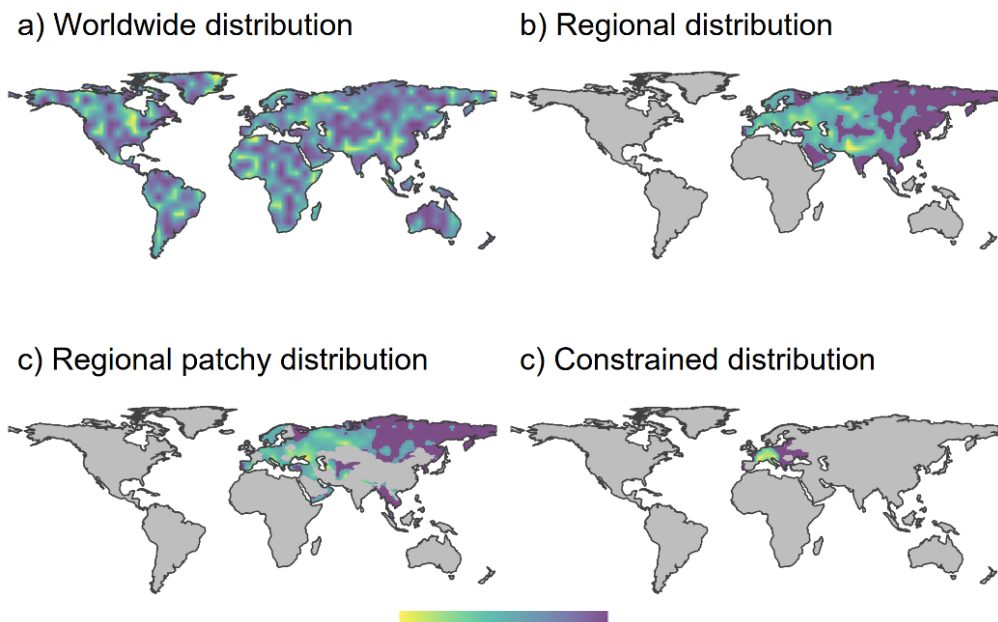


Figure 3.1. Example of data availability from simulated species (a) worldwide: widespread over the world, (b) regional: widespread but not globally, (c) (b) regional patchy: widespread regionally with data gaps, (d) constrained: specific locations. Purple color indicates where the species is absent. Grey color indicates species distribution limit range.

they have not been introduced (Carpio et al., 2017; Linnell et al., 2020). The variability in species distribution and data availability ultimately influences modeling decisions, as inferences derived from the models will depend on both factors, even when all data comes from the same source (*i.e.*, hunting statistics; Guillera-Arroita et al., 2015).

Previous studies have shown that both the frequency of abundance observations and their spatial coverage influence model performance. In addition, metrics such as accuracy, resolution and precision are affected by the treatment of abundance (*e.g.*, whether zeros are removed or maintained), and increasing the number of abundance observations does not necessarily improve model overall performance (Waldock et al., 2022). In fact, across large spatial extents, a single model may fail to capture the substantial variability exhibited by plastic and generalist species, as this implies that the species-environment relationships may not remain constant across the space (non-stationarity; Hochachka et al., 2012). In contrast, other studies have proposed using the same modeling framework for different species across broad spatial extents, although have documented biases related to habitat affinity and taxonomy (Stralberg et al., 2025). In this context, the main aim of this study was to provide a framework for modeling the relative abundance of common species across Europe considering their distribution and data availability.

3.2. Materials and methods

3.2.1. Study area

The study area extends in Europe roughly between 35°N and 70°N latitude and 10°W to 60°E longitude, with the Ural Mountains as the eastern limit, covering more than 40 countries (**Figure 3.2**). Mainland Europe comprises several mountain ranges (*e.g.*, the Alps, the Pyrenees, the Carpathians, the Caucasus, the Scandinavian Mountains) whose highest peaks exceed 4,000 m above sea level, as well as the Great European Plain, which contain extensive navigable river systems. It is bordered by the Mediterranean Sea at the south, the Atlantic Ocean at the west, and Norwegian and Arctic Sea at the north. Its

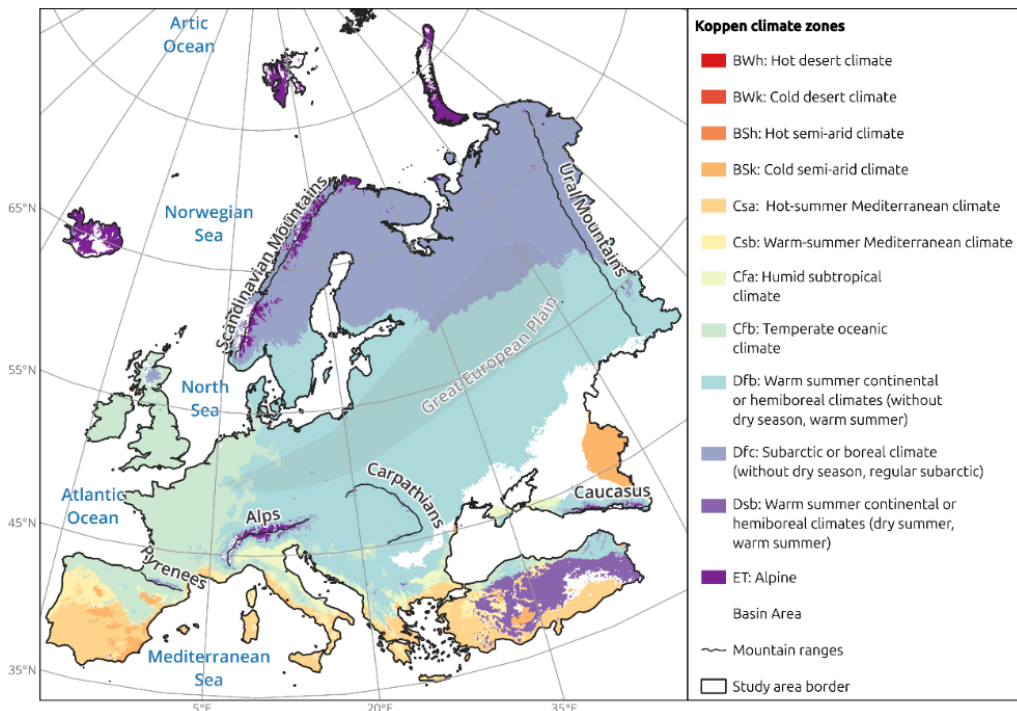


Figure 3.2. Climates and main topographical features of Europe. Source: Based on Kriticos et al. (2012).

geographic position combined with its topographic diversity confers a wide range of climates largely moderated by the warm Gulf Stream. These include the Oceanic West coast in western Europe, Mediterranean in southern Europe, Humid Continental in central and eastern Europe, Subarctic and Tundra in the north, and Highland climates in high mountain regions (**Figure 3.2**). The area encompasses diverse ecosystems, from boreal forests and tundra to temperate and Mediterranean woodlands, and is subject to intense human land use, including agriculture, forestry, hunting, and urbanization, which influence wildlife distribution.

3.2.2. Data handling

Hunting yields (*i.e.*, number of animals harvested) for wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), red fox (*Vulpes vulpes*), Alpine ibex (*Capra ibex*), aoudad (*Ammotragus lervia*), Northern chamois (*Rupicapra rupicapra*), Iberian wild goat (*Capra pyrenaica*), Pyrenean chamois (*Rupicapra pyrenaica*), European moose (*Alces alces*), European mouflon (*Ovis aries*), reindeer (*Rangifer tarandus*), sika deer (*Cervus nippon*), and European badger (*Meles meles*) have been collected in Europe from 2014/2015 to 2021/2022 hunting seasons (ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023). The spatial resolution of the data, as well as the number of records available, varied among species depending on their distribution range, ecological characteristics,

hunting legislation and data reporting practices across European countries and regions (**Table 3.1; Figure 3.3**). As a result, species differed markedly in both the spatial completeness of HYs and the frequency of zero values. These differences required the adoption of distinct modeling strategies, and species were therefore grouped according to them.

Table 3.1. Number of territorial units used for modeling by species across Europe.

	Species	Territorial units			Total	Percentage of 0 values
		Hunting ground	Municipality (or equivalent)	NUT0, NUT1, NUT2, NUT3		
Widespread species	Wild boar	32475	2184	290	34949	12.49%
	Red deer	33247	821	459	34527	69.88%
	Roe deer	30166	752	482	31396	58.50%
	Fallow deer	31313	269	419	32001	51.37%
	Red fox	37063	883	360	38306	21.00%
	European badger	7179	703	333	8215	18.21%
Spatially constrained species	Alpine ibex	-	15	278	293	93.17%
	Aoudad	6856	-	-	6856	97.31%
	Northern chamois	321	26	330	677	75.92%
	Iberian wild goat	22170	-	-	22170	93.77%
	Pyrenean chamois	7252	-	6	7258	96.57%
	Moose	5758	525	48	6331	74.43%
	European mouflon	31083	194	392	31669	96.15%
	Reindeer	-	-	15	15	73.3%
	Sika deer	4969	26	337	5332	98.46%

For all widely distributed species, regardless of these data contingencies, zero hunting yields were assumed to report limitations rather than true environmental unsuitability. Consequently, models were fitted only to territorial units with non-zero hunting yields. In contrast, constrained-distribution species are characterized by restricted geographic ranges and a high proportion of zero hunting yields across the study area (**Table 3.1**). For countries reporting hunting of a constrained species in at least one territorial unit ($HY > 0$), we assumed that $HY=0$ in all remaining territorial units of that country. For these species, zero values were assumed to carry important ecological information related to environmental limitations and the spatial boundaries of the species' distribution, and therefore, in contrast to widely distributed species, zero hunting yields were considered informative and retained in the response variable.

3.2.3. Response variable

We retained the maximum number of individuals hunted among hunting seasons and divided by the area of the respective territorial administrative or management unit (km^2) to obtain hunting yield density (HDs; **Figure S3-2.1**); it was considered as individuals by $10,000 \text{ km}^2$ for modeling purposes. For all species, values above the 99.9% percentile of individuals hunted per square kilometer were excluded from the analysis because they were considered as data entry errors.

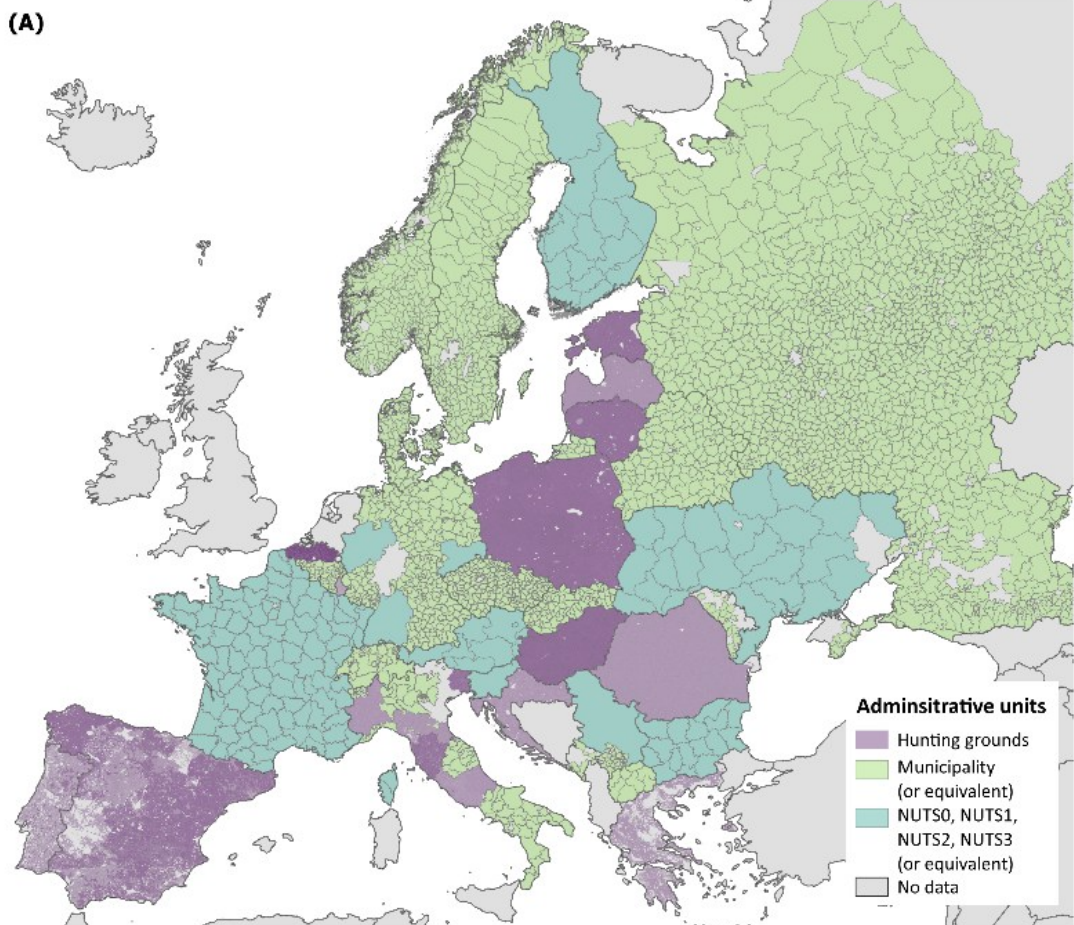
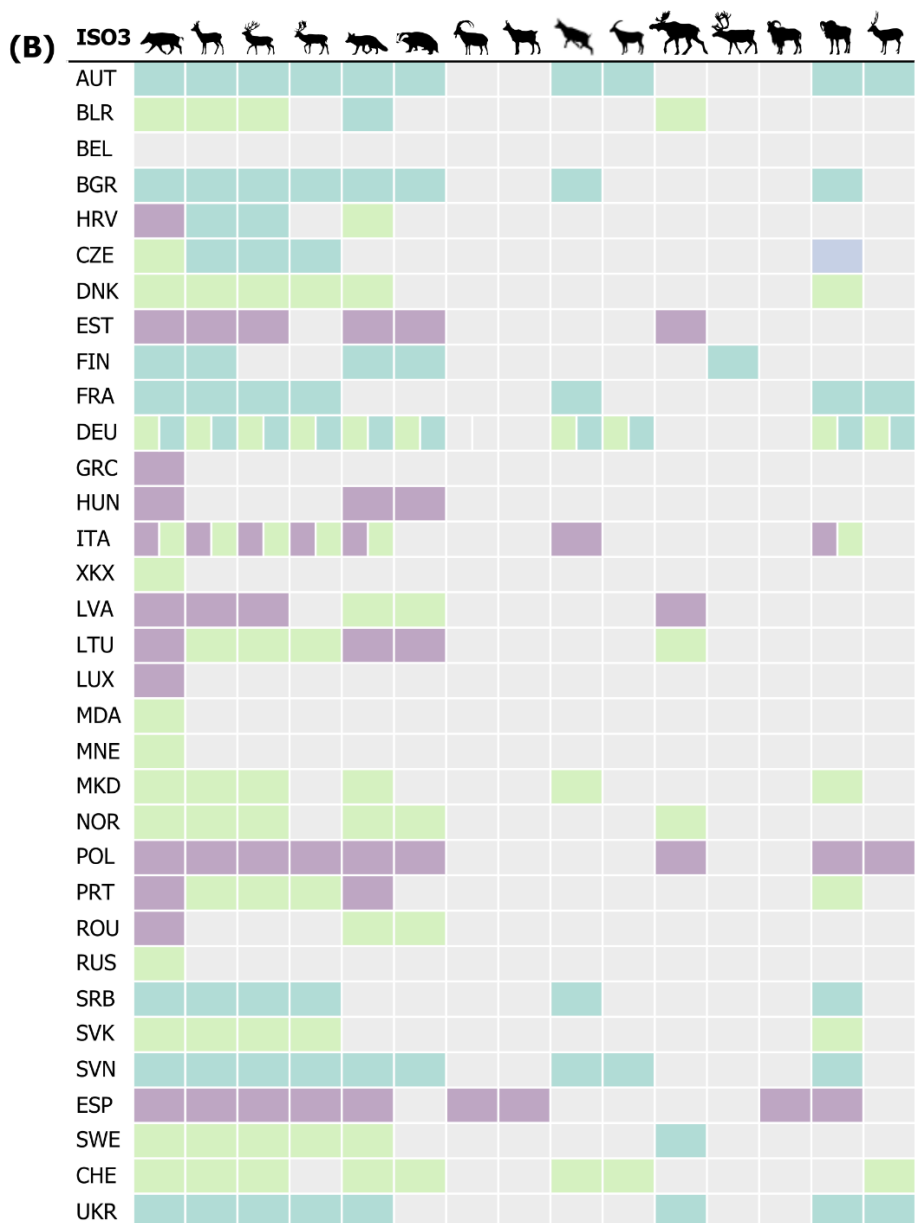


Figure 3.3. (A) Example map illustrating different administrative area units, ranging NUTS2, or NUTS3). (B) Administrative area levels vary by country and species. are wild boar, roe deer, red deer, fallow deer, red fox, European badger, Alpine ibex, European mouflon, reindeer, and sika deer. Hunting yield data were used for modeling does not necessarily cover the entire surface of a given country.



from the lowest level (“hunting ground”) to the highest level (NUTS 0, NUTS1, Countries are identified by their ISO3 codes. Species, shown from left to right, aoudad, Northern chamois, Iberian wild goat, Pyrenean chamois, moose, according to the availability of hunting data of each species (Figure S3-2.1), which

3.2.4. Ecogeographical variables

We considered environmental variables related to climate, topography, land cover, and human pressure as explanatory variables (see **Table S3-3.1**). Climate variables were obtained from the Worldclim 2 project database (Fick & Hijmans, 2017). Mean altitude was extracted from the USGS Space Shuttle Radar Topography Mission (SRTM - GL30; Farr et al., 2007). Land cover surfaces were downloaded from the Climate Change Initiative Land Cover project (SA/CCI-LC project version v2.0.7; ESA, 2017). The percentage of *Eucalyptus spp.* was considered as environmental variable, as ignoring these plantations has been shown to produce misleading predictions on ungulate abundances (European Forest Institute; Brus et al., 2012; ENETWILD-consortium et al., 2020). Snow cover was download from MODIS/Terra Snow Cover project (Monthly L3 Global 0.05Deg CMG, Version 6; Hall & Riggs, 2021), human footprint index was provided by The Last of the Wild Project version 2 (Venter et al., 2018), and vegetation growing period was obtained from the Agro-Ecological Zones project (FAO; Fischer et al., 2021). We also considered as covariates the longitude and latitude coordinates from the centroids of each territorial unit. All continuous ecogeographical covariates were scaled according to their mean and standard deviation. Furthermore, we considered the four climatic bioregions (see [S3-4](#)) described in ENETWILD-consortium et al., (2019). The packages and software used for data management were tidyverse 2.0.0 (Wickham et al., 2019), sf 1.0-19

(Pebesma, 2018), and R Statistical Software (v4.1.3; R Core Team, 2025), and QGIS 3.22.9.

3.2.5. Modeling choices

Species-specific models were developed following different modeling frameworks depending on the spatial distribution range of each species and data characteristics. All models shared a common preprocessing and variable-selection workflow, although the final statistical structure was explicitly adapted to each species, or group of species, to ensure ecological realism and statistical robustness.

3.2.5.1. General modeling framework

For all species, relative abundance N_i was modeled using a negative binomial distribution to account for overdispersion in HD estimates:

$$N_i \sim \text{NB}(HD_i, \kappa)$$

where HD_i is the expected density of individuals harvested in a territorial unit i (with $i = 1, 2, \dots, I$; I varies from 15 to 38,306 regarding species data; **Table 3.1**) and κ is the overdispersion parameter. The expected HD_i was modelled on the logarithmic scale as a linear function of the covariates, $\log(HD_i) = \beta * X_i$, where β are the linear effect of X covariates. This formulation represents the baseline model structure for all analyses and was fitted with the `glm.nb` function of MASS 7.3-65 (Venables & Ripley, 2002). Extensions of this framework were implemented to accommodate spatial stratification, management regulations, and zero inflation, depending on

species-specific characteristics (**Figure 3.4; Table 3.2**). For each species (or bioregion, where applicable), data were randomly split into a calibration dataset (80%) and a validation dataset (20%).

Prior to model development, multicollinearity among candidate ecogeographical predictors was assessed using the Variance Inflation Factor (VIF) with the `vifstep` function from `usdm` 2.1-7 package (Naimi et al., 2014). This procedure was applied independently for each species or bioregion. Predictors with VIF values ≥ 2 were excluded, and only non-collinear variables were considered in subsequent modeling steps as fixed effects (Zuur et al., 2010). Predictor selection was finally conducted when modeling using bidirectional stepwise procedures based on Akaike's Information Criterion (AIC) by species or bioregion. `stepAIC` function from `MASS` 7.3-65 package (Venables & Ripley, 2002) was used in the general baseline model.

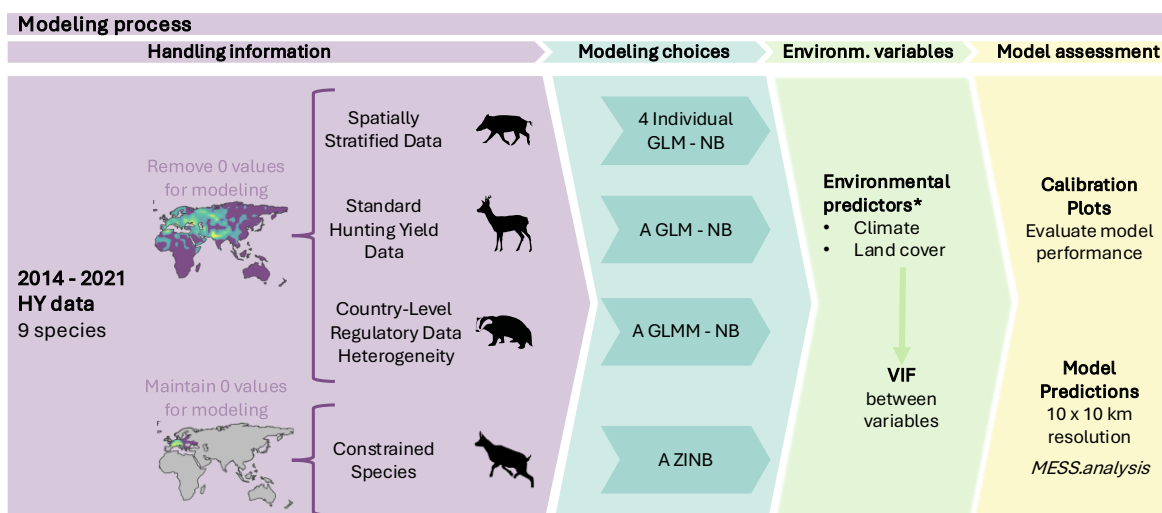


Figure 3.4. Modeling framework according species. Icons represent example species for each data treatment. *Environmental variables differ between modeling approaches, species or bioregions (**Table 3.2**).

3.2.5.2. Widely distributed species

Strong ecological and management heterogeneity across Europe led to the division of the wild boar dataset into four bioregions. Differences in climate, land use, and population dynamics across broad regions required accounting for regional variability in the relationships between hunting-derived density estimates and environmental predictors. This was addressed through a spatially stratified modeling approach in four bioregions (see [S3-4](#); de Jong et al., 2023; ENETWILD-consortium et al., 2022; von Essen et al., 2025). The baseline negative binomial model was fitted independently within each bioregion. Both intercepts and covariate slopes were allowed to vary among bioregions, capturing differences in species-environment relationships. This approach follows the general modeling philosophy proposed for wild boar by Acevedo, Quirós-Fernández, et al. (2014) and the ENETWILD-consortium, Acevedo, et al. (2019).

For several large and medium-sized ungulates and carnivores, reported hunting yields were typically lower than those observed for wild boar (**Figure S3-2.1**). For these species, HD were modeled using the baseline negative binomial model with logarithmic link function, fitted independently by each species.

Some species are affected by heterogeneity in hunting regulation between countries. This is the case of the European badger which hunting is only allowed in some European countries (Kurek et al., 2022), resulting in a mixture of absence of data, true zeros and unreported harvests. As indicative, approximately one third of the study area lacked HYS information for this species

(Figure S3-2.1). Moreover, hunting effort, reporting systems, and management practices may vary substantially among countries, generating a hierarchical data structure that required explicit consideration in the modeling framework (Griffiths & Thomas, 1997). Therefore, the European badger HD was modeled using a negative binomial generalized linear mixed-effects model, with country included as a random intercept, with the glmmTMB function of the same called package (1.1.14; Brooks et al., 2017).

$$\log(\text{HD}_i) = \beta * \mathbf{X}_i + (1|\text{country})$$

3.2.5.3. Constrained distributed species

For constrained species the baseline model was extended to a zero-inflated negative binomial model (ZINB), which jointly model the count process and the probability of an additional zero generating process.

$$N_i \sim \text{ZINB}(\text{HD}_i, \pi_i, \kappa)$$

$$\text{Zero inflation: } \text{logit}(\pi_i) = \beta_{\text{ZI}} * \mathbf{X}_i$$

$$\text{Count: } \log(\text{HD}_i) = \beta_{\text{C}} * \mathbf{X}_i$$

where π_i is the probability of the additional zero generating process, HD_i is the expected density of individuals harvested, κ is the overdispersion parameter, and where β_{ZI} and β_{C} are, respectively, the linear effect of $\mathbf{X}$ covariates for the zero-inflation and count process.

The same set of covariates was evaluated for both the count and zero-inflation components of the model. Model selection was conducted using a manual forward stepwise procedure, whereby covariates were sequentially

added to the count and zero-inflation components and retained only if their inclusion resulted in a lower AIC. As a consequence, the set of covariates retained in the count and zero-inflated components may differ. Non-convergent or non-identifiable models were excluded, and the procedure stopped when no further improvement in AIC was achieved. The final model was the model with lowest AIC. ZINB models were fitted using the `zeroinfl` function of the `pscl` 1.5.9 package (Jackman, 2024).

3.2.6. Model validation

Model performance was evaluated using an independent validation dataset (20% of the dataset) per each species or species/bioregion. Consequently, validation datasets contained no zero values for widespread species but did include zeros for constrained species. Calibration plots were constructed by comparing observed values and predicted HDs across nine quantiles-based intervals (Pearce & Ferrier, 2001), with perfect calibration indicated by alignment along the identity line. Predicted HDs were obtained from the fitted models using the response scale and subsequently back-transformed to the original HD units. Within each class, mean predicted HD and mean observed HD were calculated. The relationship between observed and predicted informs about the reliability of predictions as an indicator of model robustness.

For wild boar, calibration was performed separately for each bioregion, reflecting the bioregion-specific modeling framework adopted for this species.

For the rest of widely distributed species, calibration plots were first assessed globally and subsequently by bioregions, considering only regions where the species were present to assess potential spatial variation in model performance and to evaluate whether calibration patterns were influenced by regional differences in data availability or density distributions.

3.2.7. Spatial predictions

The models were statistically projected to make continuous predictions of HD across Europe at 10 x 10 km using the EEA reference grid (European Environment Agency, 2024). The same environmental predictors were extracted for each grid cell following the same procedures applied to the datasets. Grid centroids were computed and used to derive spatial coordinates. All predictors were scaled by the mean and standard deviation of the dataset to ensure consistency with the fitted models.

For wild boar, spatial predictions were generated separately for each of the four bioregions, reflecting the bioregion-specific modeling framework and merged to obtain a single continental prediction layer. For the rest of widely distributed species, predictions were generated across the full 10 x 10 km grid. For European badger, the random intercept corresponding to Switzerland, whose estimate was closest to the overall mean, was used for predictions, which were generated across the countries that reported HYs of this species; this was carried out to make general inferences about the potential abundance of the species

according to ecogeographical characteristics by avoiding the effects of hunting regulation in the predictions. For species with constrained distributions, spatial predictions were generated exclusively within the cell grids of the countries that reported species HYs.

For all species, model predictions at 10 x 10 km were obtained on the response scale and subsequently back-transformed to HD units by reversing the scaling applied during model fitting. To exclude areas where predictions were made outside the environmental conditions considered in model calibration, multivariate environmental similarity surfaces (MESS) were computed (Elith et al., 2010; MESS 0.6.0 package Ekstrøm, 2025). MESS analyses compared predictor values in the prediction grid against those in the calibration dataset using only the variables retained in the final models. These surfaces were used to remove grid cells of spatial predictions characterized by extrapolation beyond the environmental domain of the training data.

3.3. Results

Data availability differed markedly between widespread and constrained species (**Table 3.1**). Widespread species (wild boar, red deer, roe deer, fallow deer, and red fox) were characterized by a larger number of territorial units and observations, whereas constrained species showed more limited spatial coverage and fewer records. At this respect, the European badger reported similar number of territorial records than constrained species given the limited availability of

data according to its hunting status across Europe. Constrained species with a greater number of records (*i.e.*, Iberian wild goat and European mouflon) were present in limited number of locations in Spain, where the spatial coverage of territorial units are at hunting grounds (see [S3-2](#) and **Figure 3.3**).

3.3.1. Modeling results

Similar predictors were included in most widespread species models, particularly those related to land cover classes. However, greater interspecific variation was observed among climatic variables. Despite this general pattern, model parameter estimates differed substantially across species (**Table 3.2**). Additionally, wild boar exhibited bioregional differences in predictor selection, particularly for climatic factors. In contrast, selected land covers were more consistent across regions, although with varying effects by bioregion. Deer species, except for sika deer, showed predominantly positive associations with most selected land cover predictors; however, greater variability was detected in the effects of climatic and spatial predictors, which seemed to exert stronger influences on HDs. The red fox displayed heterogeneous responses to land cover covariates, whereas European badger responses were predominantly positive for all significant land cover effects. Scandinavian countries reflected a marked increase in the global mean (β_0), whereas Baltic and Eastern countries exhibited a pronounced reduction (**Table 3.3**). Finally, the dispersion parameter, κ ,

indicated a strong over dispersion relative to a Poisson process, given their low values (**Table 3.2**).

Model performance and parameter estimates varied markedly among constrained species, highlighting the heterogeneity of HDs patterns (**Table 3.2**). Out of the nine constrained species analyzed, seven yielded convergent ZINB models with identifiable parameter estimates. In contrast, models for two species (Alpine ibex, and reindeer) exhibited extremely large parameter estimates and standard errors in the zero-inflation component, indicating a lack of parameter identifiability. Consequently, we only report results for species whose models converged and exhibited identifiable parameters estimates. Among the converged models, both the count and the zero-inflation components contributed to explaining variation in hunting yield densities. Dispersion parameters were consistently low across species, indicating a strong overdispersion relative to a Poisson process (**Table 3.2**).

Spatial predictors were retained in all models and had the strongest effects on the zero-inflated component compared to the other predictors. However, their importance in the count component varied across species (**Table 3.2**). Regarding the latter, the signs of many of moose's selected predictors changed between processes, whereas other species (*e.g.*, Pyrenean chamois) did not exhibit this consistent trend. Some variables showed to negatively influence the presence and abundance of constrained species (*e.g.*, annual range of temperature (bio07) for European mouflon; **Table 3.2**), while other variables

Table 3.2. Model types, zero-treatment approach, selected environmental framework, individual models were developed for wild boar in each bioregion.

	       													
	MT	N	S	E	W	NB	NB	NB	NB	NB	CM	ZIC	CM	ZIC
		NB GLM	NB GLM	NB GLM	NB GLM	GLM	GLM	GLM	GLM	GLMM	(NB)	(Binom)	(NB)	(Binom)
	ZT	Rm	Rm	Rm	Rm	Rm	Rm	Rm	Rm	Rm	Rt		Rt	
bio02		1.13			0.09									
bio03			0.31							0.10	0.13	0.22		
bio04			0.11							0.32				
bio07						0.37	0.10							
bio08			0.13			0.14								
bio09			0.33	2.70									0.32	1.08
bio10														
bio13				0.21										
bio14														
bio15				0.16	0.35	0.24	0.45	0.26	0.13	0.05				
bio18		1.71			0.41									
bio19									0.14					
lc10			0.04	0.39	0.12		0.07	0.09	0.01	0.127	0.05			
lc11		1.09			0.29	0.10								
lc12			0.01						0.02					
lc30			0.05		0.12	0.07	0.20		0.07	0.051	0.25	0.35		
lc40			0.69	0.05			0.25	0.26		0.02	0.16	0.43		
lc60			0.36	0.24	0.16		0.10	0.23	0.03	0.01	0.23	0.32	0.28	0.20
lc70				0.17	0.05	0.04	0.02	0.27	0.24	0.06	0.07		0.20	0.15
lc90					0.06			0.17		0.02	0.01			
lc100				0.13	1.18	0.23	0.16	0.31	0.25		0.06	0.13	0.48	0.270
lc120				0.08				0.17	0.14					
lc130				0.16	0.14	0.10	0.04	0.10	0.14	0.08	0.03		0.61	
lc180		0.09												
lc190					0.07					0.05				
lc210		0.09												
hfp									0.08					
snow		0.48	1.14			0.30	0.30	0.25	0.17		0.14	0.29		
alt					0.14					0.121			0.40	1.08
Eu			0.05		0.24	0.27	0.14	0.13	0.07					
xscale						0.31	0.49	0.23	0.02	0.029	0.06	0.97	1.53	2.82
yscale						0.09	0.25	0.11	0.25	0.547	0.12	1.29	2.24	4.38
θ		1.90	1.17	1.03	0.98	1.66	0.92	0.66	1.33	1.79	1.22		1.10	
MS		C	C	C	C	C	C	C	C	C	C		C	

MT	Model type	ZT	Zero treatment
GLM	Generalized linear model	Rm	Removed zero values of dataset for modeling.
GLMM	Generalized linear mixed model		
CM	Count component (negative binomial with log link) of Zero Inflated model	Rt	Retained zero values of the dataset for modeling,
ZIC	Zero inflation component (binomial with logit link) of Zero Inflated model		
NB	Negative binomial distribution		
θ	Dispersion parameter of the negative binomial distribution.		
CM	Count component (negative binomial with log link) of Zero Inflated model		

variables and model fixed results for each species. According to the modeling
Bold font indicates that environmental covariates were significant.

															MT
	CM (NB)	ZIC (Binom)	CM (NB)	ZIC (Binom)	CM (NB)	ZIC (Binom)	CM (NB)	ZIC (Binom)	CM (NB)	ZIC (Binom)	CM (NB)	ZIC (Binom)	CM (NB)	ZIC (Binom)	
	Rt		Rt		Rt		Rt		Rt		Rt		Rt		ZT
															bio02
	0.26												2.17		bio03
															bio04
											0.18	0.09			bio07
															bio08
	0.60	0.86													bio09
													0.52		bio10
															bio13
											0.32	0.14			bio14
	0.37						0.23	0.48						0.84	bio15
															bio18
	0.47	0.68									0.23				bio19
							0.29	0.12				0.24	0.32	1.04	0.79
															lc10
															lc11
															lc12
						0.07				0.54			0.01		lc30
						0.05	0.34				0.47	0.18	0.24		lc40
		0.94				0.16	0.50					0.17	0.38		lc60
		1.39				0.46	0.66					0.06	1.14	0.39	lc70
						0.28	0.14						1.11		lc90
							0.14								lc100
										0.69		0.55			lc120
		0.80				0.08						0.17	0.01		lc130
															lc180
															lc190
															lc210
															hfp
															snow
							0.23					0.16	0.14		alt
												0.11			Eu
	0.60	1.85				0.03	1.26			0.33	2.13	0.13	0.45	1.28	0.08
	1.64	4.46				0.47	2.92			0.24	1.88	1.05	0.06	0.13	0.84
	1.10		-		2.06		-		1.52		0.58		0.34		θ
	C		NI		C		NI		C		C		C		MS

Environmental Variables

MS Model status

C Converged model.

NI Not identifiable model.



The ZINB model did yield identifiable parameter estimates; consequently, neither covariate effects nor dispersion parameters were reported.

Environmental variables



Squared box indicates EV selected for modeling after vifstep analysis.



EV selected after backwise AIC selection with a positive coefficient.



EV selected after backwise AIC selection with a negative coefficient.



Grey color indicates that EV was not selected after backwise AIC selection.

Table 3.3. Estimates differences from the European badger GLMM. Black text shows country-specific intercepts on the log scale, while dark teal text shows the exponential random effect [$\exp(\text{ranef}())$], representing multiplicative deviations from the global mean (β_0). Countries are identified by their ISO3 codes.

Country	Intercept	Country	Intercept	Country	Intercept
ROU		POL		SWE	
	4.850 0.142		6.383 0.658		7.576 2.172
LTU		CHE		HUN	
	5.066 0.177		6.895 1.099		7.633 2.299
LVA		AUT		NOR	
	6.084 0.489		7.021 1.247		7.654 2.346
SVN		DEU		FIN	
	6.309 0.612		7.557 2.131		8.868 7.901
EST					
	6.371 0.651				

seemed to influence positively the presence and abundance of constrained species (e.g., isothermality (bio03) for Iberian wild goat, forest (lc60, lc70) for moose; **Table 3.2**). In contrast, other variables seem to influence species absence, but when the species is present, they promote species abundance. For instance, vegetation mosaic (lc40) for moose and deciduous forest (lc60) for Iberian wild goat favor the absence of the species, but once the species is present, they respectively promote abundance (**Table 3.2**). Conversely, other variables increase the probability of presence while limiting species abundance, such as needle forests (lc70) for sika deer or precipitation seasonality (bio15) for moose (**Table 3.2**).

3.3.2. Model calibration and predictive performance

Across all widespread species, calibration plots generally showed monotonic relationships between observed and predicted values, although with some interspecific differences (**Figure 3.5** and **Figure 3.6**). Wild boar showed good predictive performance across all bioregions, except in the Northern region where low densities led to overprediction (**Figure 3.5a**). In contrast, roe deer, red deer and fallow deer showed differences in the calibration plot depending on the bioregion (**Figure 3.5**). The general calibration plot for roe deer showed an overall good prediction pattern and linear trend over density classes (**Figure 3.6**). Bioregion specific results indicated more consistent predictive performance in the Eastern and Western bioregions, whereas the Northern bioregion showed

variable patterns across density classes (**Figure 3.5b**). For the red deer calibration plots indicated generally a linear pattern and an overprediction trend in the predictive performance (**Figure 3.6c**). Bioregion-specific calibration showed good predictive performance in the Eastern bioregion, while the remaining bioregions showed weaker performance. The overall calibration plots for fallow deer indicated systematic overprediction (**Figure 3.6d**), which was also indicated by bioregion-specific calibrations. Predictive performance in the Northern bioregion could not be reliably assessed due to the scarcity of data on that bioregion (**Figure S3-2.1**). For red fox, calibration plots showed good predictive performance in the lowest density classes, with slight overprediction in intermediate and high-density bins (**Figure 3.6e**). Bioregion-specific calibration indicated good performance in the Eastern and Southern bioregions, whereas overprediction occurred in the Northern bioregion for low to medium density classes. The Western bioregion showed poor predictive performance, with no discernible pattern (**Figure 3.5e**). The calibration plots for European badger showed overall good predictive performance across most density classes (**Figure 3.6f**). Bioregion-specific calibration revealed good predictive performance in the Eastern bioregion and a linear pattern in the Northern bioregion, whereas poorer performance occurred in the Western bioregion, especially at from intermediate to high density bins (**Figure 3.5f**). Some constrained species showed satisfactory linear calibration patterns, while others showed systematically underestimated relative densities (**Figure 3.6g-m**).

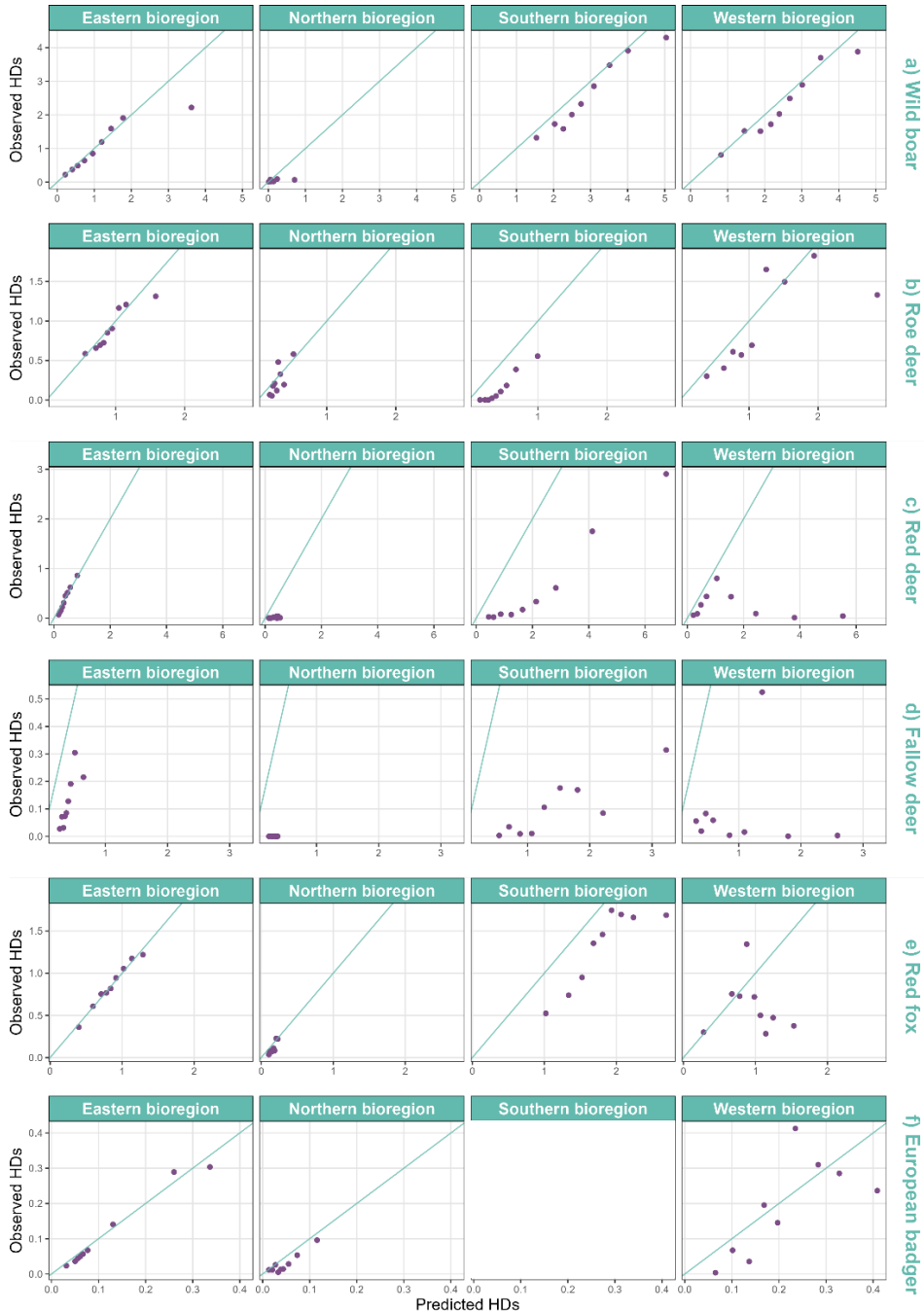


Figure 3.5. Calibration plot for assessing predictive performance, hunting yields models for each bioregion. Plots show the relationship between the predicted hunting yield densities (HD) and the observed ones on the validation datasets of wild boar (a), roe deer (b), roe deer (c), fallow deer (d), red fox (e) and European badger (f).

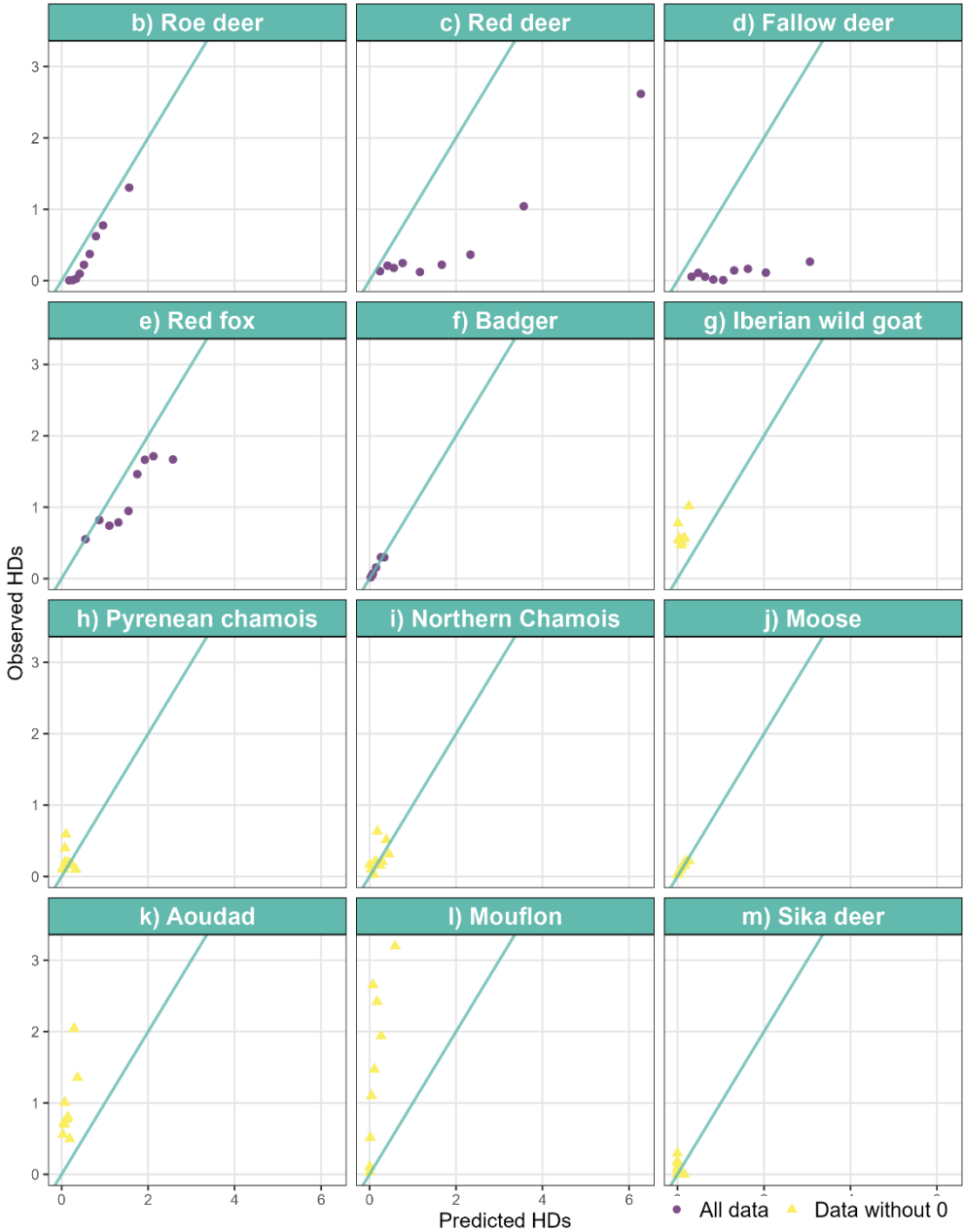


Figure 3.6. Calibration plot for assessing predictive performance HD models for all Europe. Plots show the relationship between the predicted hunting yield densities (HD) and the observed ones on the validation datasets of roe deer (b), roe deer (c), fallow deer (d), red fox (e), European badger (f), Northern chamois (g), Iberian wild goat (h), Pyrenean chamois (i), moose (j), European mouflon (k), and sika deer (l).

3.3.3. Spatial predictions

Predicted HDs differed among widespread species in both values and spatial distribution. Maximum predicted values ranged from 0.45 for the European badger to 24.7 for wild boar, and spatial predictions revealed species-specific HDs patterns across Europe (**Figure 3.7**). Wild boar predictions showed medium to high HDs across Central, Western, and Southern Europe, with lower predicted values in northern and eastern regions (**Figure 3.7a**). Roe deer predictions showed the highest HDs in Atlantic and temperate regions, with progressively lower predicted values towards northern, eastern, and southern Europe (**Figure 3.7b**). Red deer predictions showed high HDs in the northwestern Iberian Peninsula, with a widely scattered abundance pattern across Europe characterized by low to medium HDs (**Figure 3.7c**). Fallow deer predictions showed high potential HD in southwestern Europe, with decreasing predicted values towards northern and eastern regions (**Figure 3.7d**). Red fox predictions showed the highest HD densities in southern Europe, particularly in the southern Iberian Peninsula, with medium predicted values across much of the continent and lower predicted densities in northern regions and mountain systems (**Figure 3.7e**). European badger predictions showed medium HDs across most of Europe, with higher predicted values in southeastern regions and lower densities in mountainous and northern areas (**Figure 3.7f**).

Spatial predictions for constrained species generally reflected heterogeneous and spatially restricted abundance patterns, highlighting core

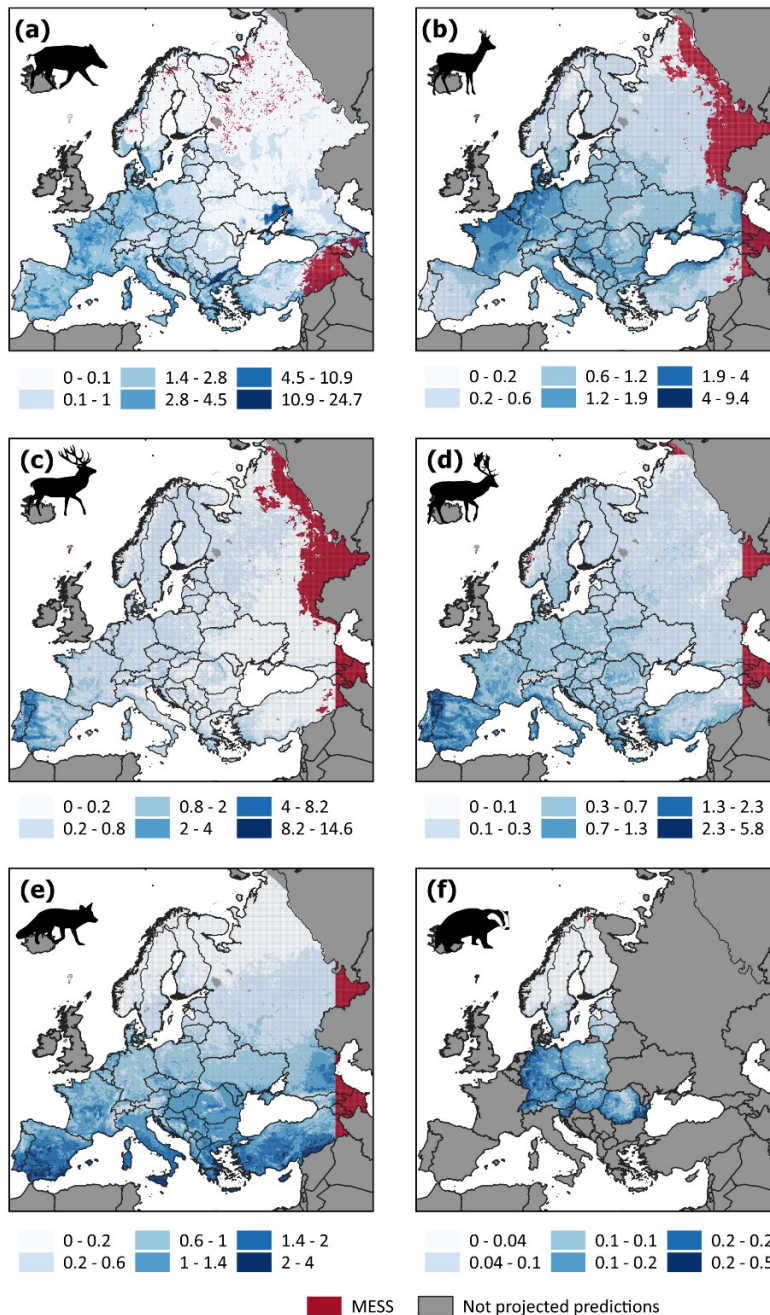
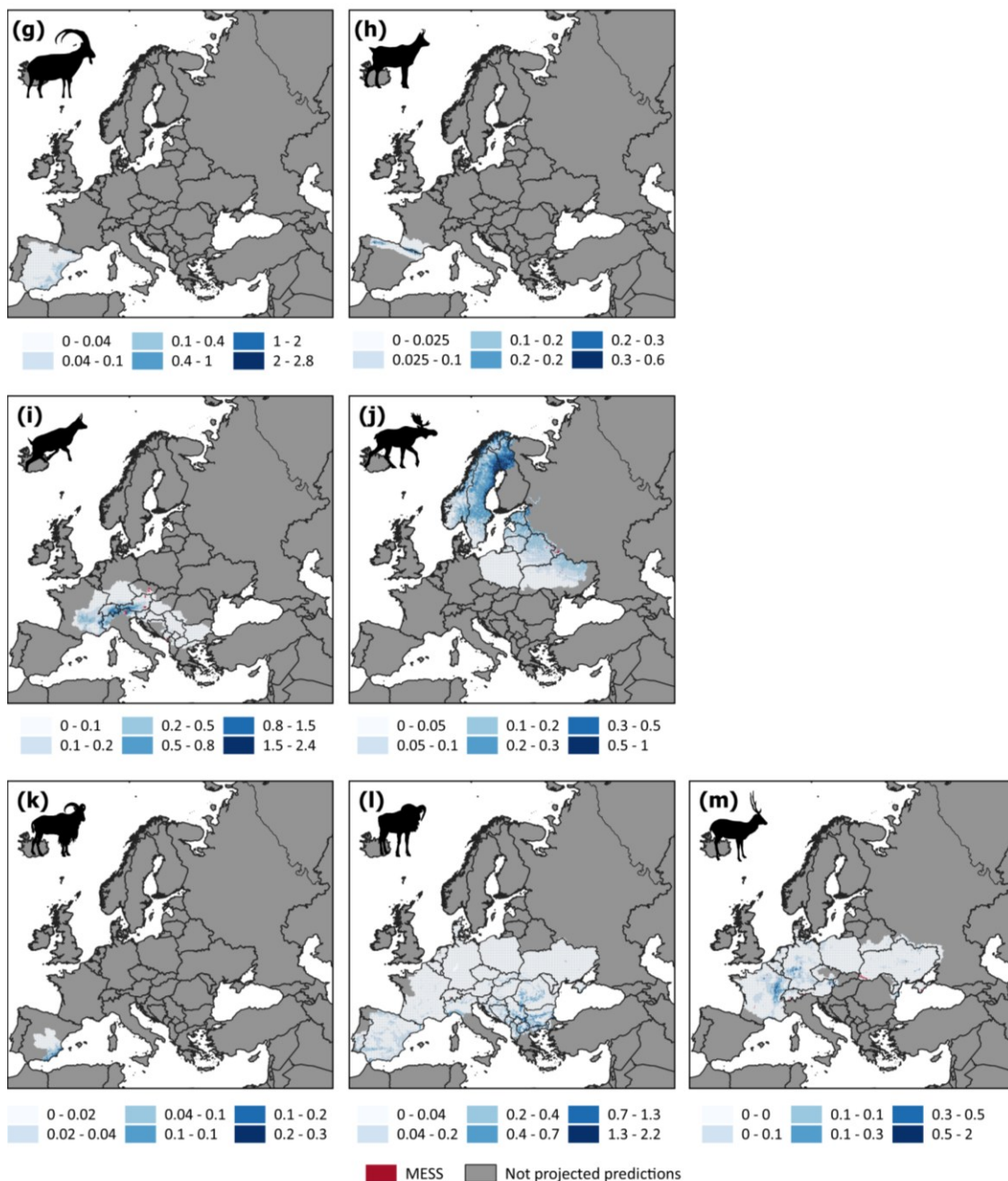


Figure 3.7. Hunting yield density (individuals hunted per km²) of red fox (e), and European badger (f) and constrained species: Iberian European mouflon (l), sika deer (m) at 10x10km. Red areas are



widespread species: wild boar (a), red deer (b), roe deer (c), fallow deer (d), wild goat (g), Pyrenean chamois (h), Northern chamois (i), moose (j), aoudad (k) beyond the environmental domain according to MESS analyses

areas with higher predicted abundance (**Figure 3.7g-m**). Three of the seven constrained species were associated to mountain systems. In the case of Iberian wild goat and Pyrenean chamois showed higher predicted densities associated to major mountain systems in the Iberian Peninsula (**Figure 3.7g-h**). Similarly, the Northern chamois higher predicted densities were concentrated in the Alpine region (**Figure 3.7i**). For moose, which distribution is restricted to northern latitudes, model predictions reflected a pronounced latitudinal gradient across northern Europe (**Figure 3.7j**). The remaining species, aoudad, European mouflon and sika deer, which have been introduced in Europe, have heterogeneous distributions across their ranges, with scattered areas of higher predicted densities (**Figure 3.7k-m**).

3.4. Discussion

This study presents different frameworks to estimate the spatial distribution of relative abundance for common game mammals at European scale using hunting yields statistics as data source and managing their idiosyncrasies. Although hunting yield datasets constitute opportunistic sources of information, they can provide a valuable overview of mammal relative abundance (Gamelon et al., 2021). Indeed, European hunting data collection frameworks are becoming more standardized, with protocols ensuring that the data are more representative and comparable. Accordingly, we accounted for data availability by considering the species-specific distribution range and the management scenario when modeling abundance. Our results show that the predictive

performance of the models is influenced by the characteristics of the species regarding their distribution and management, which directly shape the structure of the datasets. These findings emphasize the need for flexible modeling strategies and reinforce that a single modeling framework is unlikely to be equally suitable for all species, even when the modeling objective remains the same (Guillera-Arroita et al., 2015).

Clear differences emerged between widespread and constrained species in terms of data coverage, model calibration, and the role of zero values pointing out that the nature of zero values, reliable true zero or not, may differ between species. Widespread species benefited from larger datasets (**Table 3.1**) and broader spatial coverage (**Figure 3.3**), allowing models to capture consistent large-scale gradients in relative abundance (**Figure 3.7**). For these species, models fitted without zero values in the response variable showed linear predictive patterns, suggesting that zero hunting yields may partly reflect reporting practices, hunting effort, or management constraints rather than true absences (**Figure 3.5** and **Figure 3.6**; Vajas et al., 2020). In contrast, constrained species showed more spatially restricted distributions and sparser datasets. For these species, models fitted with zero values in the response variable achieved satisfactory calibration for endemic species, underscoring that zero values carried relevant information on spatial limits and local absences within reported hunting areas (**Figure 3.6g-j**), while an underprediction pattern was consistently observed for introduced species (**Figure 3.6k-m**). These contrasting patterns highlight that

the nature and interpretation of zero values differ among species as well as the importance of tailoring model formulation to species distribution and data characteristics rather than applying uniform preprocessing decisions across taxa (Stralberg et al., 2025).

Across all modeling frameworks strong to very strong overdispersion was detected (**Table 3.2**), suggesting that HDs may arise from the aggregation of some biological processes, such as an inhomogeneous Poisson Point Process (iPPP), from which harvested individuals are drawn (Fernández-López et al., 2025; Gotway & Young, 2002). Accordingly, negative binomial models provided a more appropriate representation of the data than Poisson models when using this type of data (Stoklosa et al., 2022).

Our results further suggest that environmental factors play a major role in structuring the spatial distribution of relative abundance of European game mammals, although their effects are strongly species dependent. Abundance patterns are often more closely linked to local habitat characteristics than to broad-scale environmental gradients (*e.g.*, Ferrer-Ferrando et al., 2025), and the prominence of land cover variables across models is consistent with this general expectation. However, the strength and direction of these effects differ by taxa, reflecting species specific habitat preferences. Constrained species exhibited stronger responses to land cover, indicating that their abundance is more tightly linked to local characteristics, whereas generalist species showed comparatively stronger responses to climatic factors, likely reflecting processes operating at

broader spatial scales and contributing to explain variation in abundance across their ranges. Within this framework, a consistent pattern across species was the negative association between hunting yield densities and eucalyptus plantations, suggesting that this land-cover class captures unfavorable conditions for the abundance of multiple species (**Table 3.2**; Ares-Pereira et al., 2022; Teixeira et al., 2023). In addition, model results consistently showed that spatial coordinates were among the strongest predictors, particularly in the zero-inflated component for constrained species, indicating that a substantial fraction of the variation is structured spatially and not fully captured by the environmental covariates (**Table 3.2**; Dormann et al., 2007). Coordinate terms may act as proxies of unmeasured spatial processes and likely reflect spatial restrictions in the distribution of constrained species (Dormann et al., 2007). Overall, differences in predictor importance among species appear to be mediated by niche breadth, life history traits, and biogeographic context.

Despite these similarities, model performance and calibration were species-dependent, revealing differences that should be considered in abundance modeling. These results may point to differences in the reporting of game hunting bags among species (Guillemain et al., 2026; Ruiz-Rodríguez et al., 2023), which may reflect relative abundance rather than true population size and may be influenced by variation in hunting effort, reporting accuracy, and regulatory frameworks. Our findings support the use of species-specific data preprocessing and flexible modeling strategies when estimating relative

abundance of European game mammals (Guillera-Arroita et al., 2015; Waldock et al., 2022). These results highlight that data preprocessing decisions should be tailored to species-specific distributional characteristics. Additionally, beyond preprocessing decisions, further sources of spatial heterogeneity emerged in the modeling of relative abundance. In particular, the environmental predictors selected for modeling wild boar HDs, as well as the estimated effects when predictors were shared between bioregions, reflect non-stationarity on the abundance process across Europe for this species (**Table 3.2**). Consequently, the implementation of a global model may produce misleading inferences and obscure region-specific environment relationships. At the same time, model evaluation also indicated that not all widespread species require this approach, as global calibration plots generally showed better performance than bioregional ones (**Figure 3.5** and **Figure 3.6**). Exceptions were observed in the Northern bioregion where calibration plots systematically overpredict. These results suggest that environmental relationships for these species in regions with limited data or extremely low densities may differ from those captured by a global model. Beyond this, European badger showed that including country as a random effect accounted for deviations from the global expected mean when environmental predictors were held constant (**Table 3.3**), reflecting residual heterogeneity among countries (Bolker et al., 2009). Spatial predictions were generated assuming a common country-level effect across space, thereby highlighting the role of environmental covariates in shaping abundance patterns

independently of national boundaries. Under this framework, GLMMs provide a robust tool for adaptive management by separating large-scale environmental drivers from unmeasured country-level heterogeneity, which may be especially relevant for species whose management status varies across the study area.

Finally, from a process-based perspective, ZINB results suggest that differences in environmental predictors between model components may reflect the different roles these variables play in determining species distribution versus abundance, and that their effects are not necessarily aligned in direction. The ZINB framework failed to produce identifiable parameters in the zero-inflated component for two species: Alpine ibex, and reindeer, and therefore their models were not considered. Nonetheless, it must be noted that the identifiability problem likely results from limited data availability, highly skewed density distributions dominated by zero or near zero values, and strong zero inflation, which together provide insufficient information to reliably model abundance patterns (**Figure S3-2.1**). These results highlight the sensitivity of zero-inflated models to data structure and sample size, particularly for rare or sparsely distributed species.

Monitoring common wildlife at broad scales remains uncommon, making spatial patterns derived from abundance modeling particularly valuable for wildlife management. Spatial predictions indicated that ungulate densities were generally higher than carnivores' densities across the continent (**Figure 3.7**). In addition, spatial predictions showed that the Northern bioregion supports lower

wildlife densities, suggesting that environmental conditions may constrain abundance in this region (Antão et al., 2022; Leonardi et al., 2022). Beyond these broad patterns, spatial predictions revealed consistent gradients and region-specific hotspots across species, supporting their utility for large-scale wildlife management. Several ungulate species, including wild boar, red deer, roe deer, and fallow deer, together with carnivores such as red fox and European badger, showed higher predicted densities in central and southern Europe, with a general decline toward northern and eastern regions (**Figure 3.7**). These gradients likely reflect a combination of climatic constraints, habitat productivity, and long-term management practices, and identify southwestern Europe as a recurrent area of high relative abundance for multiple game species (Linnell et al., 2020). For some species, notably fallow deer, and other introduced ungulates such as European mouflon or sika deer, spatial predictions likely represent potential abundance, reflecting populations that remain locally distributed and may not yet have reached ecological equilibrium, with possible future increases in estimated abundance (Ionescu et al., 2025). The contrasting spatial patterns between red fox and European badger in some countries (*e.g.*, Germany, Poland) suggest that predicted abundance maps may integrate both ecological processes and differences in hunting traditions. By comparison, species with more constrained ecological niches, particularly mountain-associated species such as chamois (Northern and Pyrenean) and Iberian wild goat, displayed spatially concentrated areas of higher predicted abundance aligned with known mountain systems,

indicating that the models reliably captured key ecological drivers of their distribution.

Overall, our findings indicate that, when appropriately implemented, hunting yield data constitutes a robust source of information for capturing large-scale spatial patterns of relative wildlife abundance across Europe. Our results underscored the need to align modeling strategies with species ecology, distribution range, and data availability when estimating relative abundance at broad spatial scales. Integrating these frameworks with complementary monitoring approaches, such as camera trapping networks, may enhance the robustness and applicability of abundance predictions for management and risk assessment (Gilbert, Pease, et al., 2021). The consistent overdispersion observed across hunting yield datasets supports the use of Negative Binomial distribution when modeling them. Furthermore, the presence of structured zero inflation in range restricted species highlights the importance of adopting alternative modeling frameworks, such as zero-inflated negative binomial models, rather than approaches applied to widespread species.

Acknowledgements

ENETWILD Wildlife: collecting and sharing data on wildlife populations, transmitting animal and human disease agents (OC/EFSA/ALPHA/2016/01).

Data accessibility statement

Data cannot be shared due to international data-sharing agreement restrictions. Code used for modeling is open and available at [github](#).

S3 Supplementary information

S3-1 Citizen science data collection

Citizen science has become an important source of biodiversity information due to the large number of persons that report species occurrence (Fraisl et al., 2022). Several platforms facilitate the submission of such data, among which iNaturalist has become one of the most used worldwide (Mason et al., 2025). We examined the different animal categories provided by iNaturalist and recorded, for each category, the number of observations, the number of species, and the number of observers. Comparisons among categories indicate that insects exhibit the highest ratios of observation, observers and recorded species. In contrast, mammals show the lowest ratio of observations (0.0809%), despite having a ratio of observers comparable to amphibians and reptiles; however, the ratio of observations of these latter groups is, respectively, 32.39 and 51.54 times higher (**Figure S3-1.1**). Similarly, mammals rank lowest in both the number of observations per number of observers and the number of observations per species. Given the relatively low number of mammal species compared to other groups, one might expect mammals to be easier to identify, and therefore to have a higher number of observations relative to species richness. Nonetheless, the comparatively low number of mammal observations suggest either difficulties in detecting these species or a preferential tendency of observers to record other taxa, such as birds or insects (**Figure S3-1.1**).

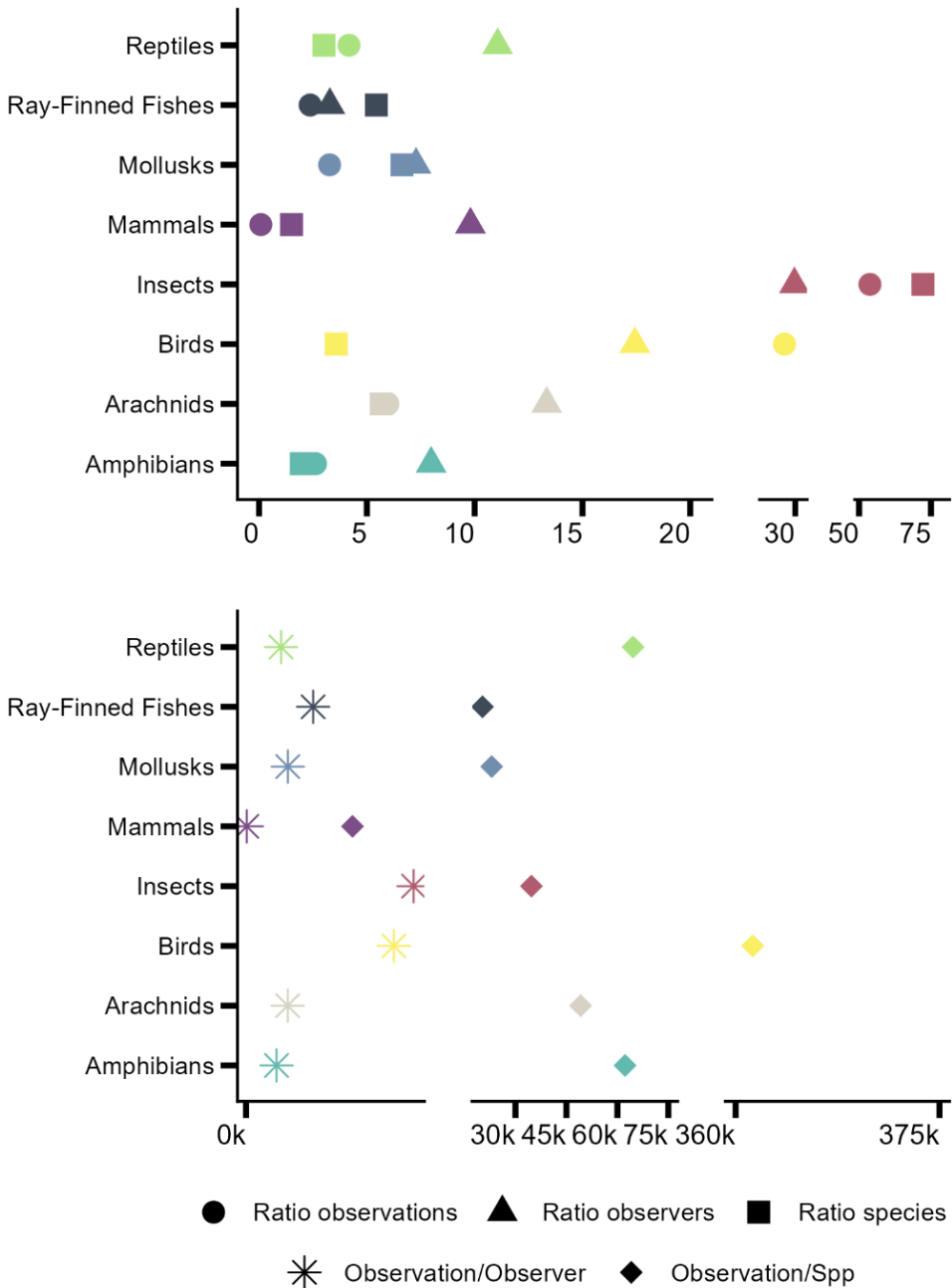
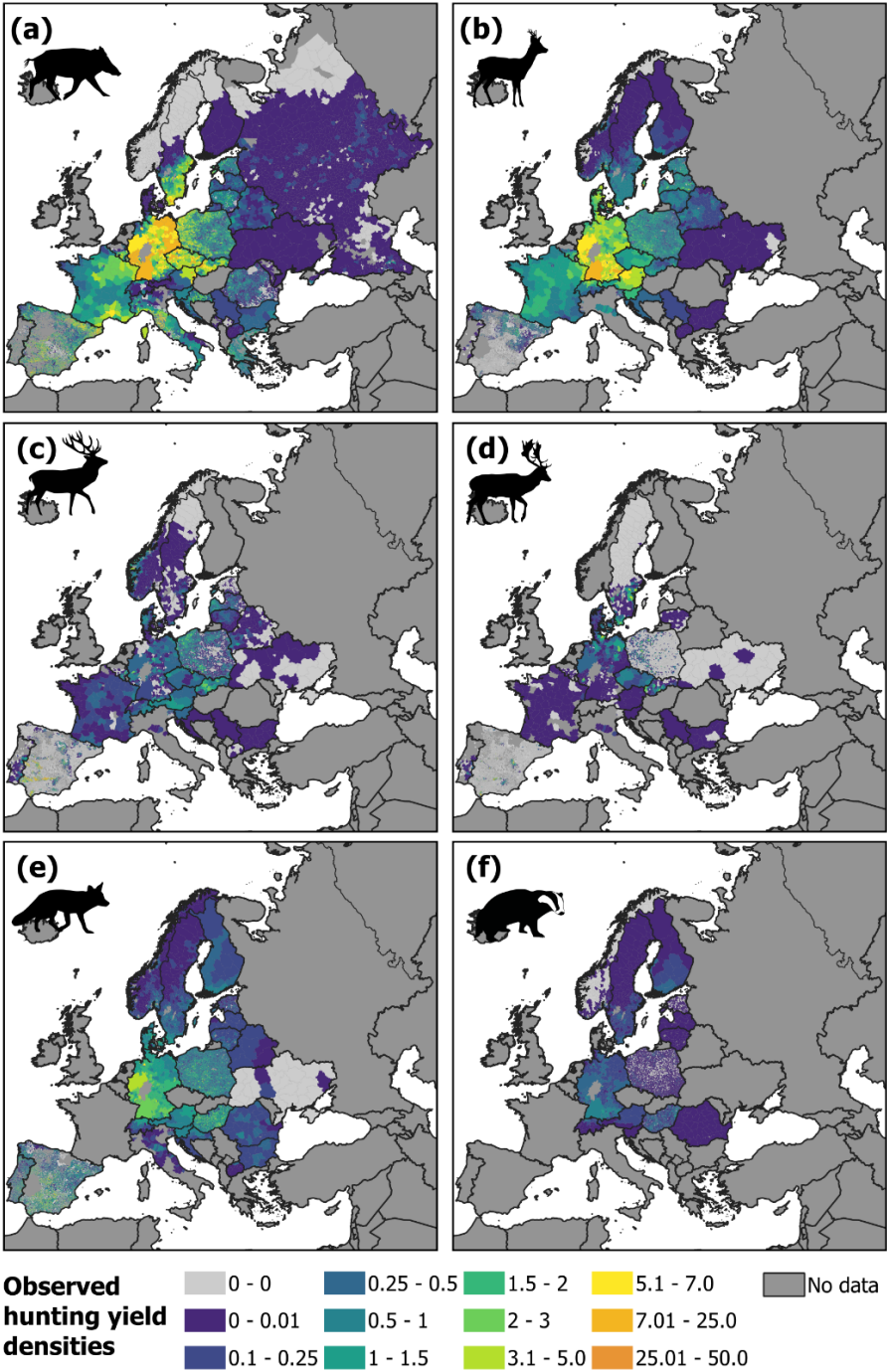
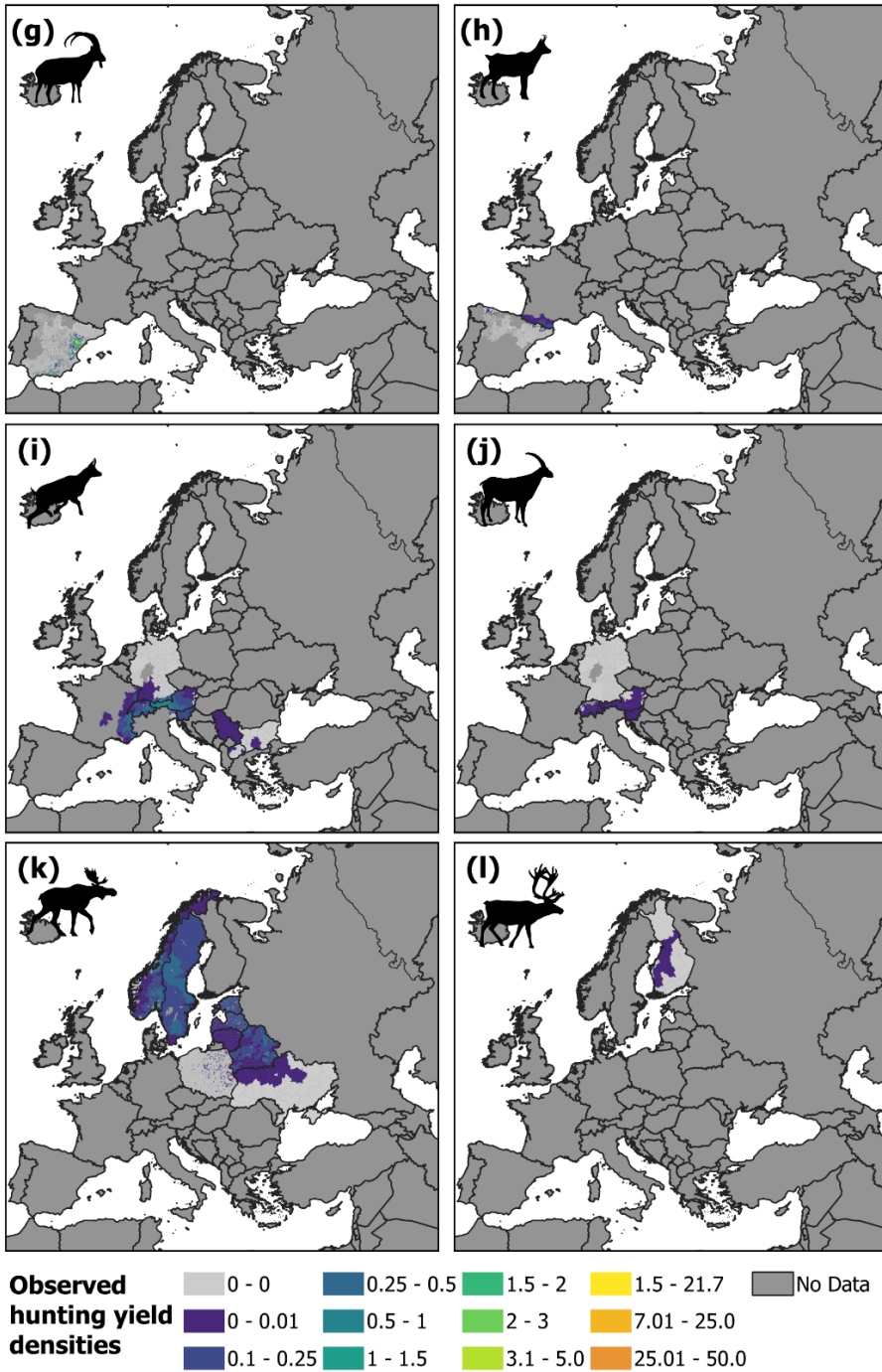


Figure S3-1.1. Distribution of iNaturalist observations across major animal groups. For each taxonomic category, we show the ratio of the number of observations, the number of species, and the number of observers recorded on iNaturalist.

S3-2 Hunting yield available data





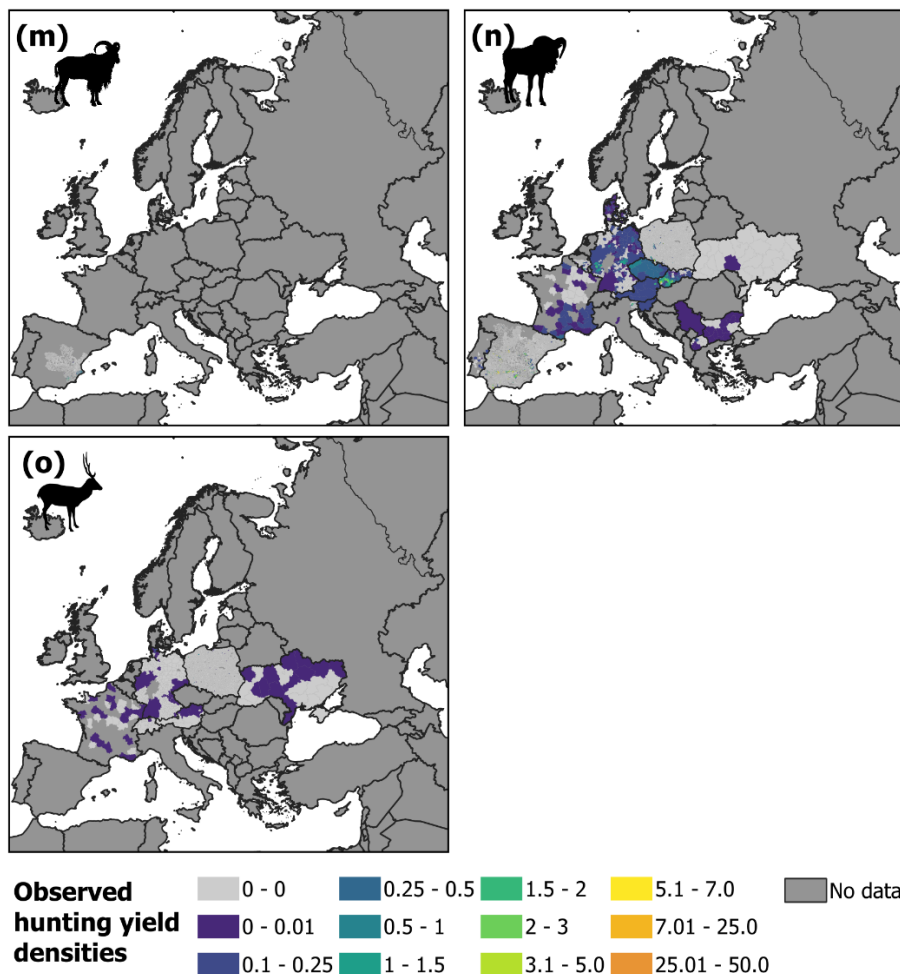


Figure S3-2.1. Maximum hunting yield density (HDs) observed between 2014/2015 and 2021/2022 hunting seasons, used as the response variable for parameterizing species models of both widespread and constrained species according to territorial units.

S3-3 Environmental variables considered as explanatory variables.

Table S3-3.1. Environmental predictors used to model the spatial pattern of HDs of widespread and constraint species.

Code	Variable description
bio01	Annual mean temperature
bio02	Mean diurnal range (mean of monthly (max temp - min temp))
bio03	Isothermality (bio2/bio7) (x100)
bio04	Temperature seasonality (SDx100)
bio05	Max temperature of warmest month
bio06	Min temperature of coldest month
bio07	Temperature annual range (bio5-bio6)
bio08	Mean temperature of the Wettest Quarter
bio09	Mean temperature of the Driest Quarter
bio10	Mean temperature of warmest quarter
bio11	Mean temperature of coldest quarter
bio12	Annual precipitation
bio13	Precipitation of wettest month
bio14	Precipitation of driest month
bio15	Precipitation seasonality (coefficient of variation)
bio16	Precipitation of wettest quarter
bio17	Precipitation of driest quarter
bio18	Precipitation of Warmest Quarter
bio19	Precipitation of Coldest Quarter
grow	Length of vegetation growing period
sunrad	Sun radiation
snow	Snow cover
alt	Mean altitude
lc10	Cropland, rainfed
lc11	Herbaceous cover

lc12	Tree or shrub cover
lc20	Cropland, irrigated or post-flooding
lc30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
lc40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)
lc60	Tree cover, broad-leaved, deciduous, closed to open (>15%)
lc61	Tree cover, broad-leaved, deciduous, closed (>40%)
lc70	Tree cover, needle leaved, evergreen, closed to open (>15%)
lc71	Tree cover, needle leaved, evergreen, closed (>40%)
lc80	Tree cover, needle leaved, deciduous, closed to open (>15%)
lc90	Tree cover, mixed leaf type (broadleaved and needle leaved)
lc100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)
lc110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
lc120	Shrubland
lc122	Deciduous shrubland
lc130	Grassland
lc140	Lichens and mosses
lc150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
lc152	Sparse shrub (<15%)
lc153	Sparse herbaceous cover (<15%)
lc160	Tree cover, flooded, fresh or brackish water
lc180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
lc190	Urban areas
lc200	Bare areas
lc201	Consolidated bare areas
lc202	Unconsolidated bare areas
lc210	Water bodies
lc220	Permanent snow and ice
hfp	Human Footprint Index
Eu	Percentage of <i>Eucalyptus</i> sp.
area	Area of sampling unit
xscale	Scaled X coordinate of the centroid of the unit area
yscale	Scaled Y coordinate of the centroid of the unit area

S3-4 Bioclimatic regions

Four bioregions were delimited as described in ENETWILD-consortium et al., (2019), which followed the methodology described in Pittiglio et al. (2018), to account for potential regional variability in the species-environment relationship ecological and management heterogeneity across Europe (Acevedo, Quirós-Fernández, et al., 2014).

The same environmental variables (climatic and land cover) were extracted to the 10 x 10 km EAA reference grid (European Environment Agency, 2024), following the same procedures applied to the datasets.

A principal component analysis (PCA) of these variables was done to reduce the dimensionality of the environmental variables into a set of linearly uncorrelated and independent components. The elbow method was first used to define the number of bioclimatic regions, using the `fviz_nbclust` function of the `factoextra` 1.0.7 package (Kassambara & Mundt, 2020). Subsequently, we performed a k-means cluster analysis, using the `kmeans` function of the `stats` 4.5.2 package (R Core Team, 2025), with the first four principal components (eigenvalues > 1), using the number of clusters suggested by the elbow method to classify the study area in homogeneous bioclimatic regions (**Figure S3-4.1**).

The homogeneous bioregions were used to divide the wild boar dataset, with individual models fitted in each bioregion. This provided a flexible framework, allowing different intercepts and slopes to accommodate species variability across Europe.

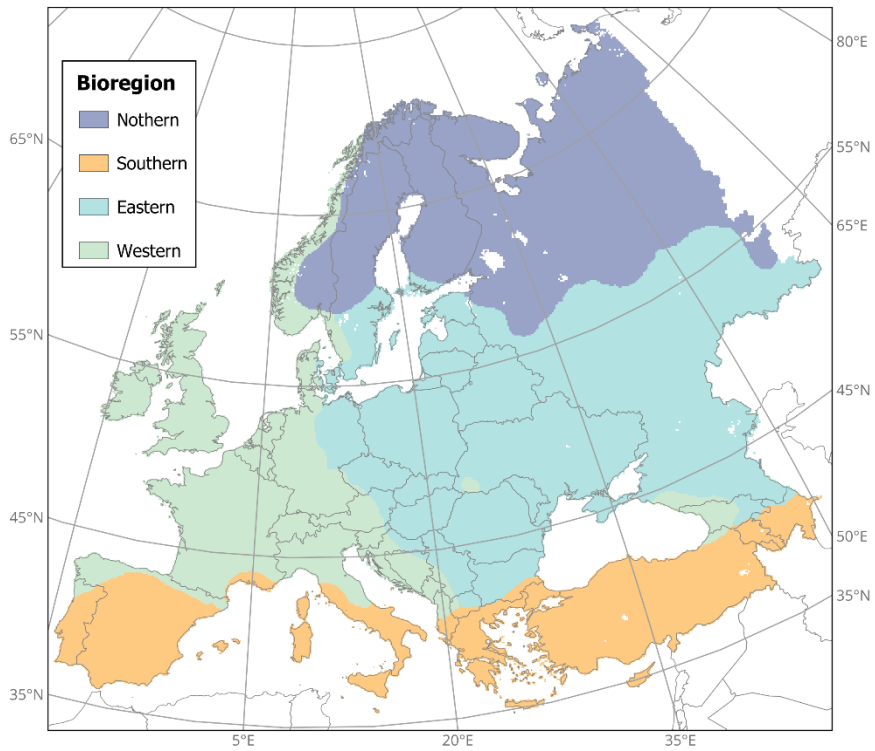


Figure S3-4.1. Map of the study area showing the four bioclimatic bioregions resulting from k-means cluster analysis and used to divide the wild boar dataset. Colors indicate each bioregion.

4. Evaluation of Modeling Approaches to Account for Hunting Data Idiosyncrasies Across Large Spatial Scales



Illanas. S., Fernández-López, J., Blanco-Aguilar, J.A. Vicente, J., & Acevedo, P. (under review). Evaluation of modeling approaches to account for hunting data idiosyncrasies across large spatial scales.

Abstract

1. Understanding the distribution and abundance of common species is essential for conservation and management. However, obtaining large-scale abundance information poses significant challenges. For game species, hunting yields (HYs) provide a valuable, albeit imperfect, source of information for this purpose. Their application is often complicated by idiosyncrasies in the data.
2. We evaluated different modeling approaches to obtain reliable abundance indices from HYs data for four species in mainland Spain. Specifically, we explored the effect of (i) data management scenario by handling uncertain data and comparing the assumptions of treating missing values as zeros (NA=0) versus omitting missing and zero values; (ii) area approach by considering the area of the territorial units by one of the three following approaches: excluding it, using it as an offset, or modeling it as a covariate; and (iii) regional approach by accounting for regional variation in species-environment relationships, namely ignoring any possible regional behavior, using bioregions as a fixed factor, developing bioregion-independent models or using a random spatially explicit model. Additionally, we assessed how the increment of spatial resolution of the prediction (*i.e.*, downscaling) influenced models' predictions both the total predicted abundance and the spatial abundance pattern.
3. The total predicted relative abundance varied across modeling approaches. These differences were influenced by the data management scenario, the area and the regional approaches. Imputing zero values to NAs produced lower biased predictions than when excluding both, except for models that used a spatial random effect. Not accounting for area size led to increased bias and wider credible intervals. Among all approaches, spatially explicit models presented the highest uncertainties.

4. Predictions made with all approaches converge to analogous spatial patterns of relative abundance except when the area size was not considered. The incorporation of the spatial random effect further highlights the difference between relative abundance patterns.
5. The modeling approach should be tailored on the objectives of the study (*i.e.*, predict numbers, species-environment relationships, spatial patterns), the species' characteristics (*i.e.*, potential variation in species-environment relationships) and the quality and intrinsic characteristics of the available data (*i.e.*, uncertain data and heterogeneity of size of the territorial units).

Key words: abundance modeling, area size, data inference, game species, hunting yields, missing data, modeling approaches, non-stationarity

Resumen

1. Entender la distribución y abundancia de especies comunes es esencial para su conservación y gestión. Sin embargo, obtener información de abundancia a gran escala plantea grandes retos. Para las especies cinegéticas, los estadísticos de caza son una fuente de información valiosa, aunque imperfecta para este propósito, ya que a menudo su aplicación es complicada por las peculiaridades de estos datos.
2. Evaluamos distintos enfoques de modelización para obtener índices de abundancia fiables a partir de estadísticos cinegéticos de cuatro especies en la España peninsular. Específicamente, exploramos el efecto de (i) el escenario de gestión de datos mediante el tratamiento de datos faltantes y comparando hipótesis sobre el tratamiento de estos valores como ceros (NA = 0) frente a omitir los datos faltantes y los valores cero; (ii) el enfoque del área, considerando el área de las unidades territoriales mediante uno de los enfoques siguientes: excluyéndola, utilizándola como *offset*, o modelizándola como covariable; y (iii) el enfoque regional, teniendo en cuenta la variación regional de las relaciones especie-ambiente, ignorando cualquier posible comportamiento regional, utilizando bioregion como factor fijo, desarrollando modelos independientes por bioregion o incorporando la dependencia espacial como un parámetro del modelo. Además, evaluamos como el incremento de la resolución espacial en las predicciones (*i.e.*, *downscaling*) influyó en las predicciones de los modelos, tanto en la abundancia predicha total como en el patrón de abundancia espacial.
3. La abundancia relativa total predicha varió entre las aproximaciones de modelización. Estas diferencias se vieron influidas por el escenario de gestión, el área y los enfoques regionales. La imputación de valores cero a los NA produjo predicciones con menor sesgo que cuando se excluyeron

ambos, excepto para los modelos que incluían la dependencia espacial. No considerar el tamaño del área de la unidad territorial dio lugar a un mayor sesgo y a intervalos de credibilidad más amplios. Entre todas las aproximaciones, los modelos con dependencia espacial presentaron las mayores incertidumbres.

4. Las predicciones hechas bajo todos los enfoques convergen en patrones espaciales de abundancia relativa análogos excepto cuando no se tiene en cuenta el tamaño del área. La incorporación de la dependencia espacial resalta aún más la diferencia entre los patrones de abundancia relativa.
5. La aproximación de modelización debe adaptarse a los objetivos del estudio (*i.e.*, predecir cantidades, relaciones especie-ambiente, patrones espaciales), las características de las especies (*i.e.*, posible variación en las relaciones especie-ambiente), así como en la calidad y características intrínsecas de los datos disponibles (*i.e.*, datos inciertos y heterogeneidad del tamaño del área de las unidades territoriales).

4.1. Introduction

The study of species distribution and the factors that drive changes in species ranges constitute an area of research that biologists and ecologists have pursued for many decades. The main goal is to understand the relationships between species and their environment to identify factors that may facilitate or hinder their long-term viability (Crisci, 2001). These relationships can be spatially inferred, revealing areas where species may expand or contract their range, both in terms of area occupied (distribution) and number of individuals (abundance). This field of study is crucial for assessing management and conservation strategies (Whittaker et al., 2005). However, the development of global models implies long-term monitoring at large-spatial scales, which require well-established programs, adequate funding and human resources. Consequently, some large regions may be underrepresented due to technical or financial constraints, potentially limiting our capacity both to generate a comprehensive picture and to detect significant changes affecting numerous species (Edwards et al., 2025; Lindenmayer et al., 2022; Oliver et al., 2021).

The implementation of efficient monitoring and data collection frames at national level (harmonizable internationally; Liquete et al., 2024), as well as the necessary financial support are especially relevant for monitoring common and widely distributed species (Wilson et al., 2007). These species experienced noticeable differences in their trends compared to rare ones, underscoring the importance of monitoring the entire community (Leuenberger et al., 2025). The

lack of financial resources for common species complicates their monitoring, which hinders the accurate estimation of population sizes (Correia et al., 2024; Moersberger et al., 2024). In the case of mammal species, some of these common and widespread species are game species, whose populations must be monitored. In many countries, hunting yields (*i.e.*, the number of animals harvested within a defined area and time frame; HYs) must be reported by hunter managers to public administrations or hunter associations (Ruiz-Rodríguez et al., 2023). Therefore, HYs can be used as wildlife relative abundance indices (*e.g.* Imperio et al., 2010; Leclerc et al., 2016). One of the main criticisms of using HYs for monitoring is the potential heterogeneity of hunting effort (*e.g.*, number of hunters, number of days, area size) across different places and times (Carvalho et al., 2024; Imperio et al., 2010; Ruiz-Rodríguez et al., 2023). Furthermore, it has been pointed out that HYs may not always provide reliable data, as they may not reflect the exact number of individuals harvested. The underlying assumptions are that HYs can be biased (either inflated or under-reported), and that, for some species, there could be a mismatch between the end of the hunting season and the reporting deadline, which may lead to the actual amount hunted to be overlooked (Moreno-Zarate et al., 2021). Nonetheless, data unreliability is not exclusive to HY datasets but can affect any type of ecological data. Several issues, such as count errors, species misidentification, imperfect detection, and zero inflation, have been reported, and the challenge lies in developing approaches that render the information contained in these datasets useful for inference

(Davis et al., 2022; Dénes et al., 2015; Ruiz-Gutierrez et al., 2016). HYS data have been shown to emerge from underlying ecological processes shaped by species-environment relationships, and latent models may reflect these influences (Fernández-López et al., 2025). Therefore, once HYS have been modeled the species-environment relationships can be properly identified and their predictions may be a useful proxy of abundance to inform wildlife conservation and management. Consequently, HYS datasets provide an opportunity to utilize the information reported every hunting season for estimating population trends (Carvalho et al., 2024; Marin-Sáez et al., 2025) and to develop models and predictions that provide a comprehensive picture of relative wildlife abundance patterns at different geographic scales (*e.g.*, national or continental; Lindström & Bergqvist, 2022; Pittiglio et al., 2018). The modeling process involves decisions that directly influence the inference drawn from the results and predictions. Defining the study objectives (explanatory versus predictive) prior to modeling is crucial to ensure the selection of an appropriate method, as outlined by previous authors (Kelleher et al., 2025; Segurado & Araújo, 2004).

Three main data issues have been identified when modeling HYS at large spatial scales. First, missing data (NAs) and zero values are not easily distinguishable in the reported datasets. Thus, HYS analysis usually consider only locations where at least one specimen has been harvested and reported (Illanas, Fernández-López, Vicente, et al., 2025; Klich et al., 2024; Marin-Sáez et al., 2025). The underlying reason behind the removal of this information is the uncertainty

of which information they represent. In the case of missing data, a knowledge gap exists. It can be attributed to either a loss of information during the digitization process or a lack of reporting due to the absence of data, indicating that no individuals were harvested during a given year. This could mean that the species is not present at the location, or that it is present, but harvesting is temporarily or permanently prohibited (Carboneras et al., 2024). The same considerations apply to zero values. These may either represent the absence of hunted individuals, as expected if monitoring programs function correctly and record all data, including zeros, or they may reflect the absence of reported information. More even, the use of zero and missing data can be different across the data reporters, mainly when working at large spatial scales. It appears that it is not always possible to dismiss either of these possibilities. In both cases, the removal of that type of data could be justified under the belief that considering them could lead to biases in the database and, consequently, in the analysis if there were unreported numbers harvested. However, the impact of considering or removing this kind of data in the analysis deserve further studies (Blasco-Moreno et al., 2019).

Second, observation units may greatly vary in size, especially at large extents. This variability largely arises from independent and non-harmonized data collection systems employed by different countries and regions, resulting in substantial spatial heterogeneity (Aubry et al., 2020). For instance, HYPs have been collected in Europe at various spatial scales, from hunting estates up to NUTS2

level, further contributing to this heterogeneity (ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023). However, the proportion of the territory effectively hunted is more similar at the level of hunting estates than at larger administrative levels, where there are many spots where hunting is not allowed (*e.g.*, urban areas, roads; Lindström & Bergqvist, 2022). Therefore, the effect of the relationship that area size plays on the HJs may not be proportional between territorial units. The differences in data resolution level may also mask the pattern-process relationship (Allen et al., 2025; C. M. Thompson & McGarigal, 2002), which could be critical if the aim of the work is inference. The size of the observation units also seems to be a challenge when predicting at lower spatial resolution than the observation unit (downscaling), as it may be a misalignment between the quantities predicted due to a change of support (Fernández-López et al., 2025; Pacifici et al., 2019), having been observed a prone pattern of overprediction especially at high abundances (ENETWILD-consortium, Acevedo, Croft, Smith, Blanco-Aguilar, Fernández-López, Scandura, Apollonio, Ferroglio, Keuling, Sange, Zanet, Brivio, Podgórski, et al., 2020).

Third, widespread species often face challenges from non-stationarity in the species-environment relationship (Allen et al., 2025). Non-stationarity refers to changes in the species-environment relationship across space, which may arise depending on the intrinsic characteristics of the species, their management, or the extent of its distribution range. This is a concern in any field of data analysis,

particularly when conducting analyses on a large scale (Doser et al., 2025; Finley, 2011; Liang et al., 2025). Applying global species-environment relationships may lead to biases in estimated species presence or abundance in a region, potentially reflecting a failure in capturing key ecological drivers of underlying ecological processes (Osborne et al., 2007). Modeling approaches that account for regional effects may produce more reliable estimates (Acevedo, Quirós-Fernández, et al., 2014). Nonetheless, approaches based on predefined regions may fail to represent smooth ecological gradients across space (Cushman et al., 2010). Pittiglio et al. (2018) proposed combining region-specific models with area-to-point-kriging of residuals to produce continuous high-resolution predictions while minimizing edge effects. However, improving the modelling process itself rather than smoothing projections techniques is still required. Models with spatially explicit structure may be better suited for capturing gradual changes across space and have shown promising predictive performance on estimates (ENETWILD-consortium, Fernández-López, et al., 2020; Norberg et al., 2019). Several methodologies have been developed for capturing spatial variability, such regression splines over spaces (*e.g.*, GAMs), geographically weighted regression (GWR), and spatial hierarchical models (*e.g.*, Gaussian Processes, INLA-based approaches). Including spatial latent effects may improve predictive performance, although care may be taken for avoiding overfitting to the observed data and spatial confounding (Finley, 2011; Hodges & Reich, 2010; Hooten et al., 2003; Paciorek, 2010).

Several approaches have been followed to address Hys data idiosyncrasies from regional to global scales (Acevedo, Quirós-Fernández, et al., 2014; ENETWILD-consortium, Acevedo, et al., 2019; Lindström et al., 2024; Ruiz-Rodríguez et al., 2022). However, there remains a need to evaluate the singular and synergic effects of specific data characteristics, and the more robust approaches to account for them. To overcome these problems the objective of this study was to evaluate different approaches for modeling high-resolution Hys at the national level, specifically addressing the influence of uncertain data, the area size and the regional effects on (1) quantitative predictions of abundance and (2) spatial abundance patterns of four common game species in Spain: wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and red fox (*Vulpes vulpes*).

4.2. Materials and methods

4.2.1. Data

Hys for wild boar, red deer, roe deer and red fox have been collected from 2014/2015 to 2021/2022 hunting seasons at municipality level in mainland Spain ($n = 8055$). We retained the maximum number of individuals hunted to be used as response variable for modeling purposes (ENETWILD-consortium, Acevedo, et al., 2019). Municipalities in Spain are characterized by a mean surface of 65.91 km² and standard deviation of 95.08 km². Hys were either zero and/or missing values (NAs) for some municipalities. We considered two scenarios to explore the

effect of uncertain data. In the first scenario, we considered both the zero and missing values as 0 hunted individuals (dataset WITH). In the second scenario zero were removed from the analysis (dataset WITHOUT). For all species, values above the 99.9% percentile of individuals hunted per square kilometer were excluded from the analysis because they were considered as data entry errors.

We considered mean precipitation (prec; WorldClim 2, Fick & Hijmans, 2017), percentage of forest (forest; SA/CCI-LC project version v2.0.7; ESA, 2017), human footprint (hfp; Venter et al., 2018), and the total area size of hunting estates per municipality (area) as covariates. All covariates, but area, were standardized using their means and standard deviations. Multicollinearity was evaluated using the Variance Inflation Factor (VIF), all variables were retained as they showed values below 3 (Zuur et al., 2010). Furthermore, we classified mainland Spain in four climatic bioregions (see [S4-1](#)).

The packages and software used for data management were tidyverse 2.0.0 (Wickham et al., 2019), sf 1.0-19 (Pebesma, 2018), and R Statistical Software (v4.4.3; R Core Team, 2025).

4.2.2. Modeling framework

For modeling HYs we used a Negative Binomial distribution, $N_i \sim \text{NB}(\mu_i, \kappa)$, where N_i is the expected relative number of animals in a municipality i (with $i = 1, 2, \dots$; i varies from 2410 to 7406 regarding the uncertain data scenarios and

species), μ_i is the expected hunting yield value which vary in space according to covariates, and k is the overdispersion parameter.

We defined the expected HY in log scale to be a linear function of the covariates as $\log(\mu_i) = \beta_0 + \beta_1 * \text{prec}_i + \beta_2 * \text{forest}_i + \beta_3 * \text{hfp}_i$, where β_0 is the intercept parameter, $\beta_1, \beta_2, \beta_3$ are the linear effect of covariates. The former basic model, which will be referred hereinafter 'EA' in the area size approach, and 'ER' in the regional approach, was modified with three approaches for exploring the regional effect and with two for addressing the area size problem (**Figure 4.1**).

Regarding the area size, we implemented three approaches. We fitted a basic model which did not consider the area size to have any effect on the expected HY, that is, the expected value was assumed to be independent of the size of the municipality where the animals were hunted (excluded area, EA); an offset model that considered that area size modified the number of animals hunted in the same proportion across all the observation units, therefore its beta value is fixed to 1 (offset area, OA); and a covariate model that considered the $\log(\text{area})$ as a covariate with beta free parameter (covariate area, CA); the area was log-transformed in order to maintain the relationship that the offset model had with the response variable.

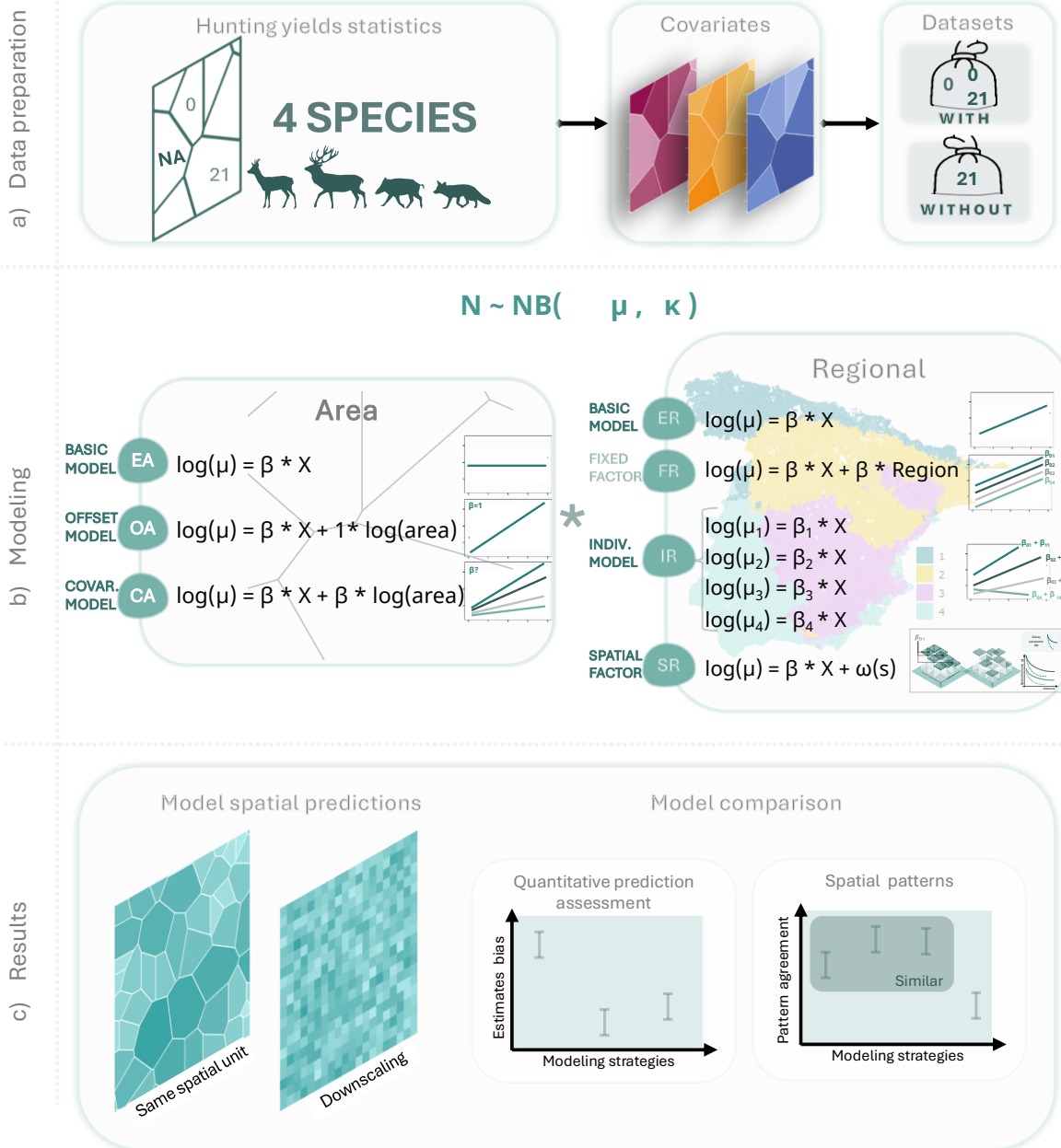


Figure 4.1. Framework: datasets used (a), strategies proposed for dealing with area size effects (b left) and regional effects (b right); spatial prediction resolution and model comparison among analytical approaches (c).

Regarding the regional effect, we fitted a basic model which does not consider regional differences, where expected HY will only vary according to covariates (excluded regionalization, ER); a regional fixed effects model, including bioregion as a fixed factor (four levels), allowing the intercept to vary between regions (fixed regionalization, FR); an individual model per bioregion, allowing the intercept and covariates effects (*i.e.*, beta coefficients) to differ between regions, thereby capturing a discrete effect form of non-stationarity across the four bioregions (independent regionalization, IR); we subset the data by bioregion (**Figure S4-1**, Figure S3-4.1) for making each individual model. Finally, we fitted a spatially explicit model by including a spatial random effect $\omega(s_i)$ modeled using a Nearest Neighbor Gaussian Process (NNGP; Datta et al., 2016), allowing the expected value to vary smoothly with respect to spatial location and covariates (spatially regionalization, SR). This explicitly incorporates spatial autocorrelation by assuming that the response variable of closer locations may have more similar values than those farther apart, due to smoothly varying spatial effects (Cressie, 1993). The spatial covariance matrix was defined by an exponential function of Euclidean distance and spatial parameters (θ), compromising the variance parameter, σ^2 , and the spatial decay parameter, ϕ . Unlike models based on fixed effects or discrete regions defined by ecological units (approaches 2 and 3), the NNGP allowed for continuous spatial estimates, capturing smooth gradients across space without relying on predefined boundaries.

All models were fitted in a Bayesian framework using Markov Chain Monte Carlo (MCMC) algorithms with the spAbundance 0.2.2 R package (Doser, Finley, et al., 2024). We used normal prior for beta coefficients (mean=0 and var=1), uniform prior for kappa (a=0, b=100), uniform prior for ϕ (a=0.0470 and b=0.2) and inverse gamma for σ^2 ($\alpha = 2$ and $\beta = 1$). We run three chains (length=100,000, burning=50,000, and thinning parameter=10). We assessed convergence of the models by visual inspection of traceplots, the Gelman-Rubin diagnosis Rhat ($0.9 < \text{Rhat} < 1.1$; Gelman & Rubin, 1992) and the Effective Sample Size (ESS; Gelman et al., 2025; Vehtari et al., 2021). Further details on the statistical models used are provided in supplementary information [S4-2](#).

For each species and analytical approach, we projected model results at two different resolutions, the same observation unit (municipalities) and the 2 km x 2 km grid cells (downscaling). We extracted the 2.5%, 50%, and 97.5% percentiles from all modeling approaches at both prediction resolutions to enable direct comparison of central estimates and credible intervals across approaches and resolutions.

4.2.3. Model comparison among analytical approaches

4.2.3.1. Quantitative prediction assessment

For each species and analytical approach (42 models per species), we estimated the overall predicted relative abundance by summing the 50% percentile predictions obtained by municipality and the range of the credible

interval. Then, we calculated the absolute difference between the total number of individuals hunted and the overall predicted relative abundance (*i.e.*, prediction bias). Prediction bias (log-transformed) was used as the response variable and related to the data scenario used (WITH, WITHOUT), area size effect (EA, OA, CV) and differentiating how the regional effect (ER, FR, IR, SR) were treated in the model. In addition, we explored the interactions between area size approach and the resolution of the predictions (municipality, grid cells), regional approach and the data scenario. Additionally, we incorporated the interaction between the area size models and the percentage of area that the calibration dataset represents regarding the total area predicted (national scale). In all models, we considered species as a random intercept. We followed the same modeling structure to determine if there was a relationship between the factors associated to the modeling approaches and the range of the credible interval predicted (log-transformed difference between 2.5% and 97.5% predicted values).

4.2.3.2. Comparing spatial patterns

We sought to assess similarities in terms of predicted spatial patterns between modeling approaches. To do so, for each species we tested Spearman's correlation (ρ_s) between each model prediction and the average of the predicted models. The model's average was calculated by i) calculating the mean of all models, and ii) calculating the mean of all models leaving one out. The model left

out was the one with which the correlation would be calculated. We then calculated the correlation for all predicted municipalities, regardless of whether their locations were used to inform the model (1), and for municipalities for which the data were zero or no reported (2). Then we used the ρ_s values as the response variable in a GLMM that included species as a random effect factor. The fixed factors were the same previously used, the data scenario, area size and regional effects, and interactions among them.

All GLMMs were fitted using lmer function from lmerTest 3.1-3 R package, which assumes a normal distribution for the response variable (Kuznetsova et al., 2017). Figures were made using plot model function from sjPlot 2.8.17 R package (Lüdtke, 2025).

4.3. Results

The relationship between environmental variables (precipitation, forest cover, human footprint) and HYs is summarized in **Figure 4.2** for each species studied, across both dataset scenarios (WITH and WITHOUT). The analysis considered several modeling approaches: excluding the regional effect, including bioregion as a fixed variable, modeling bioregions independently, incorporating a spatially explicit structure, and accounting for area, as whether excluded, as an offset, or as a covariate. All models recovered the expected environment-species relationship (**Figure 4.2**). Forest associated species such as red deer, roe deer and wild boar showed a positive relationship with forest cover, whereas red fox

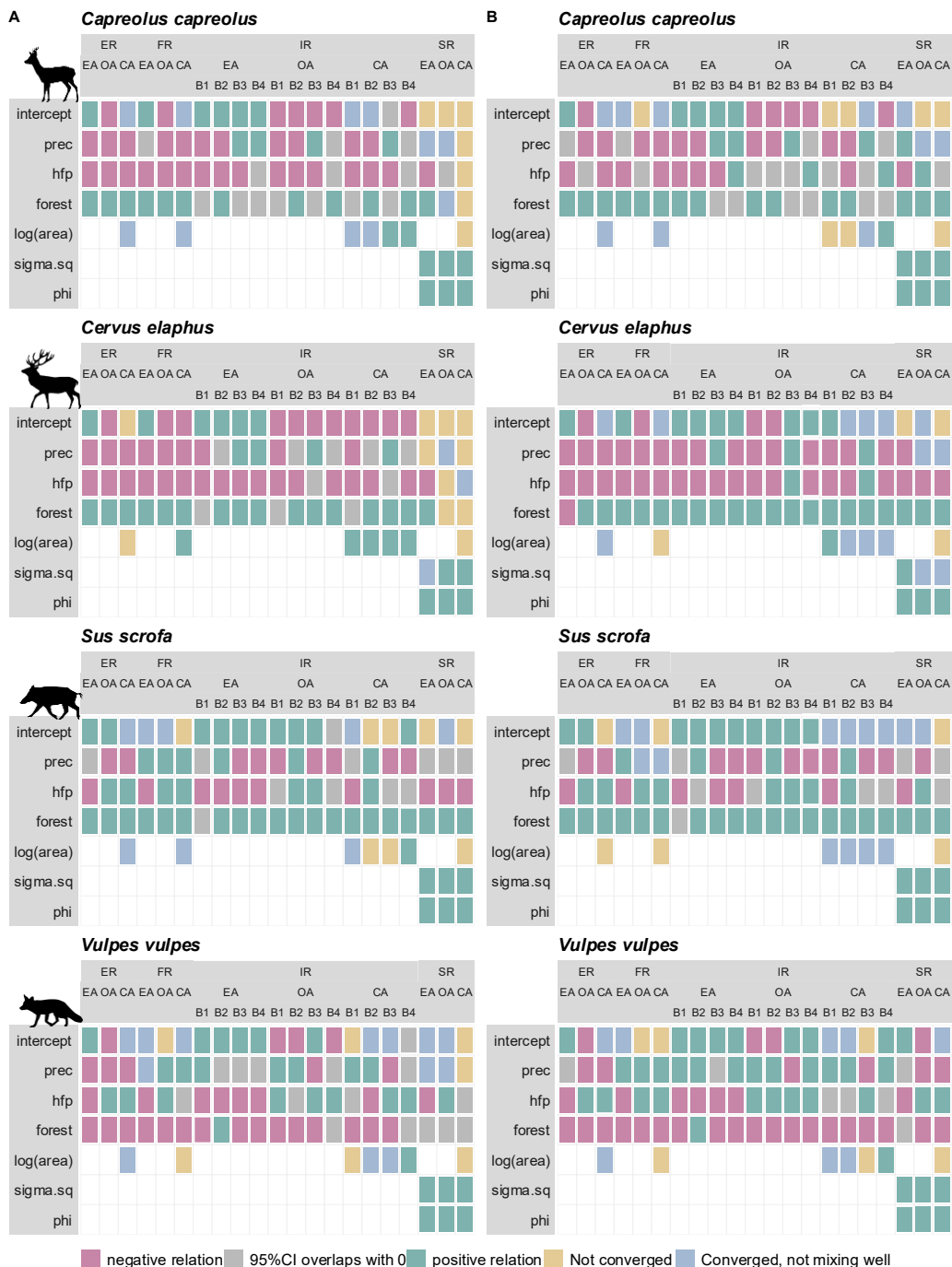


Figure 4.2. Model estimates per species studied (A) with NA-0 dataset (*Capreolus capreolus* $n=7404$, *Cervus elaphus*, $n=7406$, *Sus scrofa* $n=7402$, *Vulpes vulpes* $n=7402$), and (B) without NA-0 dataset (*Capreolus capreolus* $n=4395$; *Cervus elaphus*, $n=2410$, *Sus scrofa* $n=6294$, *Vulpes vulpes* $n=6103$). Model estimates refer to the effects of the explanatory variables (prec = precipitation, hfp = human footprint, forest = forest cover) across different modeling approaches: (ER) excluding regional effect, (FR) with bioregion as a fixed variable, (IR) with bioregions modeled independently (B1–B4), (SR) with a spatially explicit.

exhibited a negative one. Regarding the human footprint, species with more restricted distribution (*i.e.*, red deer and roe deer) showed negative relationships, while more widespread species (*i.e.*, red fox and wild boar) displayed a mixed pattern of positive and negative relationships. Similarly for precipitation, all species exhibited variability in their relationship with the IR approach. All species showed non-convergence or to have MCMC mixing issues on the intercept as well as on that covariate when employing the CA approach. Regarding the dataset scenario, all species except roe deer showed consistent environmental responses between dataset scenarios, being favored when NA and zero values are removed, as this also reduced the non-convergence issues to MCMC mixing issues (**Figure 4.2**). In contrast, roe deer showed increased overlap of its credible interval with 0 under the WITHOUT scenario. All species indicated that the model estimates tended to experience non-converge or MCMC mixing issues when using the spatially explicit approach (SR; **Figure 4.2**; see **Figures S4-4**), although the spatially explicit parameters (ϕ and σ^2) generally converged.

There is a discrepancy in the predicted relative abundance between approaches (**Table 4.1**; see **S4-5**). The biases are conditioned by the data scenario. The interaction between the data scenario and the regional approach results in lower biases when considering the scenario WITH, except when considering the spatial explicit model (**Figure 4.3A**). The biases seem to be greater when predictions are downscaled to the grid cell (**Figure 4.3B**).

Nonetheless, it should be noted that accounting for area as an offset yielded the most balanced results when predicting at any of the considered resolutions (municipality or grid cell). As the proportion of the dataset used and the area of the predictions increases, the spatial information used to train the model and that used for predictions becomes more similar (values approaching to 1), leading to a reduction in biases (**Figure 4.3C**). This decreasing effect is more pronounced when $\log(\text{area})$ is included as a covariate, whereas omission of area size results in a slight decrease in biases. Spatially explicit models have the lowest precision (**Figure 4.3D**).

Table 4.1. Evaluation of the relative importance of covariates and interaction terms through model comparison, using *drop1*, for the quantitative assessment of predictive performance (above) and spatial patterns (below).

Quantitative prediction assessment	Model bias	Model credible interval
model.br		$F(3,176)=211.28^{***}$
dataset		$F(1,178)=3.86 \cdot$
model.area*prediction	$F(2,173)=151.66^{***}$	$F(2,176)=67.27^{***}$
model.br*dataset	$F(2,173)=12.72^{***}$	
model.area*per_area	$F(2,173)=5.90^{***}$	$F(2,176)=7.12^{***}$
Spatial patterns	Model prediction to all locations	Model prediction to zero locations and missing (NAs) areas
correlation.type	$F(1,173) = 2.97 \cdot$	$F(1,173)=5.23^*$
model.br*model.area	$F(6, 173) = 2.60^*$	$F(6, 173)=3.62^{**}$
model.area*dataset	$F(2, 173) = 8.72^{***}$	$F(2, 173)=7.17^{***}$

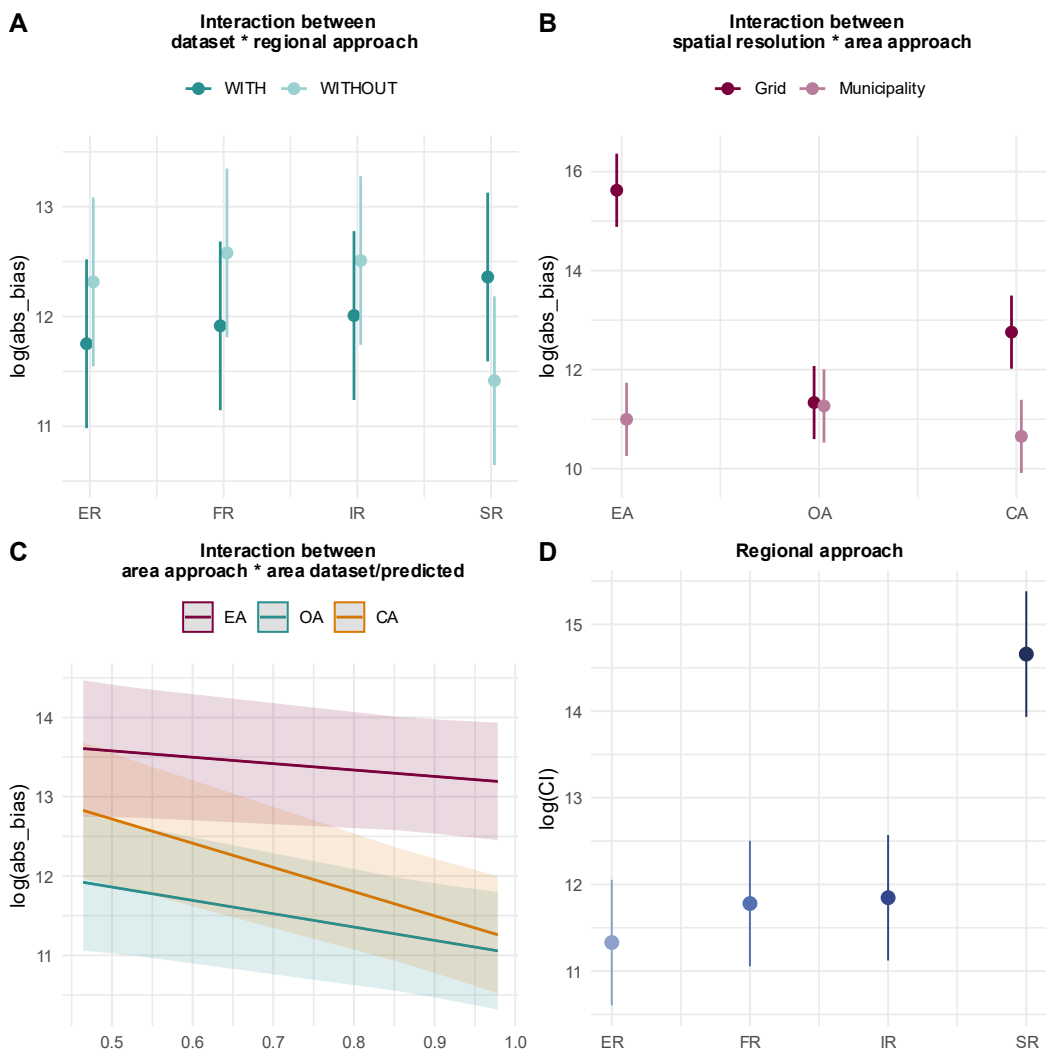


Figure 4.3. Estimated effects and interactions plots from the bias (observed-predicted50p) fitted GLMM between the dataset scenario (WITH/WIHOOUT) used for modeling and the regional models (A), the spatial prediction resolution and the area size models (B) the area size models and the proportion of area used for modeling respect to the area predicted the type of dataset used for modeling (C), and from the credible interval fitted GLMM with the regional models (D).

Analogous spatial patterns emerge for all approaches, except when area size is not considered (**Figure 4.4A** and **Figure 4.4B**). Differences between spatial patterns become more pronounced when accounting for the interaction between regional approaches and area size, with the most distinct pattern observed when area size is not included in any way in the models (**Figure 4.4B**). Notably, the SR approach generated the most similar relative abundance patterns regardless of whether area was included or excluded (see [S4-3](#)). Nonetheless, the red fox exhibited an unreliable spatial pattern in western Spain when using the SR approach under the WITH dataset scenario, a pattern that appears to be corrected under the WITHOUT dataset scenario (see [S4-3](#)). Moreover, the FR and

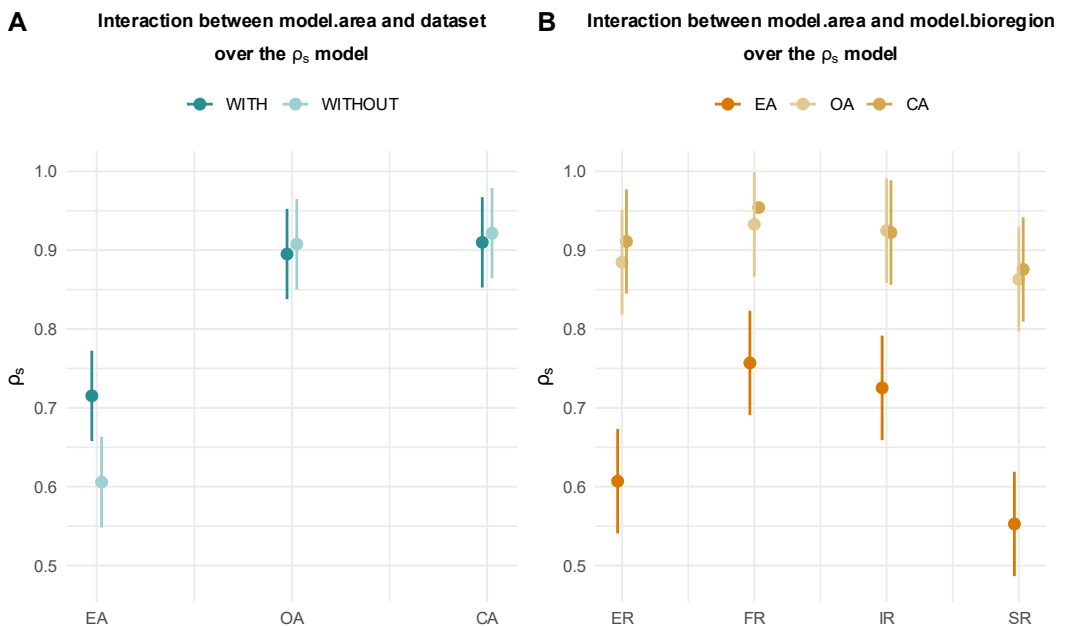


Figure 4.4. Estimated effects and interactions plots from the full rho Spearman's correlation coefficient (ρ_s) between area size models and the dataset scenario (WITH/WITHOUT) used for modeling (A), and the interaction effect of area size models and the regional models (B).

IR approaches produced abrupt transitions between bioregions for all species, which were smoothed when using the SR approach. These abrupt changes appeared to be more pronounced when downscaling predictions to the 2×2 km grid than when using the same spatial resolution (municipality) for prediction.

4.4. Discussion

Our findings support that HYs statistics provide valuable insights for modeling species relative abundance patterns of game species at large scales (Fernández-López et al., 2025; Iijima, 2020; Ruiz-Rodríguez et al., 2022), especially when other data sources (*e.g.*, camera traps, aerial vehicles, acoustic sensors) are difficult to implement at these scales (ENETWILD-consortium et al., 2024; Forsyth et al., 2022; Hofmeester et al., 2021; Kissling et al., 2024; Palencia et al., 2022; Pereira et al., 2023; M. E. Thompson et al., 2010). Nonetheless, modeling HYs requires a series of methodological decisions that directly influence the interpretation of the models and their predictions. In particular, choices must be made regarding the inclusion of missing data and zero values, the handling of area size, and the consideration of regional effects. These decisions affect results, meaning that inferences drawn from different approaches may not be equivalent. For instance, depending on the analytical approach, HYs models could be indicative of species relative abundance, if they are able to capture species-environment relationships, or may primarily refer to the species hunting yields (*i.e.*, the data source). Moreover, the implications of considering regional and area size effects depend on the species, spatial scale and the quality of data

(**Figure 4.3** and **Figure 4.4**). Therefore, selecting an appropriate modeling strategy for HYS must consider research objectives, species characteristics, spatial and regional context, and the idiosyncrasies of the available data.

No reported information, zero values and extreme values in the HYS are a recognized issues when the hunting effort is not collected (Lindström & Bergqvist, 2022; Ruiz-Rodríguez et al., 2023). It is recommended to address data inconsistencies by contacting the original data provider (Lindström & Bergqvist, 2022). However, the workload that wildlife managers who collect the HYS may face will be unsustainable in the actual circumstances of many countries. Implementing digital data collection systems may also help to minimize the risk of misinterpretation, although it would be necessary to properly define and agree with the original data providers the meaning of NA and zero values. Consequently, it may be necessary to consider the variety of potential outcomes that may result from imputing zero values as missing data in the HYS, as well as disregarding these data. According to our results, imputing missing data as zero values in the HYS interacts with the regional effect. In all regional approaches, this treatment leads to lower bias relative to the reported HYS. In contrast, in the spatially explicit model, the bias is higher when zeros are imputed and is reduced only when zeros are removed. This may be indicating that imputing zeros affects the spatially explicit model more strongly than the regional models, likely because the false absences disrupt the spatial structure and the model's interpolation across neighboring nodes. Conversely, removing these uncertain

values allows the spatially explicit model to borrow information from neighboring nodes, resulting in predictions closer to HYs, which is also reflected in more precise credible intervals. It is important to note that this only indicates better agreement between the observed and predicted values. Furthermore, the analytical approach used may be more important than the proportion of missing data for obtaining accurate and precise estimates, which has also been observed in data imputation studies (Onkelinx et al., 2017). Accuracy and precision may also depend on the amount of reliable information available as well as the nature of the missing data (*i.e.*, missing completely at random vs. missing not at random; Bowler et al., 2025; Panzera et al., 2016). The nature of missing data may differ between species. For widespread species, such as wild boar or red fox, imputing zero values to NAs may occur at random locations, as almost 80% of the Spanish territory (in our case study) reports HYs for these species. By contrast, for species with a patchy distribution, such as roe deer and red deer in Spain, HYs are reported across approximately the 55% and 30% of the country respectively, meaning that missing data may be informative. Consequently, imputing zero values for missing data may have different effects. It may potentially lead to the establishment of inaccurate relationships between species and their environment for widespread species, while providing more accurate information for species with restricted ranges, assuming that zero values reflect the true absence of these species. Therefore, we recommend avoiding imputing NA as zero values for widespread species, while doing so for species with constrained

distributions (**Table 4.2**). The importance of data management extends beyond modeling purposes, making it crucial in any field of study. It is essential to recognize that data management is the foundation of the decision-making process. The decisions made at this stage directly influence subsequent steps in the analytical approach (**Figure 4.3**). Therefore, the study of the dataset on a case-by-case basis before making decisions regarding the modeling approach is a critical step that must be done and also considered when interpreting the results.

The coarse resolution of HYs in some countries limits the use of this information to guide wildlife management at local scales (Bauder et al., 2021; Gilbert, Pease, et al., 2021). Conversely, when the collected HYs are at fine resolution, it allows for precise analysis (Lindström & Bergqvist, 2022). Our results indicated that area size plays a crucial role in modeling species abundance and is particularly relevant for predictions at finer spatial resolutions (**Figure 4.3** and **Figure 4.4**). Specifically, downscaling predictions led to higher bias and wider credible intervals, highlighting the importance of accounting for area size to address potential changes of support (Fernández-López et al., 2025). The predictions generated by the CA modeling approach did not provide the most accurate predictions, despite allowing for greater flexibility in fitting the data. This approach appears to highlight a problem with the intercept parameters' identifiability (**Figure 4.2**). This could lead to two possible explanations. The first is that our datasets reflect a highly likely proportional relationship with area, which explains why offset approach leads to more accurate predictions (J. A.

Smith, 2024). The second is that including $\log(\text{area})$ as a covariate increases model flexibility, but not enough to capture relationships more complex than linear (Lindström et al., 2024). Consequently, the model may attempt to compensate through the intercept but may fail to find a stable solution due to non-identifiability (Gelman et al., 2025). On other hand, it is important to note that the relationship may change if the covariate area size has greater variabilities, as they are found across Europe (ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023; Lindström & Bergqvist, 2022). This may result in more complex relationships in which area treatment in the modeling approach may vary (J. A. Smith, 2024). Therefore, in this context, it is crucial to advocate for the reporting of data at the hunting estate resolution (*i.e.*, finest spatial data resolution available), even though it could pose computational challenges. Nevertheless, even with the finest data resolution available, we emphasize that area size should still be considered when modeling to avoid greater bias when predicting at different spatial scales (**Table 4.2**).

Our results support that some variables may have regional differences in the species-environment relationship when analyzed at broad-scale, national, or larger and that they reflect the underlying relationship of the ecological process known between environmental variables and species (**Figure 4.2**; Acevedo et al., 2005, 2014; Díaz-Ruiz et al., 2013; Mattioli et al., 2022; Scandura et al., 2022). Therefore, the effects of non-stationarity on covariates must be considered when modeling (Acevedo, Quirós-Fernández, et al., 2014; Ruiz-Rodríguez et al., 2022).

It may be advisable to examine potential non-stationary variables prior to modeling, and, if necessary, to accommodate non-stationarity by methods that allow changing relationships across the space (Doser, Kéry, et al., 2024; Finley, 2011; Hochachka et al., 2012). Additionally, the spatially explicit model exhibited three main behaviors consistent with previous research, suggesting that its inclusion or exclusion warrants further discussion. First, while fixed covariates often failed to converge or showed poor mixing in this approach, spatial effect parameters did not exhibit such issues. This suggests that there are potential identifiability problems among the fixed effects when a spatial random effect is included (**Figure 4.2**; Page et al., 2017), possibly induced by differences in the autocorrelation range of the climatic and land cover variables that are difficult to account for using a random spatial effect (Mäkinen et al., 2022). This approach may not be ideal if the objective of the study is to examine species-environment relationship, as including a spatial effect could confound the effects of the covariates (**Figure 4.2**; Hodges & Reich, 2010; Keil et al., 2014). Second, the spatial random effect models achieved accuracy similar or higher to other models. The similarity between the other models and SR may be explained by the use of a Negative Binomial distribution, which overdispersion parameter captures non-spatial variation. Therefore, the overdispersion parameter could absorb some part of the variability that would otherwise be attended by the spatial random effects. However, our results suggest that uncertainty is more strongly influenced by the inclusion of the spatial random effects. These models

Table 4.2. Practical recommendations for modeling game species abundance and spatial patterns based on hunting yield data, considering data management, regional effects, and area size effects.

Objective of the study	Data management	Regional effect	Area size effect	Predictions
Studying species-environment relationships	Depending on species distribution range and data distribution.	1. Avoid using spatial random effects: identifiability and confounding problems between fixed effects and random spatial effects. 2. Consider possible non-stationarity effects on covariates by considering regions	Avoid using log(area) as covariate since it may develop convergence problems. Area size should be considered as an offset	
Quantitative abundance (predict your data counts)	Avoid imputing zero values to missing data.	Use spatial random effects for more accurate results, although this approach provides greater uncertainty.	Consider area size, preferably, as an offset.	Downscaling is possible, if area size is considered.
General spatial patterns	Imputing zero values to missing data seems to be especially important when area size is not considered.	Use, preferably, regions as fixed effect (2) or individual models by region (3).	Consider area size as an offset or covariate.	

consistently produced wider credible intervals than those based only on covariates (**Figure 4.3**; Keil et al., 2014; Mäkinen et al., 2022). Third, the spatial patterns showed that they were different compared to those of the other models (**Figure 4.4**; Osborne et al., 2007; Page et al., 2017). While they provided accurate predictions within the scope of the data, predicted values outside of this range may have large credible intervals (Keil et al., 2014). Moreover, we observed that the behavior of the spatial random effects is closely related to the species data input. As expected, SR predictions of relative abundance patterns were close to introduced quantities in comparison to models that do not consider the spatial effect and that will only consider covariates, since SR is prone to overfitting. Under that condition, we could consider that in our study case the dataset with NA data transformed to zero (WITH dataset) may behave poorer for widespread species than for constrained ones, which effects for the latter may be advisable. We have observed an unreliable predicted pattern under this approach on the red fox, when using the WITH dataset as it comprised a regional data gap. Therefore, model predictions in that area approximated to zero, what is unreliable for this widespread species. On the contrary, when uncertain data were removed (WITHOUT dataset) spatial random effects may extrapolate values, which may be undesirable, in this case, for constrained species, but could be desirable in the case of red fox. Therefore, models that include spatial random effects may behave unpredictably in certain regions, depending on the data input used, and could produce relative abundances estimates that differ from those

expected based on environmental conditions (see [S4-3](#)). Under our point of view, it seems reasonable to avoid using spatial random effects whether the objective of the study is obtaining species-environment relationships as well as general spatial patterns, while we support using SR approach if the aim of the study is obtaining accurate results regarding to the data used (**Table 4.2**). We also advocate to warn that model predictions while being data overfitted and that including unknown data values may produce unreliable predictions.

Consequently, modelers must consider whether it is pertinent for the target species to allow for that flexibility, especially when predicting the abundance of species in global change forecasted scenarios or when predicting species that are expanding their geographical range. Considerations that could be especially relevant for alien species or vector species in an epidemiological context (Medley, 2010; Youngflesh et al., 2025).

Inferences related to HYs models that do not consider the relationship between the ecological and the observational processes are useful tools for predicting abundance as a proxy or potential distribution of the species. However, predicted values should not be interpreted as the total number of individuals, that is, actual abundance (Guélat & Kéry, 2018), unless the predictions are validated with independent abundance data. We recognize and stress that reporting hunting effort is essential for enhancing or obtaining actual abundance of game species (Andreotti et al., 2022; Carvalho et al., 2024; Gilbert, Pease, et al., 2021; Iijima, 2017; Ruiz-Rodríguez et al., 2023). The disaggregation

of the hunting yield season data into daily or monthly hunting yields will also allow more reliable abundance estimates (Bauder et al., 2021; Crum et al., 2017). Other alternatives for better estimates include building a model which integrates the ecological and observational processes by considering approaches to measure the hunting effort (Fernández-López et al., 2025) or by integrating different sources of information (Gilbert, Pease, et al., 2021).

Our findings highlight that the type of data and the analytical approach utilized are crucial for developing species distribution or abundance models. The modeling approach should be contingent on the objectives of the study, the idiosyncrasies of the species and the data (Guillera-Arroita et al., 2015). Based on our results, we provide some practical recommendations that may aid in modeling species relative abundance according to the study objectives while accounting for the idiosyncrasies of each dataset. Next steps in the development of abundance models based on HYs datasets would be to delve deeper into the relationship between the latent state and the ecological process in order to transform the relative abundance obtained in these models into actual abundance and to compare results with independent abundance dataset.

Authors contribution

Sonia Illanas, Javier Fernández-López, Pelayo Acevedo and Joaquín Vicente conceived the ideas and designed methodology; Sonia Illanas and José A. Blanco-Aguar collected the data; Sonia Illanas performed the data analysis, supported by Javier Fernández-López and Pelayo Acevedo; Sonia Illanas led the writing of

the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest statement

The authors report no conflict of interests.

Data accessibility statement

Data and code used for modeling are open and available at Zenodo repository (<https://doi.org/10.5281/zenodo.17507317>).

S4 Supplementary information

S4-1 Bioregion covariate construction for the fixed bioregion models and independent bioregion models within the regional effect proposed strategy.

This supplementary provides information about the methodology developed to construct the bioregions. Bioregions were considered according to the climatic conditions of the study area. We obtained 19 bioclimatic variables related to temperature and precipitation from ([WorldClim version 2 project](#)) at 1 km² resolution (Fick & Hijmans, 2017).

We divided the study area in a 2 km x 2 km cell grid (ETRS89-LAEA; EPSG:3035) and transferred the mean of each of the bioclimatic values using the zonal statistics tool with QGIS ([QGIS Geographic Information System 2024](#)). We conducted a Principal Component Analysis with the `dudi.pca` function from `ade4` R package (Dray & Dufour, 2007) to group the 19 bioclimatic variables. We assigned to each cell the corresponding score of the first and second axis of the PCA representing the climatic gradient in the study area. The variance percent contribution accumulated by the two axis ~77%. We clustered the scores of the first and second PCA axis in 4 groups (Figure S4-1) to represent similar climatic conditions using the k-means method (Hartigan & Wong, 1979).



Figure S4-1. The four bioregions obtained for the study area.

S4-2 Modeling framework equations.

This supplementary material provides further details on the statistical models introduced in the [section 4.2.2](#) of the main text. In order to address the characteristics of hunting yields (HYs) we elaborated on the model formulation, and computational strategies used (see [section 4.2.2](#)). A script employing the modeling approach followed can also be found at [Zenodo](#) repository (Illanas, Fernández-López, Blanco-Aguilar, et al., 2025), as recommended by Kellner et al. (2025).

We determined that the expected relative abundance, N_i , followed a Negative Binomial distribution. The negative binomial is characterized by two parameters that influence its shape: μ and κ ,

$$N_i \sim (\mu_i, \kappa)$$

where μ_i is the mean expected hunting yield value and κ captures the overdispersion of the data. A low value of κ , close to zero, indicates high overdispersion; that is, there is great variability in the HYs data that will not be captured by a Poisson distribution. A high value of κ indicates low overdispersion and suggests that a Poisson distribution could be appropriate for modeling HYs data. A Poisson distribution has one parameter λ_i which models its shape according to the expected mean. Therefore, modeling the data over a Poisson distribution is preferable when there is no convergence or overdispersion

problems. In such cases, using a negative binomial distribution could be advisable.

It is recognized that HYs data have several intrinsic characteristics that may impede their use. series, their extensive coverage and the long data series make dealing with their idiosyncrasies worthwhile. There are three main issues related to HYs: uncertainty due to unreported and zero data, the regional nature of the species-environment relationships due to their extensive coverage, and their relationship with the size of the hunting estates where individuals were harvested. In this work, we proposed several approaches to understand the effects of these characteristics on modeling. All models were fitted with the spAbundance 0.2.2 R package (Doser, Finley, et al., 2024).

Area effects

a.- The basic model, (EA), was the same as the previous one, which assumed that the covariates were solely responsible for the expected HYs of the species (μ_i). In this case, that the HY was independent of the size of the area where the animals were hunted (Figure S4-2.1),

$$\log(\mu_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i$$

where β_0 is the intercept parameter, β_1 is the linear effect of precipitation (prec_i) β_2 is the linear effect of forest (forest_i), and β_3 is the linear effect of human footprint (hfp_i),

b.- The offset model, (OA), considered that the covariates explained the expected HY of the species (μ_i), but that this value was expressed as a rate relative to the size of the hunting estate where individuals were harvested. The offset model accounted for the fact that, all else being equal, a larger sample area should yield a proportionally higher number of individuals. Thus, if one municipality was twice the size of another, and the covariates were the same, the expected HYs would also be proportionally higher (Figure S4-2.1). Unlike the β coefficients of the covariates, the offset was a fixed term in the model, and its coefficient was not estimated because it was assumed to be known based on the proportional relationship with the response variable. This allowed the model to focus on estimating the effects of the covariates, while already accounting for differences in the area size.

$$N_i \sim \text{Negative Binomial} \left(\frac{\mu_i}{\text{area}_i}, \kappa \right)$$

$$\log\left(\frac{\mu_i}{\text{area}_i}\right) = \log(\mu_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i$$

$$\log(\mu_i) - \log(\text{area}_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i$$

$$\log(\mu_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i + 1 \cdot \log(\text{area}_i)$$

where β_0 is the intercept parameter, β_1 is the linear effect of precipitation (prec_i) β_2 is the linear effect of forest (forest_i), and β_3 is the linear effect of human footprint (hfp_i) and $1 \cdot \log(\text{area}_i)$ is the offset.

c.- The covariate model, (CA), included the area size as a log-transformed covariate. We maintained the relationship between the area size and the

response variable as an offset ($\log(\text{area})$), while freeing the β parameter. This meant that we did not assume a proportional relationship between the response variable and the area size; rather the model estimated it from the data, as it did with the other covariates. Therefore, this model calculated a β value for its effect (Figure S4-2.1).

$$\log(\mu_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i + \beta_4 \cdot \log(\text{area}_i)$$

where β_0 is the intercept parameter, β_1 is the linear effect of precipitation (prec_i), β_2 is the linear effect of forest (forest_i), and β_3 is the linear effect of human footprint (hfp_i), β_4 is the linear effect of $\log(\text{area})$.

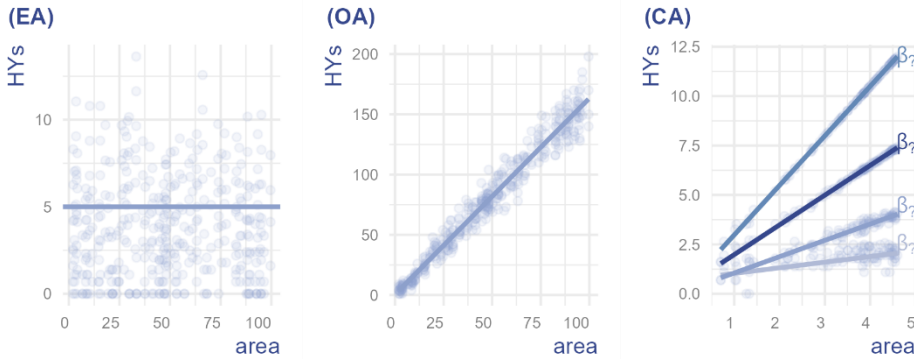


Figure S4-2.1. Three modeling approaches were followed for facing the area size problem: basic model (a), offset model (b), covariate $\log(\text{area})$ model (c). This figure was created solely for illustrative purposes and is based on simulated data.

Regional effects

1.- The basic model, (ER), considered the covariates to be solely responsible for the expected mean abundance value of a species (μ_i), which was assumed to be equal regardless of where the animal was hunted (Figure S4-2.2),

$$\log(\mu_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i$$

where β_0 is the intercept parameter, β_1 is the linear effect of precipitation (prec_i), β_2 is the linear effect of forest (forest_i), and β_3 is the linear effect of human footprint (hfp_i).

2.- The fixed regional model, (FR), considered each bioregion (Figure S4-2.2) as a fixed effect covariate, accepting that the expected abundance in a bioregion could be higher, or lower, and that the intercepts would differ accordingly (Figure S4-2.2),

$$\log(\mu_i) = \beta_{01} \cdot \text{Bioregion}_1 + \beta_{02} \cdot \text{Bioregion}_2 + \beta_{03} \cdot \text{Bioregion}_3 + \beta_{04} \cdot \text{Bioregion}_4 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i$$

where $\beta_{01/02/03/04}$ is the intercept parameter for bioregion 1, 2, 3 or 4, respectively, β_1 is the linear effect of precipitation (prec_i), β_2 is the linear effect of forest (forest_i), and β_3 is the linear effect of human footprint (hfp_i).

3.- The individual regional model, (IR), considered not only that the estimated abundance may differ between regions (intercept) and that the relationship between the covariates and the HYs may differ. This results in a different effect of the covariates (β values). We split the dataset related to each bioregion, developing an independent model for each (Figure S4-2.2).

Table S4-2.1. Equations for each independent bioregion model

Bioregion	Model equation
Bioregion 1	$\log(\mu_{i1}) = \beta_{01} + \beta_{11} \cdot \text{prec}_i + \beta_{21} \cdot \text{forest}_i + \beta_{31} \cdot \text{hfp}_i$
Bioregion 2	$\log(\mu_{i2}) = \beta_{02} + \beta_{12} \cdot \text{prec}_i + \beta_{22} \cdot \text{forest}_i + \beta_{32} \cdot \text{hfp}_i$
Bioregion 3	$\log(\mu_{i3}) = \beta_{03} + \beta_{13} \cdot \text{prec}_i + \beta_{23} \cdot \text{forest}_i + \beta_{33} \cdot \text{hfp}_i$
Bioregion 4	$\log(\mu_{i4}) = \beta_{04} + \beta_{14} \cdot \text{prec}_i + \beta_{24} \cdot \text{forest}_i + \beta_{34} \cdot \text{hfp}_i$

where $\beta_{01/02/03/04}$ is the intercept parameter, $\beta_{11/12/13/14}$ is the linear effect of precipitation (prec_i), $\beta_{21/22/23/24}$ is the linear effect of forest (forest_i), and $\beta_{31/32/33/34}$ is the linear effect of human footprint (hfp_i) for bioregion 1, 2, 3 or 4, respectively.

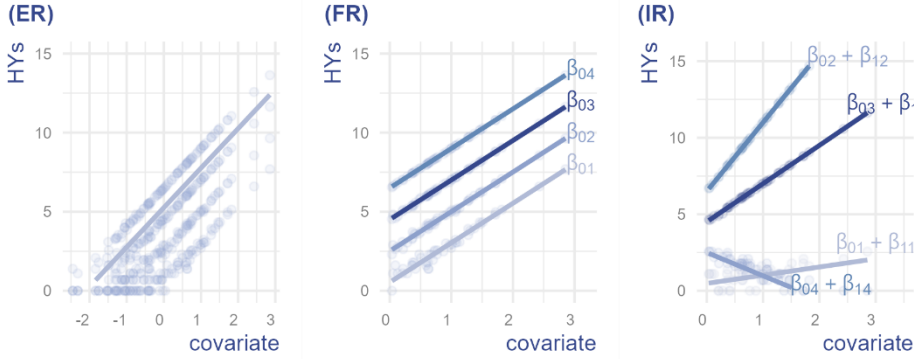


Figure S4-2.2. Approaches followed for facing the regional effects: basic model (1), regional model (2), individual regional models (3). This figure was created solely for illustrative purposes and is based on simulated data.

4.- The spatially explicit model, (SR), incorporated a spatial random effect, $\omega(s_i)$, which assumed that the expected mean abundance, (μ_i) , varied across space due to unobserved spatial factors inducing correlation among nearby locations. We assumed that the space was part of a full Gaussian process (GP), in which each location depends only on its nearest neighbors. In other words, locations that are closer tend to have more similar abundances than locations that are farther apart (Figure S4-2.3; Cressie, 1993). We used a nearest neighbor gaussian process (NNGP), a sparse approximation of a full GP, that reduces computational complexity in large datasets (Datta et al., 2016), by applying the spAbundance package's default settings of 15 neighbors (Doser, Finley, et al., 2024).

$$\log(\mu_i) = \beta_0 + \beta_1 \cdot \text{prec}_i + \beta_2 \cdot \text{forest}_i + \beta_3 \cdot \text{hfp}_i + \omega(s_i)$$

where β_0 is the intercept parameter, β_1 is the linear effect of precipitation (prec_i), β_2 is the linear effect of forest (forest_i), and β_3 is the linear effect of human footprint (hfp_i), and $\omega(s_i)$ is a spatial random effect.

We determined that the structure of the spatial random effect, $\omega(s_i)$ followed a covariance matrix with θ parameters. We also assumed that an exponential function, $\rho(s, s') = \sigma^2 \cdot e^{(-\phi \cdot (s, s'))}$, governed the spatial process, where σ^2 is the spatial variance parameter, ϕ is the spatial decay parameter, and s, s' is the Euclidean distance between each pair of locations. The spatial variance parameter follows an inverse gamma distribution, $\sigma^2 \sim \text{Inverse Gamma}(\alpha, \beta)$ where α is the shape and β the scale hyperparameters. The spatial decay parameter follows a uniform distribution, $\phi \sim \text{Uniform}(a, b)$, where a is the minimum value and b the maximum value of the hyperparameters.

To establish the initial and prior values of the spatial variance and decay parameters, we followed (Doser, 2024). In the initial approach, we implemented uninformative priors for the spatial variance, an inverse gamma (2, 1), and for the spatial decay a uniform distribution $(\frac{3}{\max(dist)}, \frac{3}{\min(dist)})$ (maximum effective range). We calculated the minimum, mean and maximum Euclidean distances (dist) between the municipalities in our dataset, which were 0.37 km, 368.77 km and 1187.55 km, respectively. Notably, we considered the maximum distance was too large to allow the expected mean abundance to vary meaningfully due to any unobserved spatial factor. Therefore, we reduced the maximum value by a factor of five, determining that the maximum distance at which an unobserved factor could affect the expected abundance was 237 km. If there were any unmeasured variables potentially affecting our response variable, we assumed that neither

management decisions nor other unconsidered factors would exert influence beyond that spatial scale. We reduced the minimum and mean distances proportionally. We defined the inits of these parameters to 0.5 and $\frac{3}{\text{mean}(dist)}$, respectively. However, the suboptimal convergence and mixing led us to restrict the values of these parameters and use more informative priors. Defining the inits and priors values of spatial parameters is not trivial, particularly when thinking about ϕ (see Doser, 2024). We made several attempts to reach convergence of the parameters, assessed by the value of Rhat, ESS and visual inspection of traceplots. These attempts included:

- changing the response variable distribution from Poisson to Negative Binomial,
- more restrictive upper and lower bounds of the spatial decay parameter,
- changing the init values of the spatial decay parameter,
- changing the init values of the spatial variance parameter to 1,
- changing the default number of neighbors in the NNGP, we tried 15, 10 and 5,
- changing the priors of beta parameters from (0,10) to (0,1).

From all the attempts, the ones that allowed us to reach convergence were: switching from a Poisson distribution to a negative binomial distribution, setting the spatial decay initial value to $\frac{4}{\text{mean}(dist)}$, restricting the uniform priors of the spatial decay to $(\frac{10}{\text{max}(dist)}, \frac{2}{10})$, and the normal priors of to $\beta(0,1)$. We further recognize and aware that the values established for the spatial parameters are sensitive to the units of the coordinate reference system of the datasets. Therefore, it is important to note that a value of, for instance, 0.3, is not

equivalent if the coordinate reference system units are in kilometers or in meters.

Caution must be taken when setting these values. For further reading on spatial modeling approaches that may inform prior selection, see (Mäkinen et al., 2022).

We used the same initials and priors values for all the species and models. We therefore set the initial values of the overdispersion parameter, κ to 0.5, and β covariate's parameters to 0. Initial values of the latent spatial random effects at each site were also set to 0 (Doser, 2024). For the spatial variance parameter σ^2 , we set the initial value to 0.5.

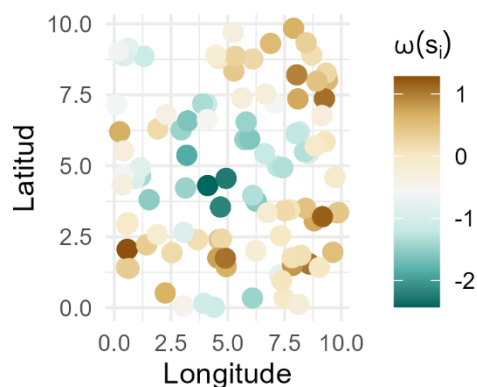


Figure S4-2.3. Values of spatial random effects $\omega(s_i)$, where closer locations have more similar values than those further apart. This figure was created solely for illustrative purposes and is based on simulated data.

S4-3 Prediction maps at municipality level and 2 km x 2 km cell grid for the four game species and both datasets.

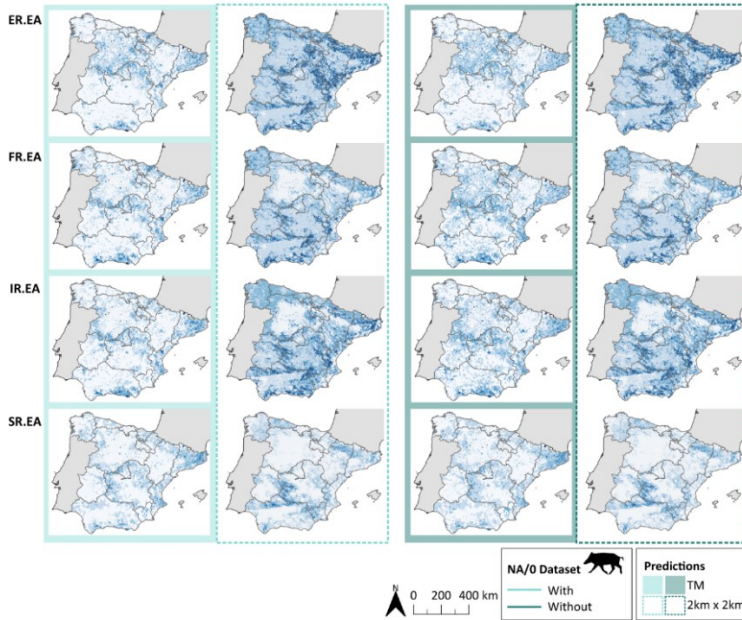


Figure S4-3.1. Wild boar predictions to municipality level and 2 km x 2 km grid for all type EA models (not consider area as explanatory variable).

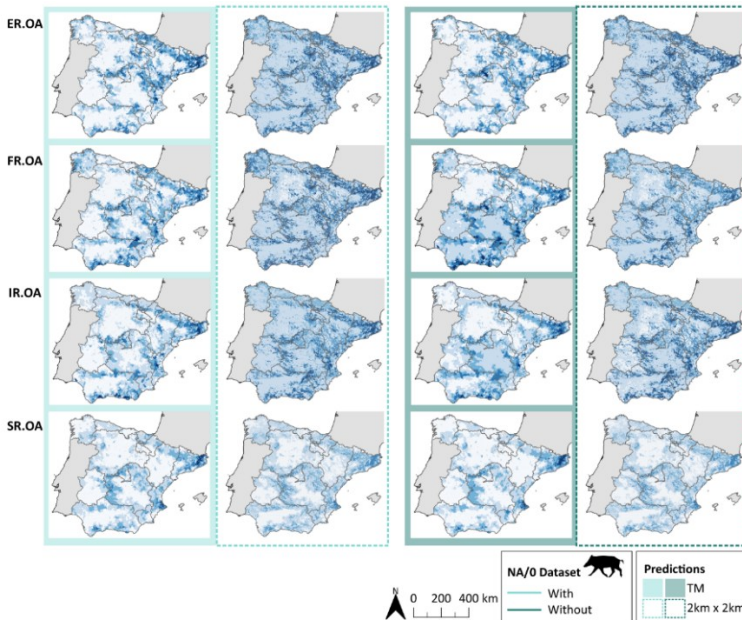


Figure S4-3.2. Wild boar predictions to municipality level and 2 km x 2 km grid for all type OA models (consider area as an offset).



Figure S4-3.3. Wild boar predictions to municipality level and 2 km x 2 km grid for all type CA models (consider log(area) as explanatory variable).

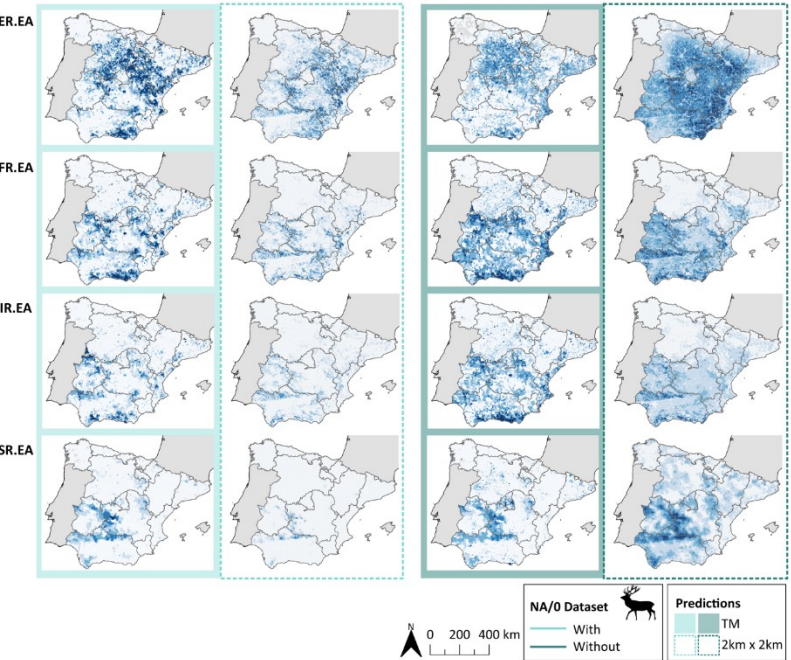


Figure S4-3.4. Red deer predictions to municipality level and 2 km x 2 km grid for all type EA models (not consider area as explanatory variable).

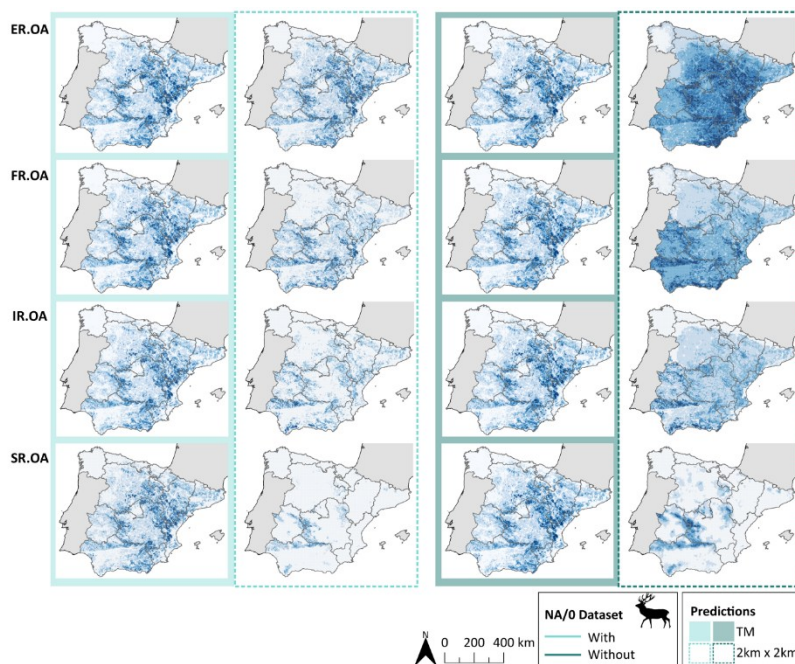


Figure S 4-3.5. Red deer predictions to municipality level and 2 km x 2 km grid for all type OA models (consider area as an offset).

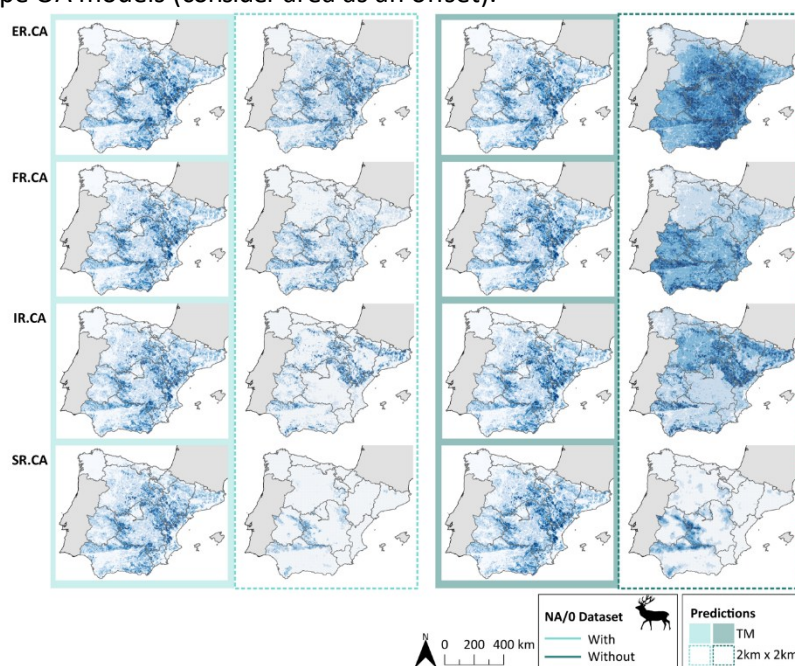


Figure S 4-3.6. Red deer predictions to municipality level and 2 km x 2 km grid for all type CA models (consider log(area) as explanatory variable).

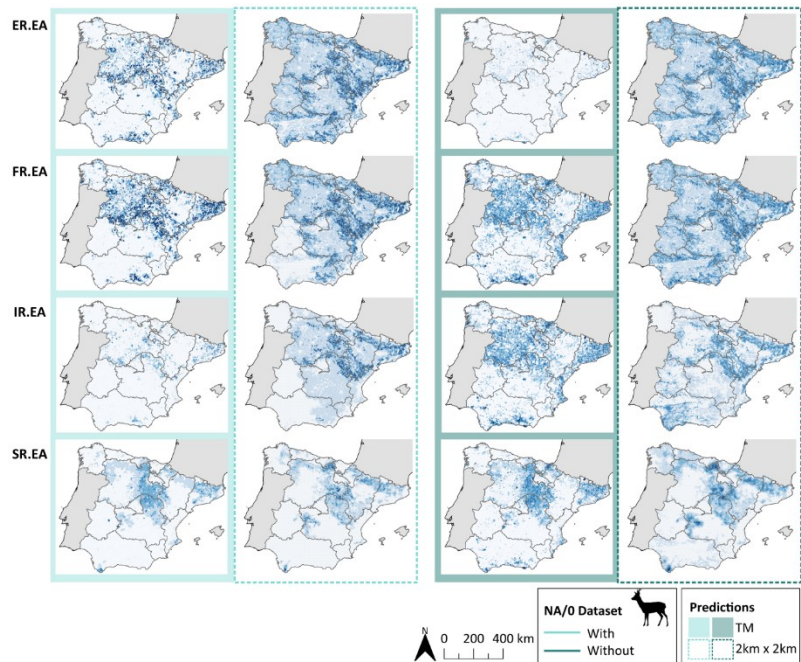


Figure S4-3.7. Roe deer predictions to municipality level and 2 km x 2 km grid for all type EA models (not consider area as explanatory variable).

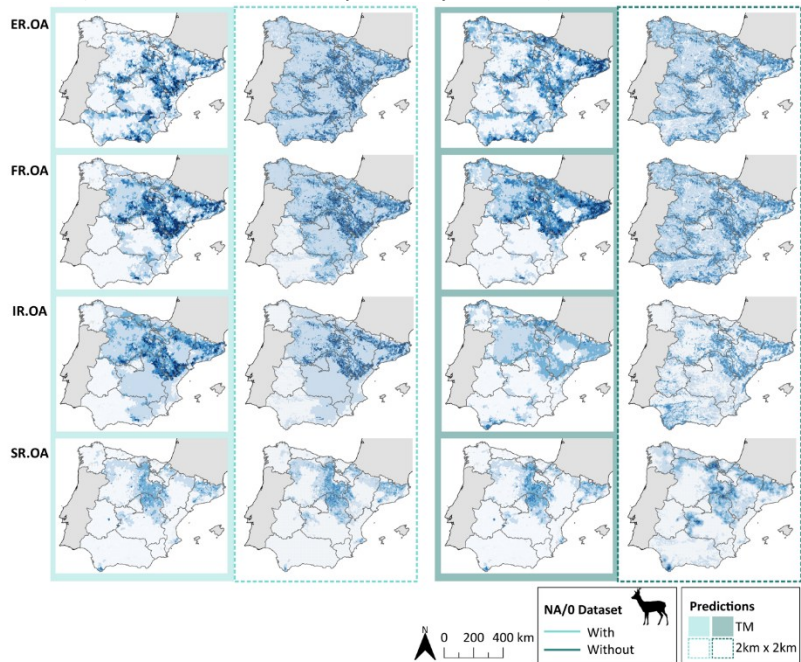


Figure S4-3.8. Roe deer predictions to municipality level and 2 km x 2 km grid for all type OA models (consider area as an offset).

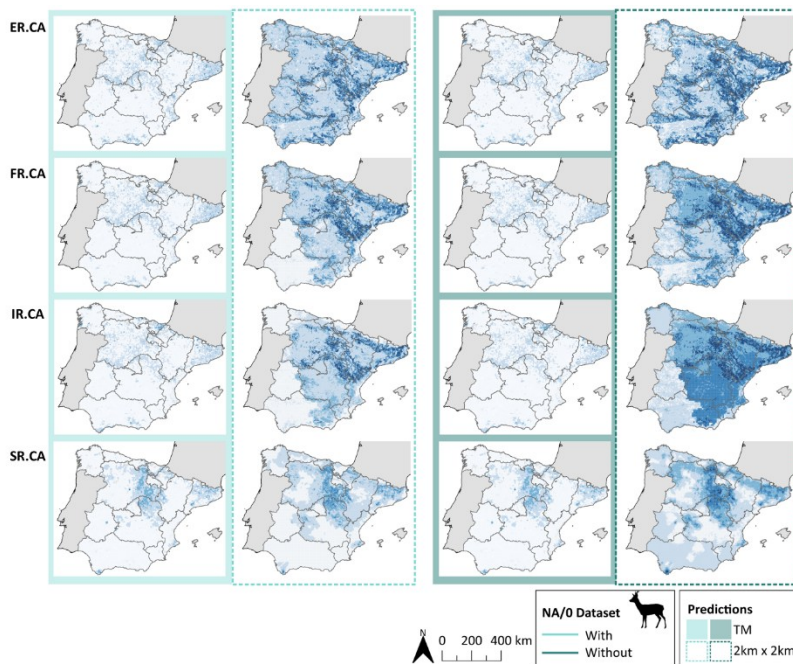


Figure S4-3.9. Roe deer predictions to municipality level and 2 km x 2 km grid for all type CA models (consider $\log(\text{area})$ as explanatory variable).

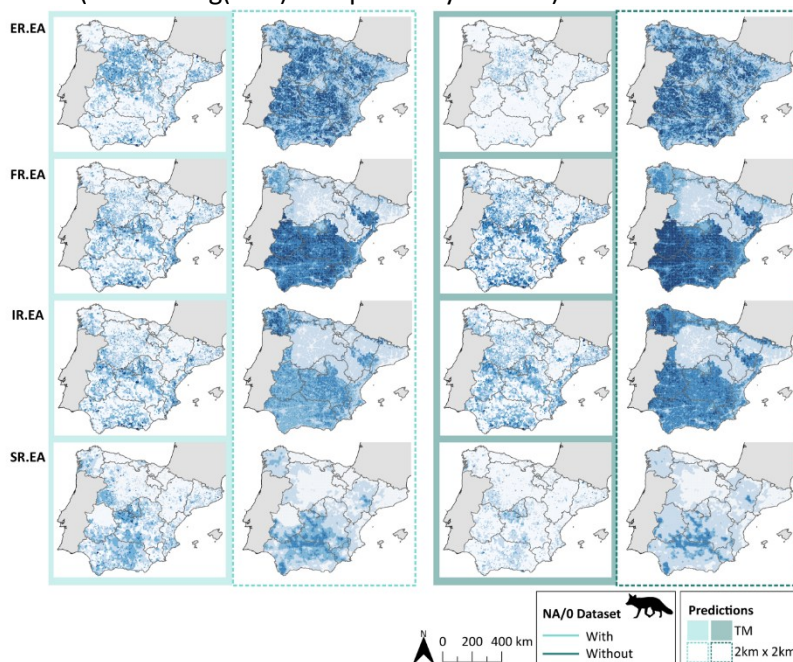


Figure S4-3.10. Red fox predictions to municipality level and 2 km x 2 km grid for all type EA models (not consider area as explanatory variable).

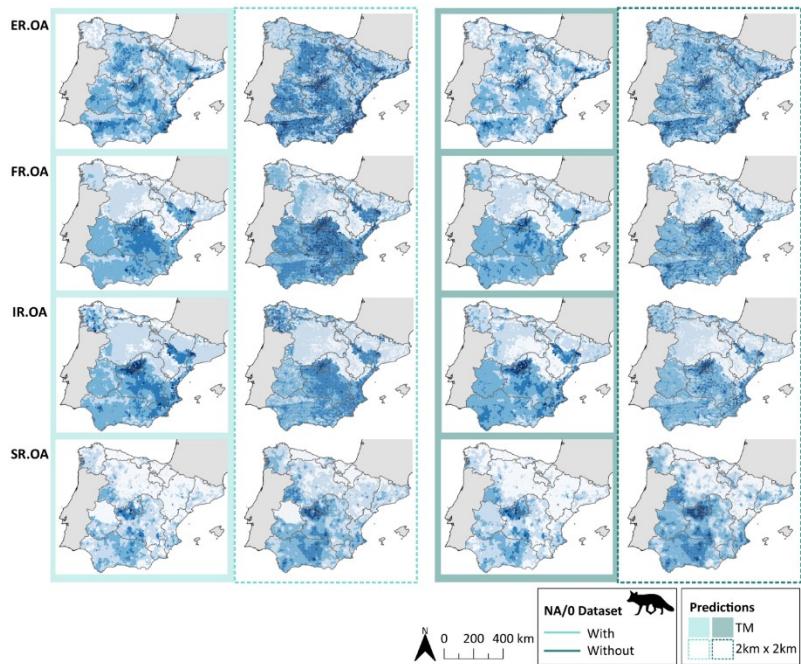


Figure S4-3.11. Red fox models predicted to municipality level and 2 km x 2 km grid cell for all type OA models (consider area as an offset).

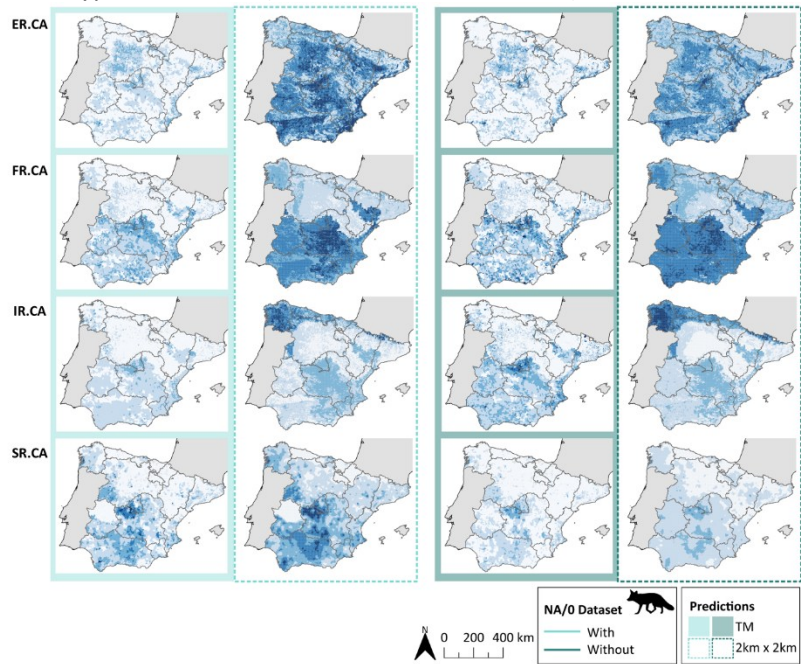


Figure S4-3.12. Red fox models predicted to municipality level and 2 km x 2 km grid cell for all type CA models (consider log(area) as explanatory variable).

S4-4 Convergence diagnostics. Trace, density plots, Rhat and ESS values to assess convergence.

This supplementary document reports the convergence results for each modeling approach used across studied species and data scenarios.

Owing to the extensive volume of image-based content contained in the supplementary material, it is not included in the print version of this thesis. The complete supplementary material is available exclusively online and can be accessed using the QR code or at [github](#).



S4-5 Summary of GLMMs of 4.2.3 model evaluation section.

This supplementary material provides further details on the GLMMs results of the model's comparison introduced in the [section 4.2.3](#) of the main text.

S4-5.1. Prediction assessment

Table S4-5.1. Estimated coefficients, standard errors, and significance levels for the bias (observed-predicted50p) model including interaction terms. Main effects should be interpreted considering the interaction terms.

Variable	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	15.939	0.733	42.246	21.748	0.000	***
model.areaOA	-3.558	0.577	172.998	-6.168	0.000	***
model.areaCA	-0.997	0.577	172.998	-1.729	0.086	.
predictionMunicipality	-4.626	0.185	173.000	-24.951	0.000	***
model.brFR	0.163	0.214	172.998	0.762	0.447	
model.brIR	0.257	0.214	172.998	1.200	0.232	
model.brSR	0.608	0.214	172.998	2.840	0.005	**
datasetWITHOUT	0.563	0.264	175.090	2.131	0.035	*
per_area	-0.806	0.662	175.956	-1.216	0.225	
model.areaOA:predictionMunicipality	4.557	0.262	172.998	17.384	0.000	***
model.areaCA:predictionMunicipality	2.521	0.262	172.998	9.615	0.000	***
model.brFR:datasetWITHOUT	0.101	0.303	172.998	0.332	0.740	
model.brIR:datasetWITHOUT	-0.062	0.303	172.998	-0.206	0.837	
model.brSR:datasetWITHOUT	-1.508	0.303	172.998	-4.982	0.000	***
model.areaOA:per_area	-0.876	0.659	172.998	-1.330	0.185	
model.areaCA:per_area	-2.246	0.659	172.998	-3.407	0.001	***

Table S4-5.2. Estimated coefficients, standard errors, and significance levels for the credible interval model including interaction terms. Main effects should be interpreted considering the interaction terms.

Variable	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	12.932	0.715	39.208	18.078	0.000	***
model.areaOA	-2.612	0.564	176.024	-4.632	0.000	***
model.areaCA	-0.143	0.564	176.024	-0.253	0.801	
predictionMunicipality	-3.276	0.181	176.026	-18.081	0.000	***
model.brFR	0.450	0.148	176.024	3.042	0.003	**
model.brIR	0.517	0.148	176.024	3.496	0.001	***
model.brSR	3.328	0.148	176.024	22.500	0.000	***
datasetWITHOUT	-0.362	0.184	178.940	-1.964	0.051	.
per_area	1.342	0.648	178.931	2.072	0.040	*
model.areaOA;predictionMunicipality	2.824	0.256	176.024	11.020	0.000	***
model.areaCA;predictionMunicipality	2.215	0.256	176.024	8.644	0.000	***
model.areaOA;per_area	-0.614	0.644	176.024	-0.954	0.341	
model.areaCA;per_area	-2.344	0.644	176.024	-3.639	0.000	***

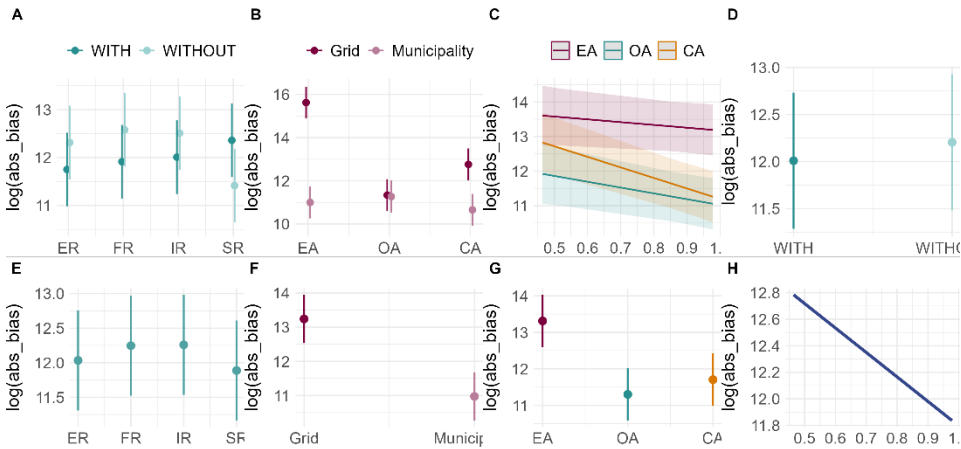


Figure S4-5.1. Estimated effects and interactions plots from the bias (observed-predicted50p) fitted GLMM. Main effects should be interpreted considering the interaction terms. Columns correspond to the interaction effect between the data scenario used for modeling and the regional effect (A), the spatial prediction resolution and the area effect (B) the area effect and the proportion of area used for modeling respect to the area predicted the type of dataset used for modeling (C), the data scenario used for modeling (D), the regional effect (E), the spatial prediction resolution (F), the area effect1 (G), the proportion of area used for modeling respect to the area predicted.

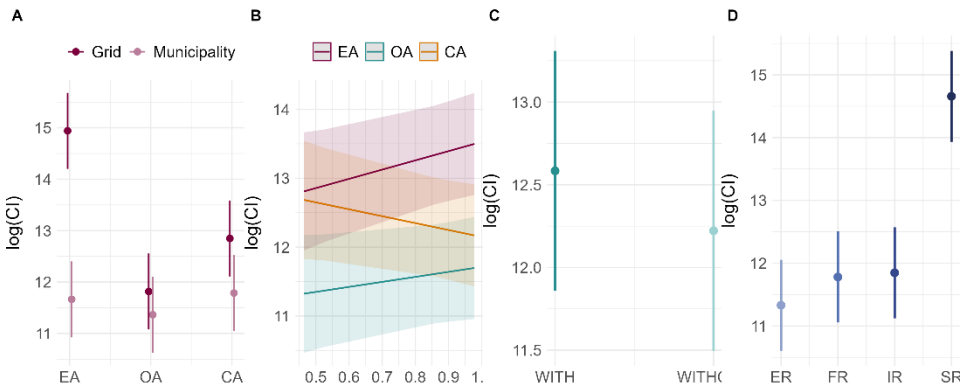


Figure S4-5.2. Estimated effects and interactions plots from the credible interval fitted GLMM. Main effects should be interpreted considering the interaction terms. Columns correspond to: the interaction effect between spatial prediction resolution and the area effect (A), the area effect and the proportion of area used for modeling respect to the area predicted (B), the data scenario used for modeling (C), the regional effect (D).

S4-5.2. Singular patterns

Table S4-5.3. Estimated coefficients, standard errors, and significance levels for the rho values for the full data model including interaction terms. Main effects should be interpreted considering the interaction terms.

Variable	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	0.674	0.036	13.654	18.584	0.000	***
correlation.typerhoL1O	-0.024	0.014	173.000	-1.722	0.087	.
model.brFR	0.150	0.034	173.000	4.465	0.000	***
model.brIR	0.118	0.034	173.000	3.523	0.001	***
model.brSR	-0.054	0.034	173.000	-1.616	0.108	
model.areaOA	0.217	0.038	173.000	5.773	0.000	***
model.areaCA	0.244	0.038	173.000	6.486	0.000	***
datasetWITHOUT	-0.109	0.024	173.000	-4.609	0.000	***
model.brFR:model.areaOA	-0.102	0.047	173.000	-2.147	0.033	*
model.brIR:model.areaOA	-0.078	0.047	173.000	-1.648	0.101	
model.brSR:model.areaOA	0.033	0.047	173.000	0.687	0.493	
model.brFR:model.areaCA	-0.107	0.047	173.000	-2.253	0.025	*
model.brIR:model.areaCA	-0.107	0.047	173.000	-2.254	0.025	*
model.brSR:model.areaCA	0.019	0.047	173.000	0.394	0.694	
model.areaOA:datasetWITHOUT	0.122	0.034	173.000	3.629	0.000	***
model.areaCA:datasetWITHOUT	0.121	0.034	173.000	3.605	0.000	***

Table S4-5.4. Estimated coefficients, standard errors, and significance levels for the rho values for the zero and absences data model including interaction terms. Main effects should be interpreted considering the interaction terms.

Variable	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	0.609	0.034	16.956	18.101	0.000	***
correlation.typerhoL1O	-0.030	0.013	173.000	-2.287	0.023	*
model.brFR	0.180	0.033	173.000	5.509	0.000	***
model.brIR	0.127	0.033	173.000	3.907	0.000	***
model.brSR	-0.031	0.033	173.000	-0.964	0.336	
model.areaOA	0.248	0.036	173.000	6.795	0.000	***
model.areaCA	0.281	0.036	173.000	7.704	0.000	***
datasetWITHOUT	-0.094	0.023	173.000	-4.083	0.000	***
model.brFR:model.areaOA	-0.126	0.046	173.000	-2.730	0.007	**
model.brIR:model.areaOA	-0.090	0.046	173.000	-1.950	0.053	.
model.brSR:model.areaOA	0.020	0.046	173.000	0.426	0.671	
model.brFR:model.areaCA	-0.131	0.046	173.000	-2.851	0.005	**
model.brIR:model.areaCA	-0.138	0.046	173.000	-2.992	0.003	**
model.brSR:model.areaCA	0.003	0.046	173.000	0.057	0.955	
model.areaOA:datasetWITHOUT	0.109	0.033	173.000	3.344	0.001	**
model.areaCA:datasetWITHOUT	0.105	0.033	173.000	3.209	0.002	**

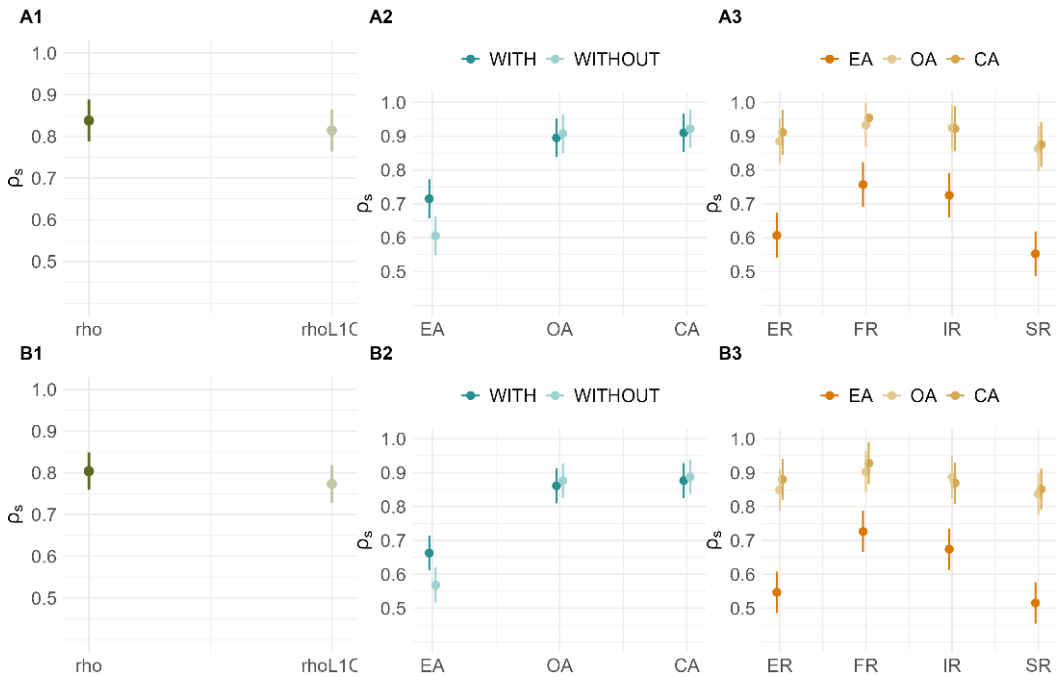


Figure S4-5.3. Estimated effects and interactions plots of the fitted GLMM for (A) all predicted municipalities, regardless of whether their locations were used to inform the model, and for (B) municipalities for which the data were zero or missing values (NAs). Main effects should be interpreted considering the interaction terms. Columns correspond to the effect of full model average or models average leaving one out (1), the interaction between area effect and the data scenario used for modeling (2), the interaction between area effect and the regional effect (3).

5. Accounting for Spatial Dependence to Smooth Regional Patterns of Wild Boar Abundance across Europe



Based on the report:

ENETWILD-consortium, **Illanas. S.**, Fernández-López, J., Blanco-Aguiar, J.A. Warren, D.A., Croft, S., Smith, G. C., Vicente, J., Acevedo, P. (*in press*). Perspectives from hunting bags for a continuous gradient of relative abundance of wild boars in Europe. EFSA supporting publication.

Abstract

Accurate spatial predictions of wildlife abundance are essential for managing disease risk and guiding conservation policy, yet they remain challenging at continental scales where data quality and ecological processes vary widely. For widely distributed species such as wild boar (*Sus scrofa*), data spatial heterogeneity and non-stationary species–environment relationships complicate efforts to generate reliable abundance estimates across large and diverse landscapes. Abundance modeling was, therefore, usually conducted within ecologically homogeneous regions. However, the regionalization approach can generate abrupt artificial transitions in predicted patterns at regional boundaries, resulting in unreliable spatial patterns and hampering their interpretation at large scales. Here, we evaluate whether statistical models explicitly accounting for spatial dependence result in reliable relative abundance spatial patterns of wild boar across Europe.

We used harmonized hunting yield data to fit a model that accounts for spatial dependence and derive two predictions surfaces from it: an environmental-only surface based on the fixed covariate estimates and a surface that also includes the spatial dependence. We then compared both predictions with previously published regional model fitted separately within biogeographic regions, assessing spatial agreement, uncertainty patterns, and consistency of predictions.

Across Europe, environmental covariates account for much of the variation in wild boar abundance on a large scale, while spatial effects primarily enhance local predictions as they can explain a substantial proportion of the variation in the response variable. Thus, spatial predictions generally produce smoother and more continuous abundance gradients than regional predictions. Nonetheless, variation in the size and number of observation units (*i.e.*, administrative and management units) can influence the spatial autocorrelation parameter and, consequently, the predicted spatial pattern. In our study, the majority of observation units are relatively small, such as hunting grounds, leading to a smooth spatial pattern in areas with high-quality, fine-resolution data. In contrast, predictions are more uncertain in regions with coarser observation units. This limitation, due to heterogeneity in unit size, may reduce precision in spatial predictions.

These results suggest that statistical models explicitly accounting for spatial dependence should not be viewed as a universal solution for large-scale wildlife abundance modeling. Instead, their effectiveness depends critically on the spatial resolution and homogeneity of input data.

Resumen

Las predicciones espaciales precisas de la abundancia de fauna silvestre son fundamentales para la gestión del riesgo de enfermedades y la orientación de las políticas de conservación, aunque siguen siendo difíciles de obtener a escala continental, donde los procesos ecológicos y la calidad de los datos varían considerablemente. En especies de amplia distribución, como el jabalí (*Sus scrofa*), la heterogeneidad espacial de los datos y las relaciones no estacionarias especie-ambiente complican la obtención de estimaciones fiables de abundancia en paisajes extensos y diversos. Por ello, la modelización de la abundancia se realizaba normalmente dentro de regiones ecológicamente homogéneas. Sin embargo, las aproximaciones de regionalización pueden generar predicciones artificialmente abruptas en los bordes de las regiones. En este estudio se evalúa si los modelos estadísticos que tienen en cuenta explícitamente la dependencia espacial producen patrones de abundancia de jabalí coherentes a escala europea.

A partir de estadísticos cinegéticos, se ajustó un modelo que considera la dependencia espacial y se derivaron de él dos patrones de abundancia predichos: uno basado únicamente en los efectos de las covariables ambientales del modelo, y otro que tenía también en cuenta la dependencia espacial. Se compararon ambas predicciones con modelos regionales previamente publicados que fueron ajustados por separado dentro de regiones biogeográficas, mediante el grado de concordancia espacial, los patrones de incertidumbre y la consistencia de las predicciones.

En toda Europa, las covariables ambientales explican gran parte de la variación a gran escala en la abundancia del jabalí, mientras que los efectos

espaciales mejoran principalmente las predicciones locales, ya que pueden explicar una parte sustancial de la variación en la variable respuesta. De esta manera, las predicciones espaciales generan gradientes de abundancia más suaves y continuos respecto a los enfoques regionales, es decir, más coherentes. No obstante, la variación en el tamaño y número de las unidades de observación (*i.e.*, unidades administrativas y de gestión) puede influir en el parámetro de autocorrelación espacial y, en consecuencia, en el patrón espacial predicho. En nuestro estudio, la mayoría de las unidades son relativamente pequeñas, como cotos de caza, lo que dio lugar a que las predicciones espaciales fueran especialmente buenas en estas áreas. Sin embargo, las predicciones son más inciertas en regiones con unidades más grandes. Esta limitación, debida a la heterogeneidad en el tamaño de las unidades de observación, puede reducir la precisión y coherencia de las predicciones espaciales especialmente cuando se trabaja con fuentes de datos heterogéneas y/o a grandes escalas espaciales.

En conjunto, los resultados indican que los modelos que tienen en cuenta explícitamente la dependencia espacial no deben considerarse una solución universal para la modelización de la abundancia de fauna silvestre a gran escala. Por el contrario, su eficacia depende de manera crítica de la resolución espacial y la homogeneidad de los datos de entrada.

5.1. Introduction

Statistical models in ecology are a simplified representation of real-world-ecological processes (Callaghan et al., 2023; Levins, 1966; Oreskes et al., 1994). Models can be decomposed into multiple facets, including data input and model parameters as key terms (Malmborg et al., 2024). Both determine model complexity and are responsible for the ability to disentangle informative species-environment relationships needed to make accurate predictions (Potts & Elith, 2006). Nevertheless, it is unrealistic to know all the factors that determine an ecological process, since multiple factors may operate at different scales and interact with each other. (Oreskes et al., 1994). Consequently, determining correctly the relationships among all interacting parameters within an ecological process to produce predictions consistent with the reality is challenging, in part due to multiple uncontrollable stochastic processes. In fact, many ecological models exhibit unmodeled heterogeneity due to missing parameters or processes, which can lead to biased inference and misleading predictions (Dormann et al., 2012; Elith & Leathwick, 2009). At the same time, modeling has become essential for active wildlife management and conservation, and accurate estimates of species abundance and distribution are fundamental to rapid decision-making, for example enabling managers to identify high-risk areas, prioritize surveillance and implement targeted interventions to prevent the spread of pathogens when there is a disease outbreak (*e.g.*, Guisan & Thuiller, 2005; Schmolke et al., 2010).

In the last decades, ecological models have increased complexity in all their facets given the increase of computational power (Malmborg et al., 2024). Many wildlife models include a spatially explicit parameter, given the ability of these parameters to capture complex spatial structures that are a combination of multiple unaccounted factors (Illian et al., 2012; Paradinas et al., 2023). While incorporating spatial dependence through the covariance structure among observations can substantially improve predictive performance, as this component is able to incorporate part of the non-modeled heterogeneity while fixed parameters are unable to, the interpretation of environmental relationships becomes less straightforward, as spatial components may absorb part of the variation otherwise attributed to ecological drivers (Finley et al., 2014; Hodges & Reich, 2010; Mäkinen et al., 2022; Norberg et al., 2019; Paciorek, 2010). This effect may be undesirable if the aim of the model is to disentangle species-environment relationships but may be less important if the aim is to accurately generalize observed spatial patterns, an objective more appropriate than drawing inference on predictors when spatial dependence is included in a model (Mäkinen et al., 2022; Norberg et al., 2019).

The wild boar (*Sus scrofa*) has become a model species for spatial distribution modeling in Europe and represents a particularly suitable case study for assessing the predictive performance of models that account for spatial dependence (Alexander et al., 2016; Bosch et al., 2017; Pittiglio et al., 2018; G. C. Smith et al., 2026). Its wide geographical distribution enables it to occupy

environments with substantial variability. This ecological plasticity implies that its environmental relationships may not remain constant throughout its range, a condition defined as non-stationarity (Dormann et al., 2007; Suárez-Seoane et al., 2002). In addition, the availability of harmonized, high-resolution data at European scale allows for rigorous development and testing of advanced spatial model approaches under realistic management conditions. Among the spatial modeling approaches, previous studies on wild boar have developed separate spatial distribution and abundance models for different regions to address the challenges posed by shifting species-environment relationships (Acevedo, Quirós-Fernández, et al., 2014; ENETWILD-consortium, Acevedo, et al., 2019). Based on hunting yield data, these models account for regional effects and provide more reliable estimates. However, regional models may fail to accurately represent continuous spatial gradients (Cushman et al., 2010) and may produce abrupt spatial frontiers between regions (see wild boar predictions of [Chapter 3](#)). Models that include spatial dependence extend purely environmental models and have shown promising predictive performance in capturing gradual spatial changes (ENETWILD-consortium, Fernández-López, et al., 2020; Norberg et al., 2019), but have not yet been assessed at a continental scale.

This study evaluates whether incorporating spatial dependence through a covariance structure into models estimating wild boar relative abundance at the European scale can produce reliable spatial patterns. Emphasis is placed on the ability of the model to capture gradual spatial variation and to generate

accurate predictions from the available dataset. This work provides practical insights into the strengths and limitations of spatial models for operational wildlife management and disease-risk assessment at the continental level.

5.2. Materials and methods

5.2.1. Data

The response variable for modeling wild boar was hunting yield abundance (HYs) across Europe. We calculated the maximum number of individuals annually hunted within 2015-2021 hunting seasons in each territorial unit. The response variable is the same one used in previous regional model used here for comparative purposes (see wild boar model in [Chapter 3](#)), and therefore results can be comparable as the input facet remains the same.

Environmental covariates that were used more frequently as predictors when fitting the individual regional models were selected for this report (**Table 5.1**; ENETWILD consortium et al., 2022). Their repeated selection across independent regional models indicates a consistent explanatory role for spatial variation, suggesting that they represent ecologically meaningful environmental gradients across the study area. Therefore, we considered the mean diurnal range (bio2; Worldclim 2, Fick & Hijmans, 2017), the mean altitude from the USGS Space Shuttle Radar Topography Mission (SRTM - GL30; Farr et al., 2007), the land use variables mainly related with forestry landscape composition (SA/CCI-LC project version v2.0.7; ESA, 2017). The percentage of *Eucalyptus spp.* was also considered (European Forest Institute; Brus et al., 2012), as wrong predictions of

wild boar abundance in western Europe have been detected when they are not considered (ENETWILD-consortium, Acevedo, Croft, Smith, Blanco-Aguilar, Fernández-López, Scandura, Apollonio, Ferroglio, Keuling, Sange, Zanet, Brivio, Podgorski, et al., 2020). In addition, given the differences in spatial resolution between the HYs, we also included the area as a covariate log transformed in the model (see Chapter 4). This variable was used as an offset in other models, as the response variable was wild boar density, that is, harvested number of individuals divided by the area size of the territory they were contained. Latitude and longitude coordinates were obtained in kilometers from the centroids of each territorial unit.

Table 5.1. Variables used to model the spatial pattern of wild boar abundance.

Code	Variable description
bio02	Mean diurnal range (mean of monthly (max temp - min temp))
alt	Mean altitude
Area	Area of sampling unit
Eu	Percentage of Eucalyptus sp.
lc_10	Cropland, rainfed
lc_30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
lc_40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)
lc_90	Tree cover, mixed leaf type (broadleaved and needle leaved)
lc_100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)
lc_130	Grassland

All covariates were standardized using their mean and standard deviation and multicollinearity among predictors was tested using Variance Inflation Factor ($VIF < 2$; Zuur et al., 2010). Raster predictor layers and grid polygons were managed using QGIS 3.4 and *sf v1.0-21* R package (Pebesma, 2018).

5.2.2. Models based on hunting yield data

A Negative Binomial distribution was used for modeling HYS, $N_i \sim NB(\mu_i, \kappa)$, where N_i is the expected relative number of animals in a location i (with $i = 1, 2, \dots, I$; $I = 38494$), μ_i is the expected hunting yield value which vary in space according to covariates, and κ is the overdispersion parameter. We defined the expected hunting yield in log scale to be a linear function of the covariates and a spatial random effect $\omega(s_i)$:

$$\log(\mu_i) = \beta * X_i + \omega(s_i),$$

where β are the linear effect of covariates (bio2, alt, Eu, lc10, lc30, lc40, lc90, lc100, lc130, area_log) and $\omega(s_i)$ is a spatial random effect.

The spatial random effect was specified through a Nearest Neighbor Gaussian Process (NNGP; Datta et al. 2016), which enables the expected response to vary smoothly across space and in relation to the covariates. This approach relies on a spatial covariance matrix, which was defined by an exponential function. The exponential function uses the Euclidean distance between sampling units and a set of spatial parameters (θ): the variance parameter, σ^2 , and the spatial decay parameter, ϕ .

$$\omega(s_i) \sim \text{MVN}(0, \mathbf{C})$$

$$\mathbf{C}(s, s', \boldsymbol{\theta})$$

when $\boldsymbol{\theta}$ defined by the exponential function: $p(s, s') = \sigma^2 * \exp(-\phi \cdot d_{\text{Euc}})$

The model was fitted in a Bayesian framework using Markov Chain Monte Carlo (MCMC) algorithms with the spAbundance 0.2.2 R package (Doser et al. 2024). We used normal prior for beta coefficients (mean=0 and var=1), uniform prior for kappa (a=0, b=100), uniform prior for ϕ (a=0.0470 and b=0.2) and inverse gamma for σ^2 ($\alpha = 2$ and $\beta = 1$). We run three chains (length=100,000, burning=10,000, and thinning parameter=10). Model convergence was assessed by visual inspection of traceplots, the Gelman-Rubin diagnosis Rhat ($0.9 < \text{Rhat} < 1.1$; Gelman & Rubin, 1992) and the Effective Sample Size (ESS; Gelman et al. 2025; Vehtari et al. 2021). The model required approximately 4.57 days (6580 min) to complete the run on a computer equipped with 64 GB of RAM and 2.90GHz processor.

Model output was downscaled to make predictions at 10x10km using the EEA reference grid (European Environment Agency, 2024). The predictions were made with both the linear effects of covariates (environmental-only predictions) and with the linear effects of covariates and the spatial random effect (spatial predictions). Predictions were only projected inside of the recognized distribution range of the species (Scandura et al. 2022).

5.2.3. Comparison of models based on hunting yield

We compared the downscaled predictions (environmental-only and spatial) with those reported for the wild boar in [Chapter 3](#) (see [S5-1](#); regional model hereafter). Quantitatively, we assessed the predictions (environmental-only and spatial) by summing the predicted harvested values at 10 x 10 km resolution. We also compared the predicted credible intervals values with the confidence interval of the regional model. To evaluate spatial patterns, we computed Spearman correlations between predictions and also with those of the regional model at distribution range level. Moreover, we performed specific comparisons for Spain, France, Italy, and Poland. The countries were selected to account for differences in the resolution of their reported datasets, ranging from the finest reported observation units (hunting grounds) to broader units (NUTS2).

5.3. Results

Our results showed no evidence of multicollinearity among selected predictors ($VIF < 2$). The results further indicated that 80% of the variables used to fit the model did not include in the zero in their credible interval, highlighting their importance for model performance (**Table 5.2**). The model results also showed that the variance of the spatial dependence parameter was the largest of all the linear effects of the covariates. All the model parameters, except for the intercept which exhibited poor mixing, reached convergence (**Table 5.2** and **Figure S5-2.1**).

Table 5.2. Covariate estimates from the negative binomial model. Mean, Standard Deviation (SD), quantiles (2.5%, 50%, 97.5%), convergence criteria (Rhat), effective sample size (ESS).

	Mean	SD	2.5%	50%	97.5%	Rhat	ESS
Abundance (log scale):							
(Intercept)	3.2626	0.0411	3.1863	3.2628	3.3416	1.1328	52
bio_02	-0.0245	0.0264	-0.0788	-0.0231	0.0246	1.0894	164
elev	-0.1058	0.0205	-0.1461	-0.1058	-0.0659	1.0718	253
lc40	0.0801	0.0093	0.0620	0.0800	0.0986	1.0114	1472
Eucmean	-0.0204	0.0104	-0.0408	-0.0204	-0.0001	1.0019	1196
lc10	-0.1822	0.0110	-0.2036	-0.1821	-0.1603	1.0545	1029
lc30	0.0116	0.0087	-0.0051	0.0116	0.0293	1.0091	1619
lc90	0.0573	0.0098	0.0379	0.0573	0.0762	1.0449	543
lc100	0.2094	0.0096	0.1904	0.2094	0.2280	1.0212	1384
lc130	0.0259	0.0085	0.0091	0.0259	0.0427	1.0625	995
area_log	1.0552	0.0132	1.0286	1.0558	1.0803	1.0204	345
Spatial Covariance:							
sigma.sq (σ^2)	1.3864	0.0298	1.3295	1.3860	1.4453	1.0032	1433
phi (ϕ)	0.0486	0.0000	0.0486	0.0486	0.0487	1.0012	13281
NB overdispersion:							
Kappa	1.6984	0.0255	1.6493	1.698	1.749	1.0109	995

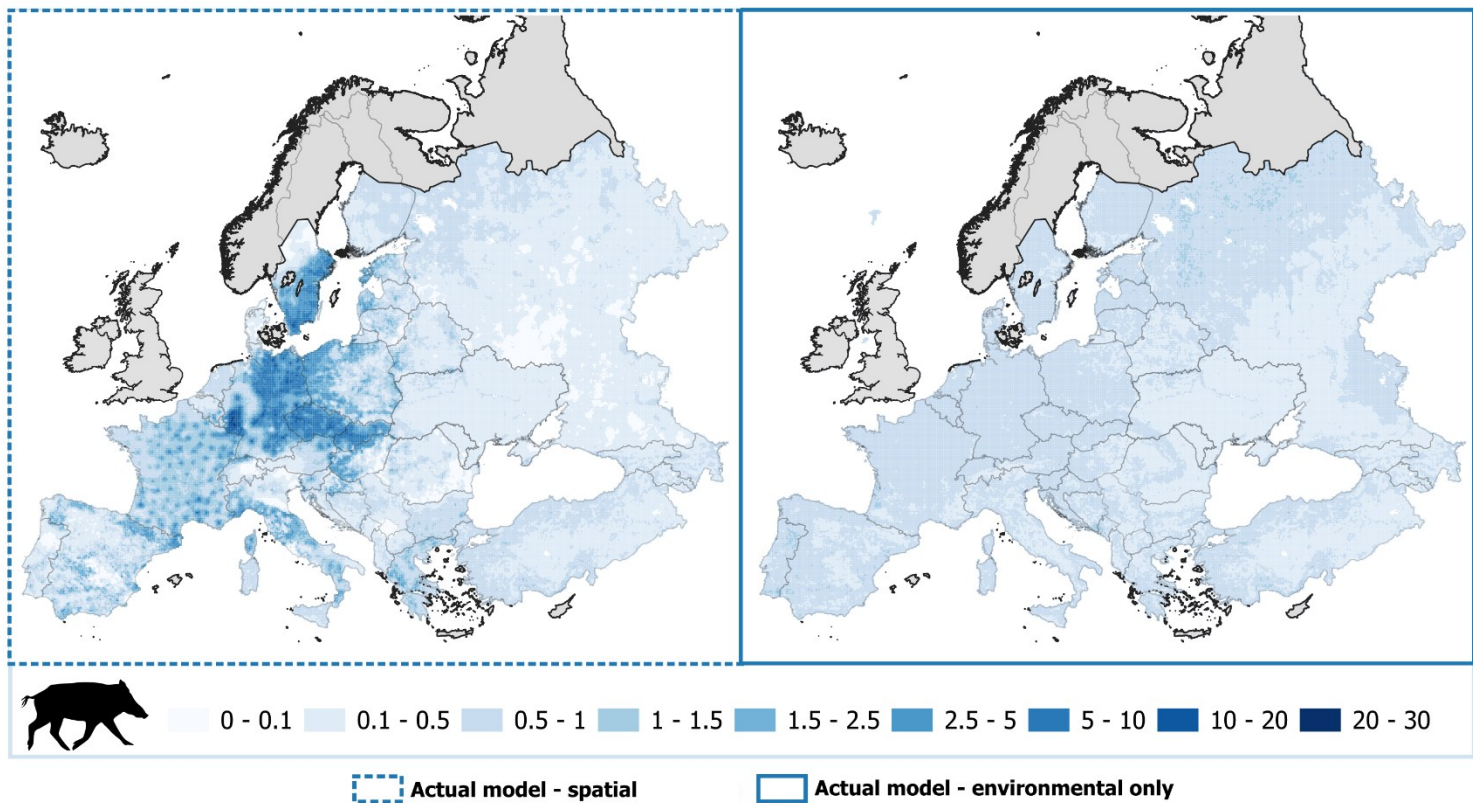


Figure 5.1. Model output downscaled to make predictions at 10x10km using EAA grid. The predicted harvested wild boar (individuals/km²) were made just with the linear effects of environmental covariates (environmental-only, right) and also including the linear effects of environmental covariates and the spatial random effect (spatial, left map).

Prediction spatial patterns appear similar to the regional model for certain countries, such as Spain, but differ for others, such as Russia. Environmental-only predictions appear to produce a pattern more similar to that of the regional model than spatial ones, except for Russia (**Figure 5.1**). Nevertheless, predicted densities (hunted individuals/km²) of the environmental-only predictions are substantially lower and displayed a narrower credible interval than the other two predictions (**Figure 5.2A**).

The correlation in spatial patterns seems to vary depending on the scale of comparison (**Figure 5.2B**). At a global scale, environmental-only and spatial predictions seem to have similar patterns, as well spatial predictions with the regional model, which would indicate a general concordance between locations with low and high values of the species abundance. At national scales, the correlation between predictions differs. Spain exhibited a moderate correlation between all predictions (correlation coefficients > 0.30), whereas other countries, such as France or Italy, showed lower correlation values between the environmental-only and spatial predictions. In contrast to these countries, Poland displayed the highest correlation between environmental-only and spatial predictions, with both predictions showing strong correlations with the regional approach.

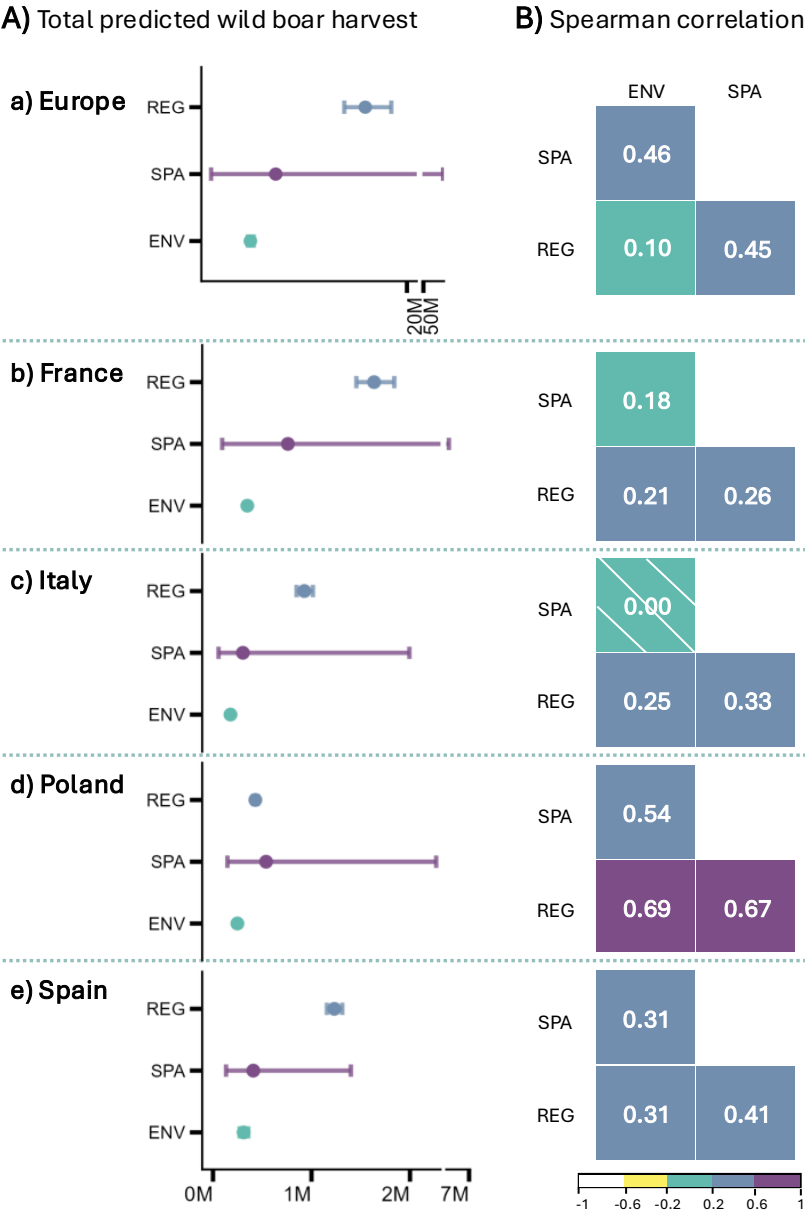


Figure 5.2. Model comparison of predicted wild boar harvested in the 10 x 10 km grid. (A) Total number is shown for environmental-only predictions (teal; ENV), spatial predictions (muted purple; SPA), and predictions from the regional previous model (slate blue; REG). Dot points show the sum of the median total predicted values. Error bars show the sum of the lower (2.5) and upper (97.5) credible intervals. (B) Spearman correlation coefficients between abovementioned prediction patterns. All figures were generated for wild boar distribution range in Europe (a), France (b), Italy (c), Poland (d), and Spain (e).

5.4. Discussion

Previous studies on wild boar distribution and abundance have developed independent regional models to address the challenges posed by spatial heterogeneity and shifting species-environment relationships. By fitting models separately for different regions, these approaches allow greater flexibility in the estimated relationships and generally improve the reliability of abundance estimates and spatial patterns (Acevedo, Quirós-Fernández, et al., 2014; ENETWILD-consortium, Acevedo, et al., 2019). However, regionalization of the models can lead to abrupt transitions between regions and may fail to represent continuous gradients across large spatial extents, resulting in unrealistic or unprecise values and patterns at regional boundaries (Cushman et al., 2010; ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022). We developed a continent-scale model incorporating spatial dependence in the covariance structure to capture gradual spatial variation in wild boar abundance across Europe and results shown that its performance is critically affected by the spatial resolution and homogeneity of input data.

The inclusion of spatial structure has previously demonstrated promising predictive performance at smaller spatial scales (ENETWILD-consortium, Fernández-López, et al., 2020; Norberg et al., 2019). As expected, our results show that adding spatial dependence produces smoother spatial patterns and a continuous abundance gradient at the continental scale (**Figure 5.1; Figure S5-**

3.1). However, the modeling framework adopted here does assume that environmental effects are constant across the study area. Selected predictors include some variables that were only relevant in subsets of regions in the regional model, while excluding others that could not be consistently incorporated across Europe (see [Chapter 3](#)). Under this framework, part of the non-stationarity and unmodeled spatial heterogeneity are implicitly absorbed by the spatial random effect, but it is not flexible enough to accommodate difference environmental responses. Consequently, differences in the sign and magnitude of estimated coefficients relative to regional approaches are not unexpected.

Despite the overall smoothness of the predicted patterns, the spatial predictions produced unusual or implausible shapes in countries characterized by coarse or heterogeneous data, such as France and Russia. These artefacts are not solely a consequence of the spatial model specification but are also strongly linked to a classic change-of-support problem (Gotway & Young, 2002; Pacifici et al., 2019). Hunting yield data are collected over territorial units that vary widely in size across Europe (*e.g.*, from 0.01 km² to 104,163 km²), whereas predictions were generated at a much finer and regular spatial resolution (100 km² grid). This mismatch between the spatial support of observations and predictions can strongly affect spatial covariance estimation, and, ultimately, the reliability of model outputs.

From a modeling perspective, spatial dependence through a covariance structure requires the specification of geographic coordinates for each observation unit to construct the covariance matrix. When using an exponential covariance function, spatial dependence is governed by the spatial variance parameter (σ^2), the decay parameter (ϕ), and the Euclidean distance between locations. If the spatial autocorrelation range defined by ϕ is smaller than the Euclidean distance between observation-unit centroids, spatial effects may not propagate effectively across space, leading to unreliable or erratic predictions. In contrast, if the spatial autocorrelation range is larger than the Euclidean distance, spatial effects may propagate over long distances and may lead to a broad over-smoothing spatial pattern. Moreover, representing aggregated observed data (e.g., hunting yields) as point-level without an explicit change-of-support step can lead to misallocation of observed quantities across space. In this study, the observed HY for each territorial unit was effectively associated with its centroid, and used to estimate the covariance structure, while predictions were generated at grid-cell centroids. This approach does not redistribute the observed quantity across the area of the original units but instead propagates the signal from its centroid according to the spatial correlation structure. Observation units were highly heterogeneous in size, though smaller units were more numerous in this case. Consequently, the spatial autocorrelation range (ϕ) tended to be small relative to some large units and when observation units are large relative to the

spatial scale captured by ϕ , predictions may lead to unreliable or misleading patterns.

Explicit change-of-support approaches that reconcile spatial misalignment have been shown to produce reliable estimates when downscaling total abundance (Fernández-López et al., 2025; Gilbert, Pease, et al., 2021). Previous studies have also highlighted the difficulty of producing reliable estimates and predictions when using large observation units for hunting yield data, emphasizing that low spatial resolution can hamper the applicability of such information for wildlife management at finer scales (Bauder et al. 2021; Gilbert et al. 2021). This suggests that patterns obtained for countries such as France, Finland and Russia should be interpreted with caution, whereas countries with finer and more homogeneous data, such as Spain, show spatial patterns more consistent with known abundance distributions. Importantly, countries differ not only in spatial resolution but also in the degree of spatial misalignment between observation units and predictions, resulting in heterogeneous change-of-support effects across Europe.

At the continental scale, comparisons further illustrate how non-stationarity, data resolution and change-of-support jointly limit the transferability of continental-scale predictions. At the European scale, spatial predictions showed only moderate correlation with both environmental-only and the regional predictions, while environmental-only predictions exhibited low

correlation with predictions from the regional model. After the visual inspection of the patterns, these differences likely arise from structural differences in covariate selection between modeling approaches, while spatial dependence effects may further contribute by absorbing variation associated with environmental covariates (Hodges & Reich, 2010; Keil et al. 2014). Consequently, environmental-only predictions may fail to capture effects that are either absorbed by the spatial component or explicitly modeled through region specific coefficients. Under these conditions, comparing spatial patterns derived from broad-scale models that do not share the same covariate structure can be inherently limiting, particularly evident in country-level correlation analysis.

At the country level, moderate correlations between the environmental-only and the predictions of the regional model were observed in Spain, France and Italy, but not in Poland. This likely reflects differences in both environmental conditions and model specification across regions, reinforcing the importance of accounting for other ways to consider non-stationarity when modeling at continental scales, since the spatial dependence is not enough to capture all environmental variability that cannot be distinguished by the covariates within a single model. Approaches incorporating spatially varying coefficients may offer greater flexibility for modeling species-environment relationships (*e.g.*, Doser et al. 2024; Finley, 2011).

Differences in the size of observation units are also likely to affect predicted patterns, making it essential to reconcile spatial misalignment between observation units and predictions regardless of the modeling framework. In France, coarse spatial units relative to the spatial decay range likely exacerbate change-of-support effects when predicting at finer resolution. In Italy, the lack of correlation between the spatial predictions with either the environmental-only or the predictions of the regional model may be driven by heterogeneous data resolution and spatial gaps. While spatial dependence effects may improve predictions under some conditions, they can also lead to overfitting and including them has been found to be especially sensitive for making predictions when data is unevenly distributed or there are spatial gaps (see 4). These results underscore the importance of homogeneous territorial units and minimal spatial gaps for the reliable large-scale spatial modeling.

An alternative strategy explored here was to generate predictions based solely on environmental covariates, which avoids some of the challenges posed by heterogeneous territorial units. This approach often produces more coherent large-scale spatial patterns, reinforcing the idea that environmental variables largely explain wild boar abundance. However, in countries with high-quality resolution data, such as Spain, spatial predictions achieved higher correlations with previous predictions than environmental-only predictions. Conversely, environmental-only predictions tend to underestimate abundance relative to

models including spatial dependence, as the variability explained by the spatial parameters is intentionally excluded. Moreover, spatial dependence can obscure the influence of environmental covariates, complicating ecological interpretation (Hodges & Reich, 2010; Keil et al. 2014). Consequently, fitting a model with spatial dependence but generating predictions without them may improve the visual coherence of spatial patterns when observation units are highly heterogeneous, while producing inaccurate estimates of abundance (**Figure 5.2A**).

In summary, including spatial dependence in models through a covariance structure provides a powerful tool for generating smooth, continuous abundance patterns at continental scale, but their performance is strongly constrained by heterogeneity in the spatial resolution of input data and by non-stationarity. Large differences in the size of observation units introduce change-of-support effects that limit the reliability and interpretability of predictions in several regions. While environmental covariates explain part of the large variation of wild boar abundance, spatial dependence can improve predictions where high-quality data are available, at the cost of reduced interpretability of environmental covariates effects. Together, these results highlight the need to explicitly consider non-stationarity, data resolution and change-of-support when selecting modeling strategies for large-scale wildlife abundance.

Acknowledgements

ENETWILD Wildlife: collecting and sharing data on wildlife populations, transmitting animal and human disease agents (OC/EFSA/ALPHA/2016/01).

Data accessibility statement

Data cannot be shared due to international data-sharing agreement restrictions.

Code used for modeling is open and available at [github](#).

S5 Supplementary information

S5-1 Modeling framework

Modeling decisions are taken throughout the entire modeling process from data input to model projection. Each decision involves trade-offs, with advantages and drawbacks, that depend on each specific context. Decisions may therefore vary according to the species being modeled, its ecology, distribution range, and management. No single option is universally optimal, as these factors govern data availability and structure, and consequently influence all the subsequent modeling steps.

Here, we present alternative options for each decision point (**Figure S5-1.1**). This framework intends to facilitate reproducibility by explicitly documenting the methodological choices underlying the statistical analyses. Dotted darker boxes indicate modeling components corresponding to the regional framework applied for wild boar described in detail in the methodology [section 3.2.5.2](#) of [Chapter 3](#).

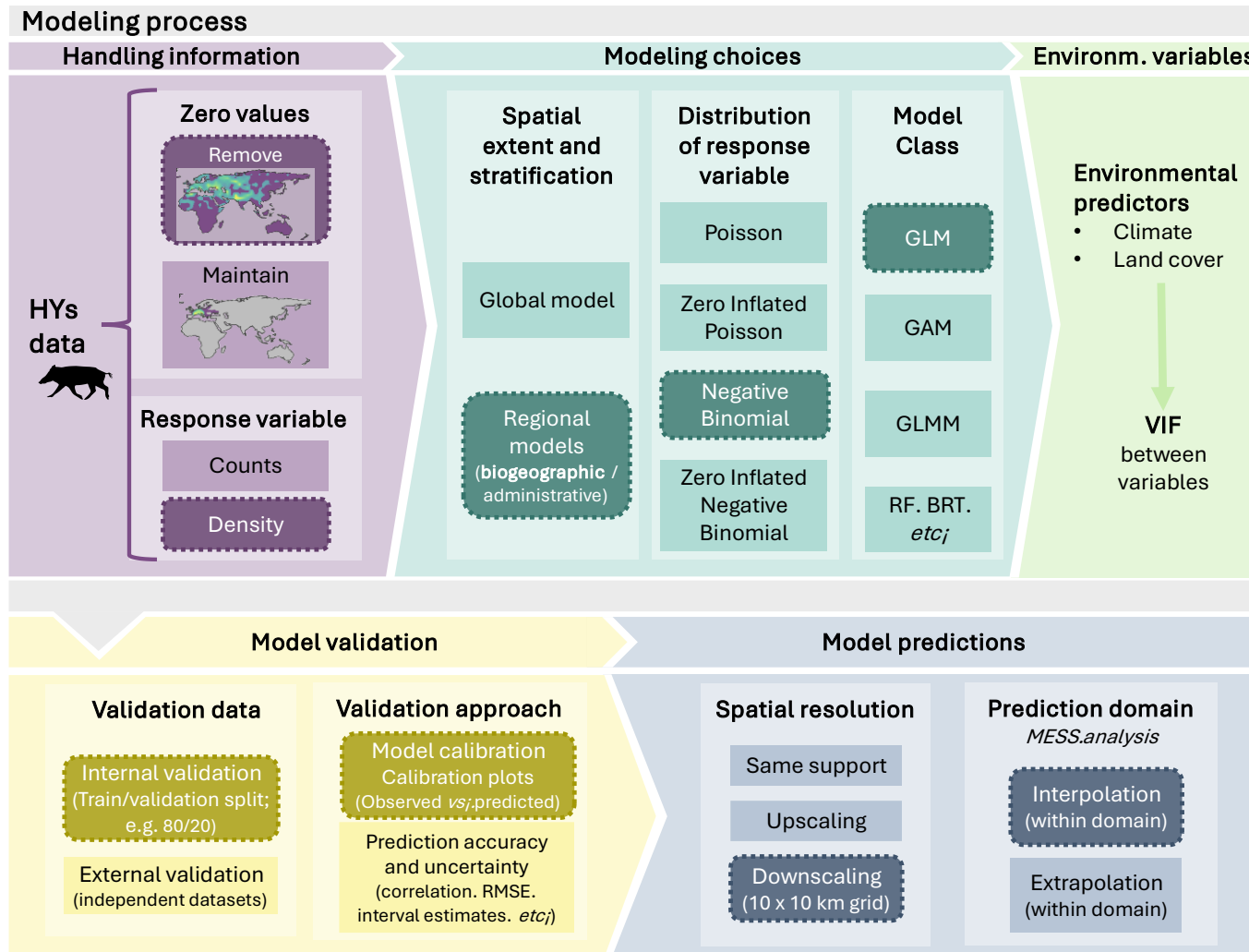


Figure S5-1.1. Conceptual framework summarizing alternative modeling choices. Selected options for regional wild boar abundance estimation appear filled with darker colors and a dotted line

S5-2 Assessing model convergence

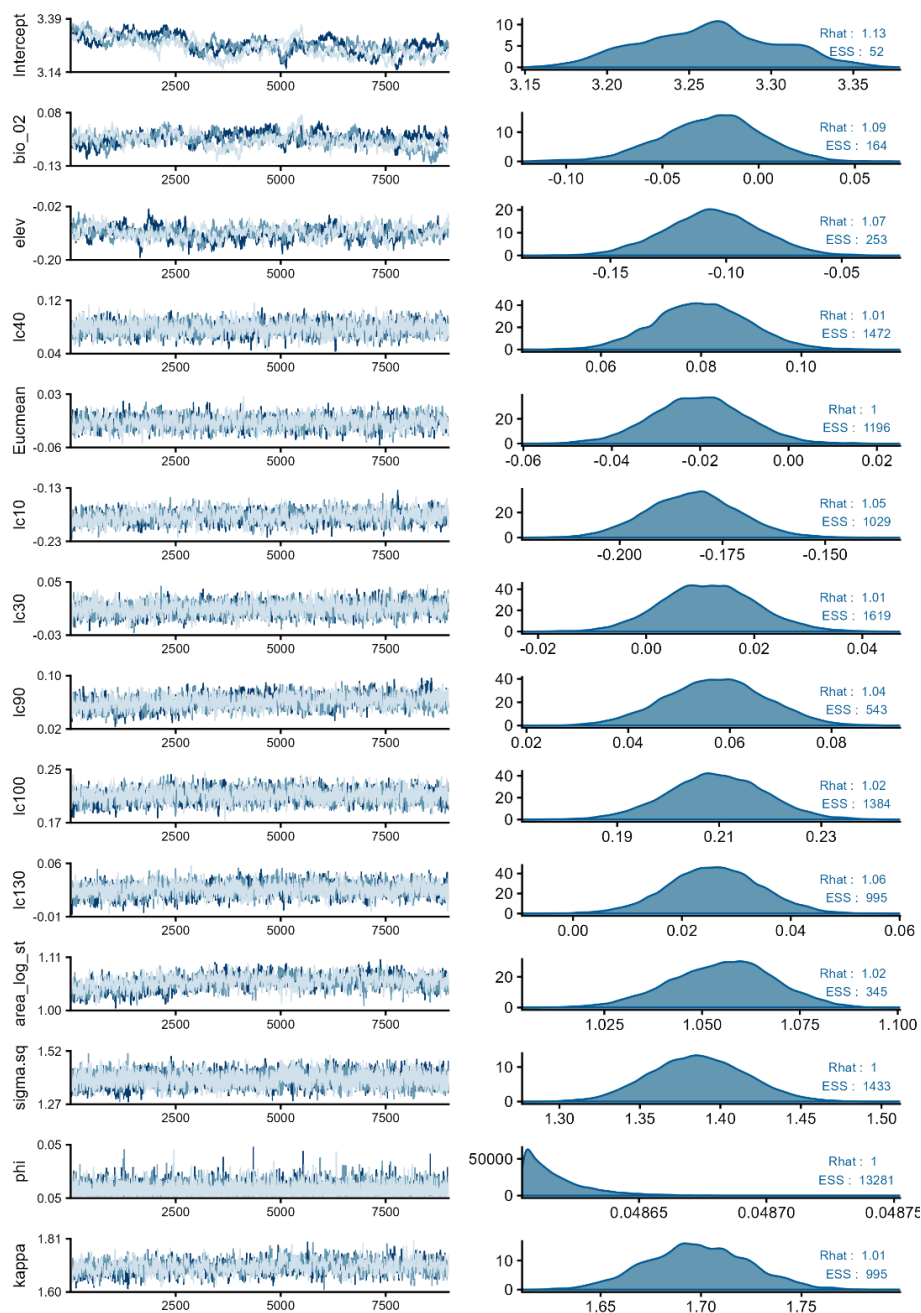


Figure S5-2.1. Trace and density plots, Rhat and ESS for assessing convergence of the modeling approach.

S5-3 Spatial patterns between regional borders from the different model approaches (accounting for spatial dependence and regional).

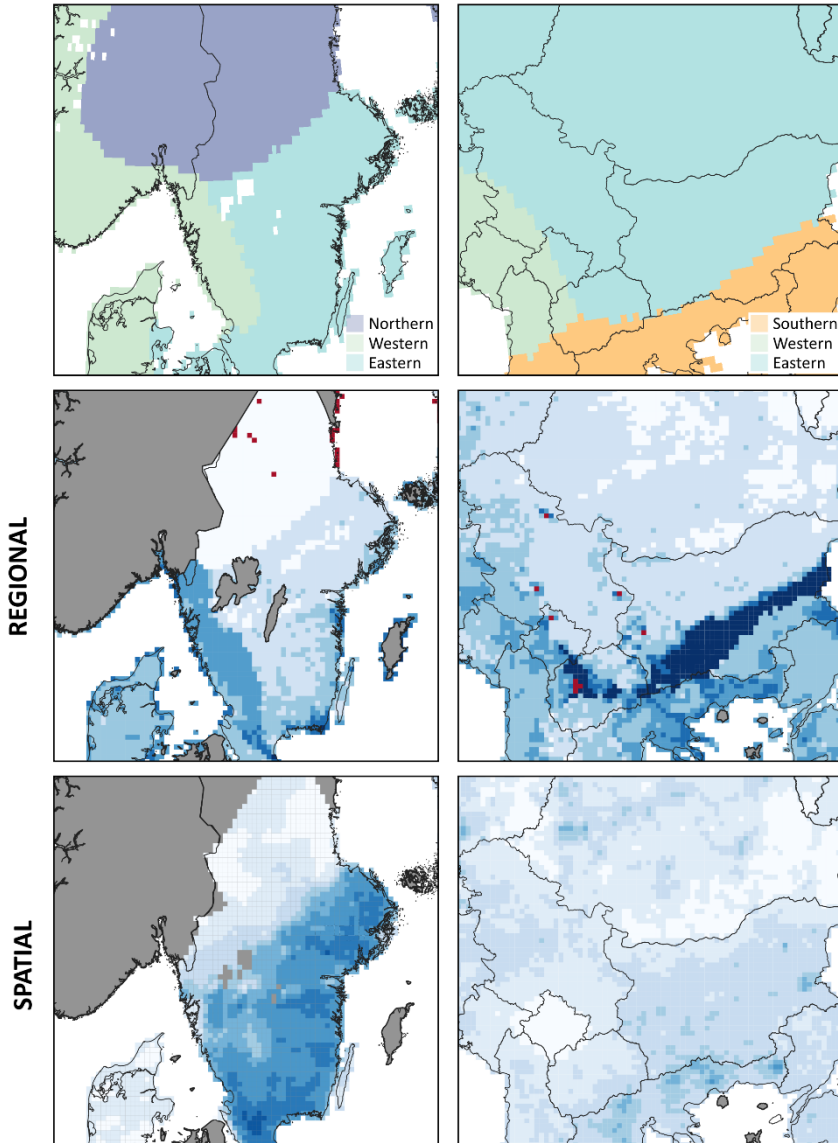
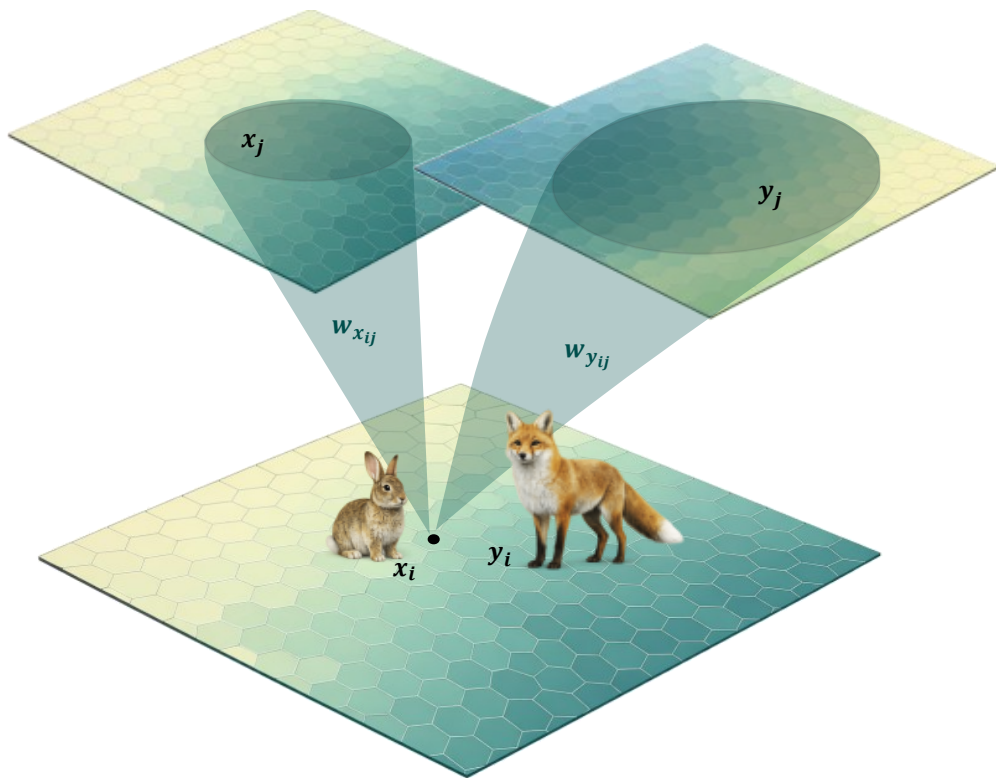


Figure S5-3.1. Comparison of spatial predictions of wild boar relative abundance at bioregion borders in selected European areas. Top panels show bioregions of the selected areas. Central panels show predictions from the regional model, exhibiting abrupt transitions at borders. Bottom panels show predictions from the spatial dependence model, illustrating smooth transitions at frontiers.

6. Assessment of Bivariate Relationships between Spatial Patterns

Revisiting the L index for Wildlife Management and Conservation



Illanas, S., Gómez-Rubio, V., Vicente, J., Acevedo, P. (2025). Assessment of Bivariate Relationships between Spatial Patterns: Revisiting the L Index for Wildlife Management and Conservation. *Ecological Indicators* 175, 113551. <https://doi.org/10.1016/j.ecolind.2025.113551>

Abstract

In wildlife management and conservation, the spatial relationship between two species (*e.g.*, abundance patterns) is often studied through overlapping local information or implementing clustering analysis. However, conventional approaches overlook processes operating at larger spatial scales than the observation unit. Analyses that consider not only a location but also its neighbors, such as the Global L bivariate index (GL) and its Local (LL) measure, can be more appropriate for addressing spatial relationships between two species. The current formulation considers a unique connectivity matrix to define neighbors' structure, assuming both species exhibit the same spatial dependence even when they may differ. We revisited the Global (GL') and Local (LL') indices to incorporate specific connectivity matrices to enhance wildlife applicability. We studied the behavior of the revisited indices through a simulation and a case study of four wildlife species with contrasting movement capabilities. The simulation study revealed the indices' intrinsic characteristics, including smaller GL' values and smoother LL' patterns as the number of neighbors increases. The case study suggested imbalanced coexistence and divergence areas for the species studied, providing meaningful scenarios for wildlife management. The application of species-specific connectivity matrices facilitates the consideration of spatial use characteristics, offering a more reliable understanding of ecological relationships, particularly when the observation unit is smaller than the species' home range. These findings are crucial for determining accurate and ecologically

meaningful connectivity matrices. Overall, the revisited indices offer high flexibility and a comprehensive description of the spatial relationships between ecological indicators.

Key words: Bivariate relationships; Lee's statistics; Spatial overlap; Spatial patterns; Wildlife management

Resumen

En la gestión y conservación de la fauna, la relación espacial entre dos especies (por ejemplo, los patrones de abundancia) son frecuentemente estudiadas a partir de la superposición de la información local o implementando análisis de clústeres. Sin embargo, los enfoques convencionales pasan por alto procesos que operan a mayores escalas espaciales que la unidad de observación. Los análisis que consideran no sólo una localización sino también sus vecinos, como el índice bivariado Global L (GL) y su medida Local (LL), pueden ser más adecuados para abordar las relaciones entre dos especies. Su formulación actual considera una única matriz de conectividad para definir los vecinos, asumiendo que ambas especies tienen la misma dependencia espacial a pesar de que puede diferir entre ellas. Hemos revisitado el índice Global (GL') y Local (LL') para incorporar matrices específicas de conectividad para mejorar su aplicación a la fauna silvestre. Hemos estudiado el comportamiento de los índices revisitados a partir de una simulación y un caso de estudio para cuatro especies con diferentes capacidades de movilidad. La simulación reveló características intrínsecas de los índices, incluyendo valores más pequeños de GL' y más suavizados de LL' cuando el número de vecinos aumenta. El caso de estudio sugiere áreas desbalanceadas de coexistencia y divergencia para las especies estudiadas, aportando escenarios importantes para la gestión de la fauna. La aplicación de las matrices de conectividad específicas a cada especie ofrece un entendimiento más realista de las relaciones ecológicas entre especies, particularmente cuando la unidad es

más pequeña que el área de campeo de las especies. Estos hallazgos son cruciales para determinar matrices de conectividad precisas y ecológicamente significativas. En general, los índices revisitados ofrecen mayor flexibilidad y una descripción exhaustiva de las relaciones espaciales entre los indicadores ecológicos.

6.1. Introduction

The analysis of spatial patterns has been well established since the 20th century, when univariate spatial autocorrelation coefficients such as Moran I or Geary c were developed (Geary, 1954; Moran, 1950). These indices assess whether a variable has a spatial pattern in a global context by testing the hypothesis that the variable is randomly distributed in space. Subsequently, Local Indicators of Spatial Association (LISA) were developed. These indicators assign a value to each location based on the relative influence of each location on the magnitude of the global statistic (Anselin, 1995; Getis & Ord, 1992). Later, bivariate relationships between spatial patterns were explored, leading to the development of new spatial indices (Anselin, 2019; Lee, 2001).

The Global L bivariate index (hereafter GL) analyzes the bivariate association between two variables including a location (i) and its neighboring areas (j) in both X and Y (Lee, 2001). It effectively captures the extent to which the bivariate association is spatially clustered by its Local L (LL) measure. LL can reveal areas of spatial heterogeneity or homogeneity in the relationship between variables. Meanwhile, the local bivariate Moran index quantifies the relationship between a variable X at location i and a variable Y at neighboring locations j. However, it does not consider the relationship between the variables X-Y at i nor the nearby j regions of X. Thus, bivariate indices are valuable tools for assessing how two variables are spatially structured and provide a more realistic picture of the spatial association between spatial patterns (*e.g.*, ecological indicators).

Despite this, their use has been limited to a few studies, ranging from social problems such as urban crime, to human health diseases and diversity gradients in terrestrial plants (*e.g.*, Cerrejón et al., 2022; Gómez-Rubio et al., 2025; Kim et al., 2018; Mateo et al., 2016).

In wildlife management and conservation studies, the relationships between spatial patterns (*e.g.*, species abundance, species richness, environmental variables, anthropogenic factors) are often analyzed using spatial overlap of locations (*i.e.*, observation units). This analysis typically involves discretizing variables into categories (*e.g.*, low, medium, high; Vargas-Amado et al., 2022), or using approaches to relate continuous variables (*e.g.*, Acevedo et al., 2010a; Ruiz-Rodríguez et al., 2024). Spatial overlap is the methodological basis of Gap Analysis (Scott et al., 1993), and it is sometimes used to identify elements of biodiversity that are underrepresented in designated conservation areas (*e.g.*, Bosso et al., 2024; Estrada et al., 2008; Hu et al., 2024). While it offers a straightforward and easily interpretable solution, it does not consider the surrounding context when assessing the relationships between variables.

It is important to acknowledge the relevance of neighboring regions in ecological studies. This is because ecological processes, and therefore their associated spatial patterns, can operate at larger spatial scales (spatial dependence) than the spatial resolution of the data (Qi & Wu, 1996). Therefore, determining the spatial relationships between spatial patterns requires defining specific and ecologically meaningful neighbors to each one, as they may be

different, for instance, due to differences in movement capabilities when assessing the interspecific relationship in species distribution patterns. However, the formulation of the GL and LL indices only permits the utilization of the same connectivity matrix to assess the spatial dependence between variables.

In the attempt to broaden the applicability of GL and LL to wildlife management and conservation studies, we aimed to revisit the formulation of the indices (GL' and LL') to enhance their flexibility by incorporating variable-specific connectivity matrices. We hypothesized that bivariate spatial indices are strongly dependent on the definition of the connectivity matrices. By incorporating species-specific neighbors' structure, we can enhance our ability to assess the spatial relationships between two (or more) spatial patterns. Realistic assessments are essential when they can support wildlife management and conservation. To assess our working hypothesis, we utilized simulated data to describe the importance of neighbors in both GL' and LL' indices by considering three different scenarios: no neighbors, the same connectivity matrix for both variables, and different connectivity matrices for each variable. We then explored the performance of the revisited indices in a case study by examining the spatial interspecific relationships at a regional scale between the abundance patterns of wildlife species with contrasting movement capabilities: European rabbit (*Oryctolagus cuniculus*), Iberian hare (*Lepus granatensis*), red fox (*Vulpes vulpes*), and wild boar (*Sus scrofa*).

6.2. Materials and methods

6.2.1. Revisiting the GL and LL indices

The GL index simultaneously captures the spatial co-patterning and spatial clustering of two variables (*e.g.*, X and Y), incorporating information about the univariate spatial association of both variables. The index is defined by the same binary connectivity matrix (**V**) for X and Y variables. Locations considered neighbors have a value of 1 in the binary connectivity matrix and those not considered neighbors a value of 0. The GL index is defined in Lee (2001) as:

$$GL_{X,Y} = \frac{n}{\sum_i (\sum_j v_{ij})^2} \frac{\sum_i [(\sum_j v_{ij}(x_j - \bar{x}))(\sum_j v_{ij}(y_j - \bar{y}))]}{\sqrt{\sum_i (x_i - \bar{x})^2} \sqrt{\sum_i (y_i - \bar{y})^2}} \quad (\text{Equation 1})$$

where n is the number of locations, v_{ij} is the value of the spatial binary connectivity matrix between location i and its neighboring location j , $\bar{x}$ and $\bar{y}$ are the mean values of X and Y variables, x_i and x_j are the values of the X variable at location i and j , respectively, and y_i and y_j are the values of the Y variable at location i and j , respectively.

The **Eq. 1** can be simplified by utilizing the spatial weight connectivity matrix (**W**). The spatial weight matrix is a row-standardized version of **V** (*i.e.*, the sum of the weights of a given location's neighbors is equivalent to one) and GL is expressed in Lee (2001) as:

$$GL_{X,Y} = \frac{\sum_i [(\sum_j w_{ij}(x_j - \bar{x}))(\sum_j w_{ij}(y_j - \bar{y}))]}{\sqrt{\sum_i (x_i - \bar{x})^2} \sqrt{\sum_i (y_i - \bar{y})^2}} \quad (\text{Equation 2})$$

where w_{ij} is the value of the spatial weight connectivity matrix between location i and its neighboring location j .

The removal of the sum of the i values over each location results in the decomposition of GL into Local measures (LL), thereby capturing the point-to-point association of a place and its surroundings. Therefore, LL was derived from **Eq. 2** and expressed in Lee (2001) as:

$$LL_{i_{X,Y}} = \frac{n (\sum_j w_{ij}(x_j - \bar{x}))(\sum_j w_{ij}(y_j - \bar{y}))}{\sqrt{\sum_i (x_i - \bar{x})^2} \sqrt{\sum_i (y_i - \bar{y})^2}} \quad (\text{Equation 3})$$

Lee (2001) realized that “locations with an identical value might be differently recognized in measuring a bivariate association if their relations with neighboring locations are different”. However, **Eq. 1-3** did not permit consideration of different neighboring locations depending on the target variables. This option is of particular importance in the context of wildlife management and conservation, as the influence of a location on its neighbors and the neighbors on a given location may exhibit different spatial dependencies depending on the species. Consequently, we defined separate binary connectivity matrices for each X and Y variable ($\mathbf{V}_X$ and $\mathbf{V}_Y$, respectively) and transformed them into spatial weight connectivity matrices ($\mathbf{W}_X$ and $\mathbf{W}_Y$). Considering species-specific spatial weight matrices, the global bivariate spatial association (GL') for generic weight matrices is expressed as:

$$GL'_{X,Y} = \frac{n}{\sqrt{\sum_i (\sum_j w_{x_{ij}})^2} \sqrt{\sum_i (\sum_j w_{y_{ij}})^2}} \frac{\sum_i [(\sum_j w_{x_{ij}}(x_j - \bar{x}))(\sum_j w_{y_{ij}}(y_j - \bar{y}))]}{\sqrt{\sum_i (x_i - \bar{x})^2} \sqrt{\sum_i (y_i - \bar{y})^2}} \quad (\text{Equation 4})$$

where $w_{x_{ij}}$ and $w_{y_{ij}}$ are the values of the spatial weight connectivity matrix between location i and its neighboring location j for X and Y variables, respectively.

And the local bivariate spatial association (LL') is then defined as:

$$LL'_{i_{X,Y}} = \frac{n (\sum_j w_{x_{ij}}(x_j - \bar{x}))(\sum_j w_{y_{ij}}(y_j - \bar{y}))}{\sqrt{\sum_i (x_i - \bar{x})^2} \sqrt{\sum_i (y_i - \bar{y})^2}} \quad (\text{Equation 5})$$

The relationship between GL' and LL' is expressed in **Eq. 6**. It should be noted that, given the row-standardization of weights, the value of the global index GL' is equal to the average of the local index LL' .

$$GL'_{X,Y} = \frac{\sum_i LL_{i_{X,Y}}}{\sqrt{\sum_i (\sum_j w_{x_{ij}})^2} \sqrt{\sum_i (\sum_j w_{y_{ij}})^2}} = \frac{\sum_i LL_{i_{X,Y}}}{n} \quad (\text{Equation 6})$$

6.2.2. Simulated dataset

Following the seminal paper of Lee (2001), we developed four hypothetical variables comprising 37 hexagon cells (locations). The values of the four variables ranged from 10 to 60 and shared the same statistical properties in terms of mean and standard deviation (mean of 34.86 and standard deviation of 22.56). Two of these variables exhibited clustered patterns, but an asymmetrical distribution of the values (1 and 1'; **Figure 6.1**). The remaining two exhibited random patterns with an asymmetrical distribution (2 and 2'; **Figure 6.1**). We considered three connectivity scenarios to assess bivariate relationships: no neighbors (*i.e.*, each cell grid was connected only to itself), same connectivity for both variables (in this case $GL'=GL$ and $LL'=LL$), and different connectivity matrices for each variable (**Figure 6.1**). To illustrate the behavior of the GL' and LL' under the different scenarios, we calculated both for each variable with itself and with its asymmetrical variable for the three different connectivity scenarios (**Figure 6.1**).

We released version 1.0.0 of this data and analysis code on Zenodo (Illanas, Gómez-Rubio, et al., 2025). It is also available at [github](https://github.com).

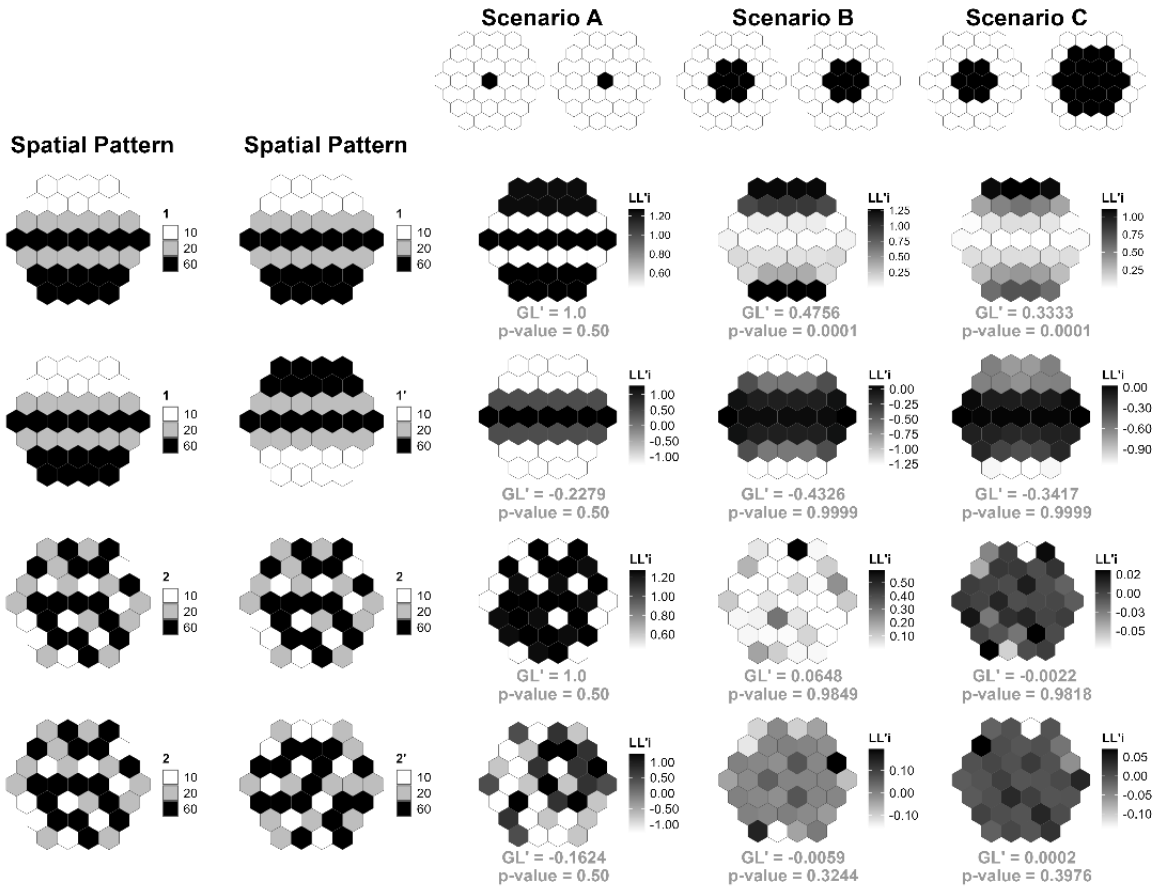


Figure 6.1. The hypothetical variables 1, 1', 2 and 2' for assessing the behavior of GL' and LL' in three connectivity scenarios: no neighbors (Scenario A), same connectivity matrix for both variables (Scenario B), and different connectivity matrices for each variable (Scenario C). The black color indicates a 1 value (connected), and the white color indicates a 0 value (no connected). The LL' values for the three connectivity scenarios are shown. The GL' values and p-values obtained for each pair of variables and scenario are included.

6.2.3. Case of study: data collection, study species and neighbor scenarios

We collected hunting data (as a proxy of relative abundance; Fernández-López et al., 2024) for the Castilla-La Mancha region (approximately 80,000 km² in central Spain; **Figure 6.2**) for European rabbit, Iberian hare, red fox, and wild boar, from the 2014/2015 to the 2021/2022 hunting seasons at hunting ground level (n= 5768). For each hunting ground, we calculated the maximum hunting

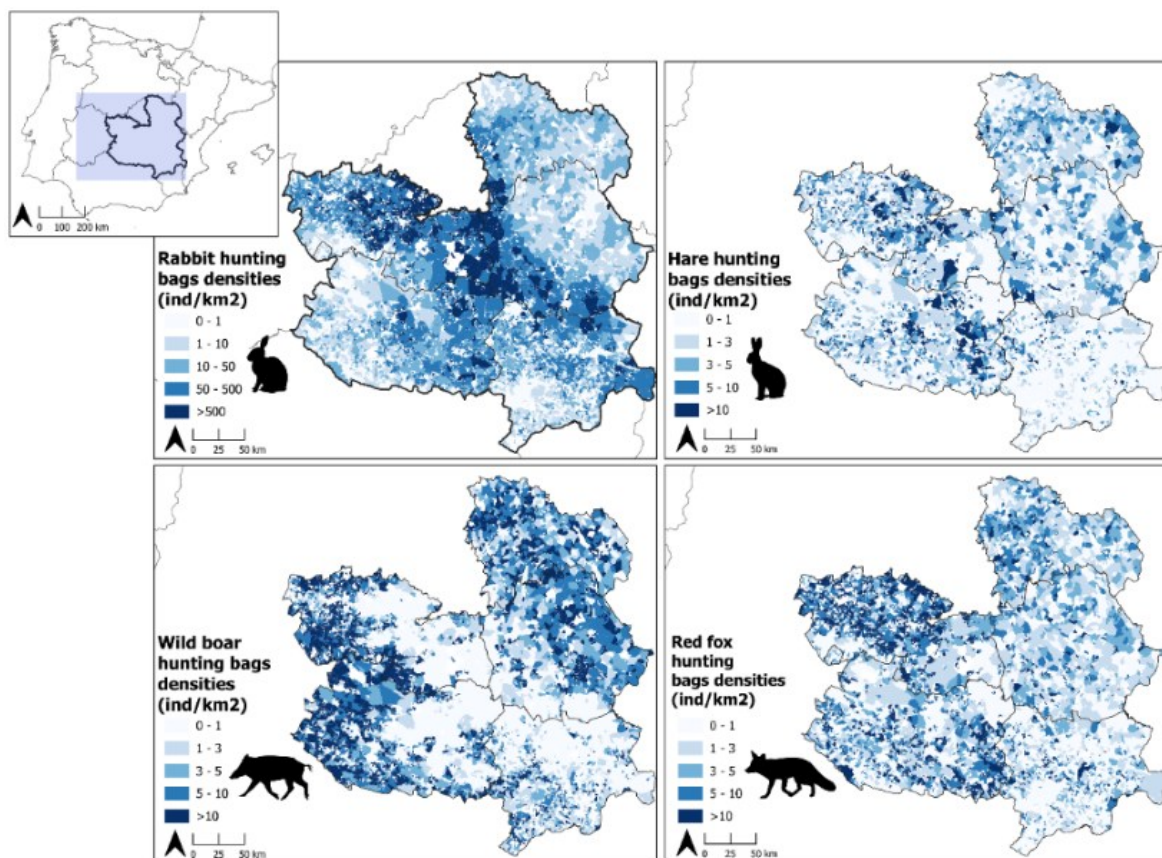


Figure 6.2. Hunting yields densities (individuals hunted/km²) of the European rabbit, the Iberian hare, the wild boar, and the red fox at hunting ground level in the Castilla-La Mancha region of central Spain.

yield recorded (Rodríguez-Ruiz et al., 2023) and transformed them to hunting yield densities (*i.e.*, the hunting yields divided by the surface area of the hunting ground), given that hunting ground surfaces differed considerably ($\mu=12.25 \text{ km}^2$, $\sigma=19.92\text{km}^2$). The packages utilized for data management were tidyverse 2.0.0 (Wickham et al., 2019) and sf 1.0-14 (Pebesma, 2018) in R Statistical Software (v4.3.1; R Core Team, 2022).

We utilized the hunting yield densities of the species to explore ecological interspecific relationships between European rabbit and red fox, European rabbit and wild boar, and Iberian hare and red fox, three ecological meaningful interspecific relationships (**Figure 6.3a**). The study species have different movement capabilities. This variation in movement give rise to distinct neighbor relationships, which are contingent on the species. We determined the neighbor scenarios by distance criteria due to the casuistic of data geometries of the hunting yields (*i.e.*, irregular polygon geometries). Therefore, we used the daily relationships mentioned, we calculated GL' and LL' (**Figure 6.3c**). We employed a range species distance, defined as the distance traveled by an individual in a day. The daily ranges were 1.5 km/day for the European rabbit, 4.1 km/day for the Iberian hare, 7.8 km/day for the wild boar, and 16.9 km/day for the red fox (Mitchell & Balogh, 2007; Palencia et al., 2022, 2023). We defined the binary connectivity matrix per species ($\mathbf{V}_{\text{RABBIT}}$, $\mathbf{V}_{\text{HARE}}$, $\mathbf{V}_{\text{RED.FOX}}$, $\mathbf{V}_{\text{WILD.BOAR}}$) and transformed each to the spatial weight connectivity matrix ($\mathbf{W}_{\text{RABBIT}}$, $\mathbf{W}_{\text{HARE}}$, $\mathbf{W}_{\text{RED.FOX}}$, $\mathbf{W}_{\text{WILD.BOAR}}$; **Figure 6.3b**) using the spdep 1.2-7 package. Finally, for each ecological

interspecific permutation test, generating 10,000 random permutations for each pair of species associations (Bivand, 2022; Bivand & Wong, 2018; Bivand et al., 2013).

To have a better understanding of the abundance pattern relationships between species, we grouped LL' values into intervals to identify areas of spatial divergence (where only one species is abundant; LL' with negative values) and different levels of spatial convergence (when both species are absent/scarse or are abundant; LL' with positive values). We used the fourth quartile to define the intervals (*i.e.*, 25%, 50%, 75%, 100%; Acevedo et al., 2010). The interval that

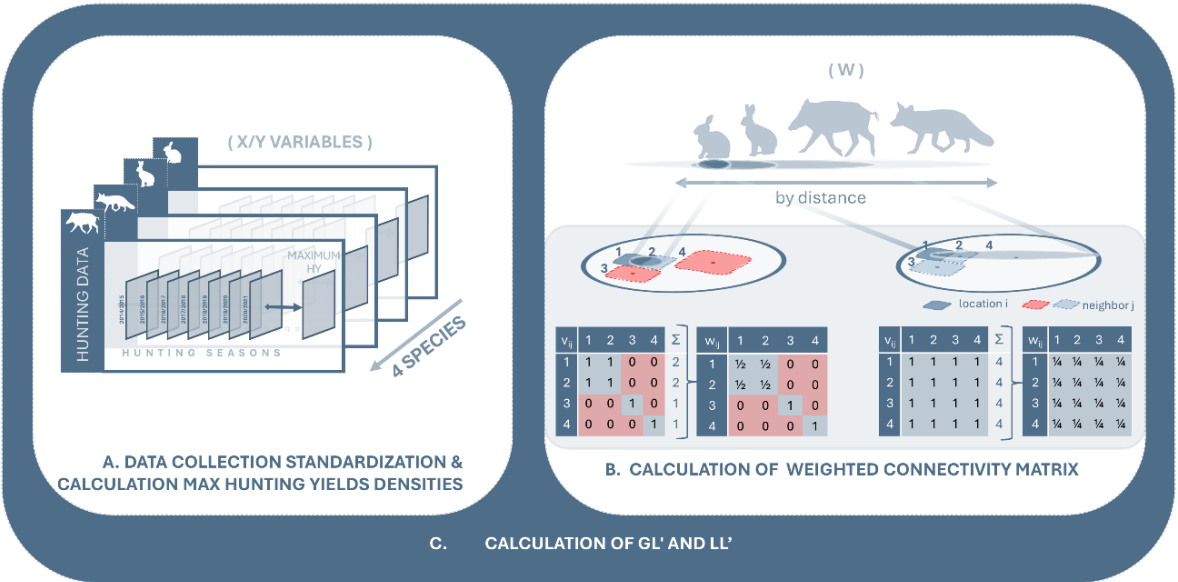


Figure 6.3. The study case analysis framework is outlined from the data collection to the calculation of GL' and LL'. Example of determination of neighbor structure by distance among centroids. In this example, location i (1) and neighbor j (2, 3, 4) are classified as neighbors (blue) if the daily range of the species is larger than the Euclidean distance between their polygons, and as non-neighbors (red) if the Euclidean distance between them is higher than the daily range distance.

encompassed by zero was divided into two to differentiate between the negative and positive values of the index within that interval. Finally, we estimated the mean and the 95% confidence interval of the hunting yield density for each species per interval. This methodological approach enabled us to elucidate the species-specific circumstances within each interval and to describe their interspecific biogeographical relationships (Acevedo et al., 2010; Real et al., 2022).

6.3. Results

6.3.1. Simulation dataset

The results demonstrate that different connectivity scenarios result in different GL' values and LL' spatial patterns. In the scenario of no neighbors (*i.e.*, Scenario A, simple overlap), LL' exhibits a spatial pattern directly related to the value of the variables at location i . However, this pattern changes when the same connectivity matrix is considered (Scenario B; **Figure 6.1**). Furthermore, the spatial patterns also change when comparing scenarios with identical connectivity matrices for both variables and different connectivity matrices for each variable (Scenario C). The latter scenario gives rise to a smoother spatial pattern, as each cell contributes with smaller LL' values (**Figure 6.1**). For variables with the same aggregated patterns and values, the largest positive LL' values (always positive) occur when the lowest or the highest values of variables coincide (**Figure 6.1** row 1). When the patterns are inversely related, we find the

opposite relationship: the lowest, negative, LL' values occur when the lowest for one variable and highest values for another coincide (**Figure 6.1** row 2). Variables with random patterns exhibit a narrower range of LL' values compared to aggregated patterns under scenarios B and C. In other words, random variable patterns result in smoother spatial patterns (**Figure 6.1**).

6.3.2. Study case

GL' indicates greater value similarities between the red fox and European rabbit or Iberian hare than between rabbit and wild boar (**Figure 6.4**). Conversely, LL' values indicate substantial differences in the spatial patterns of the bivariate associations (**Figure 6.4**).

A common pattern of convergence areas (*i.e.*, when the abundance of both species is over or under the mean) is exhibited by all pair in the southeastern part of the region, where hunting yield densities for the study species are mostly low (**Figure 6.2** and **Figure 6.4**). In contrast, the distribution of negative values, which represent divergence areas (*i.e.*, where the abundance of one species is over the mean and the abundance of the other species is under the mean), appears more patchy and highly dependent on the specific species pair associations (**Figure 6.4**).

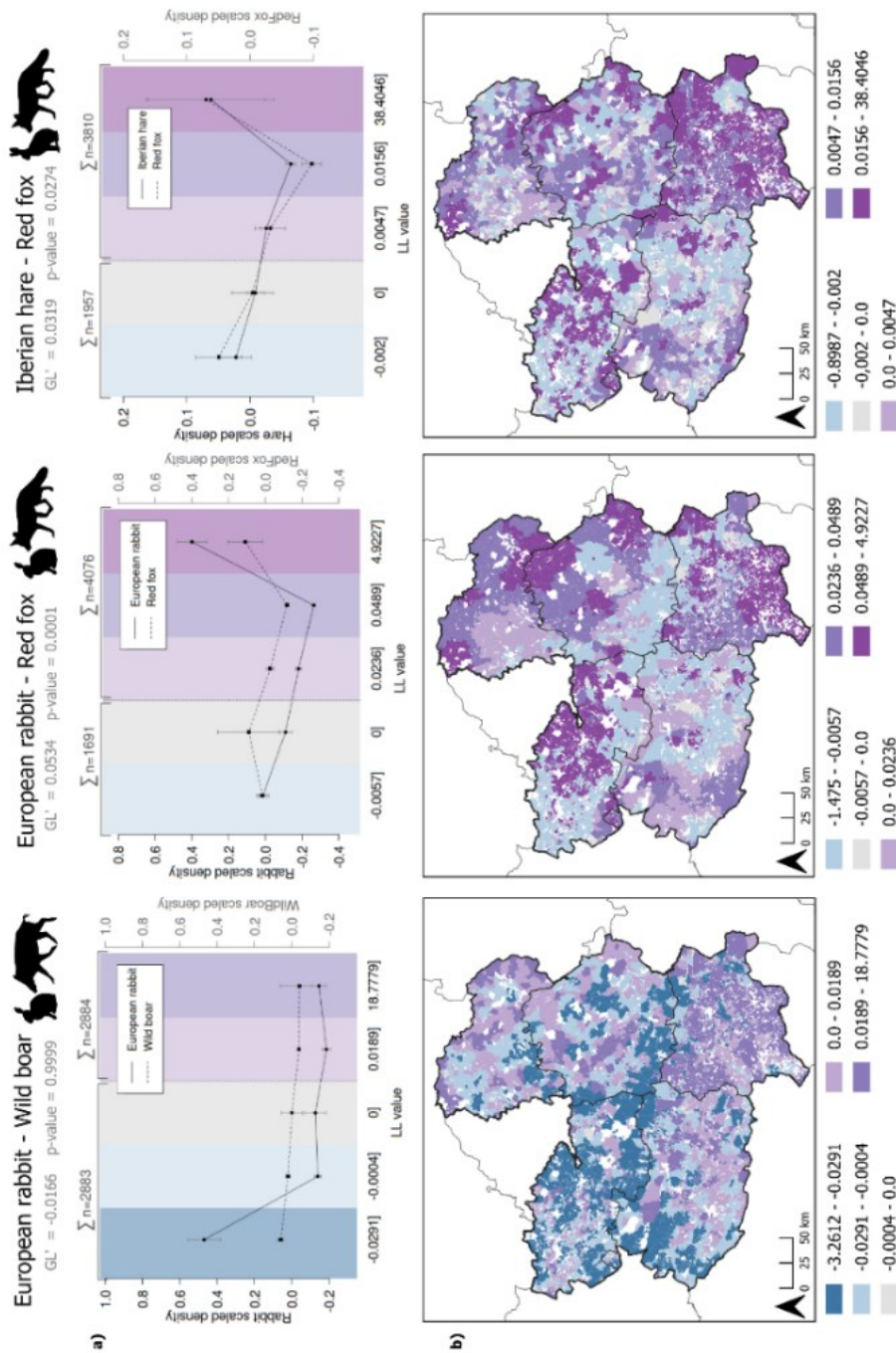


Figure 6.4. Characterization of divergence and convergence areas for each pair of species associations derived from LL' values in terms of species hunting yield density (a) and spatial location (b). $\sum n$ represents the number of locations for the divergence area (LL' negative values) and for the convergence one (LL' positive values); see text for further details. GL' values and p-values obtained in the study case for each pair of associations are included.

6.4. Discussion

Spatial indices, including GL and LL, have been used in studies on diseases, pollution or contaminants, ecosystem services, inert beings, sessile species analysis, or a combination of them (Canton et al., 2023; Cima et al., 2022; Ding et al., 2022; Liu et al., 2020; Mateo et al., 2016; Ochoa-Hueso et al., 2021). Nonetheless, the application of these methods in wildlife management and conservation has been limited primarily due to the challenge of incorporating different spatial dependence depending on the species under analysis. We revisited the GL and LL bivariate indices with the aim of incorporating the possibility of considering different connectivity matrices depending on the species. The flexibility in defining different neighbors allows for consideration of the different scale that a process can operate or influence its spatial range. Consequently, the incorporation of species-specific connectivity matrices is expected to broaden their versatility in this field (*e.g.*, Geary's c or Getis-Ord, G_i^* extensions; Wang & Lam, 2020).

Simulations revealed that the consideration of different connectivity matrices for each variable has implications for the GL', and therefore LL' values obtained. To better understand how spatial dependence affects the connectivity matrix and, consequently, GL', we implemented three different connectivity scenarios on a set of hypothetical variables with varying spatial patterns. It was observed that the differences between a location and its surroundings diminishes with an increase in the number of neighbors, particularly in scenarios where the

variables exhibit a random pattern. In both scenarios, GL' and LL' values decreased (**Figure 6.1**; see also Canton et al., 2023). This intrinsic characteristic of GL' and LL' underscores the importance of considering appropriate connectivity matrices when implementing the indices.

For the case study, we considered the distance neighbor approach to define the connectivity matrices, using the movement distances traveled for the wildlife species under consideration. This formulation allowed for analyzing the relationship between species with contrasting movement patterns, such as wild lagomorphs with small home ranges and carnivores and/or ungulates with larger ones. The results showed a positive GL' when the species abundance patterns were more similar, indicating convergent patterns (*e.g.*, Iberian hare – red fox), while negative GL' was obtained when the species displayed divergent patterns (*e.g.*, European rabbit – wild boar; **Figure 6.2**). The LL' index provides more detailed insights into species associations than spatial overlap, enabling a description of the spatial pattern of their relationship and identifying areas where these patterns change. Interestingly, we found that divergence areas for all species associations predominated on the western side of the study region, while convergence areas, identified with positive LL' values, were most common in the eastern part (**Figure 6.4b**).

In general, areas of divergence were not predominant. These areas could be interpreted as zones where one of the species may be excluded, which might be related to biotic factors (*e.g.*, competitive exclusion) and/or to environmental

changes (Real et al., 2022). Nevertheless, the association between European rabbit and wild boar appears to be almost balanced, with divergence and convergence areas almost equally represented (**Figure 6.4a**), suggesting a possible recent shift in the distribution patterns of these two species traditionally linked to forest areas (Calvete et al., 2004). The divergence in the abundance patterns of wild boar and rabbit is expected to be primarily mediated by land use changes and diseases, rather than by a direct effect of competitive exclusion (Delibes-Mateos et al., 2009; Santoro et al., 2023). Meanwhile, the red fox exhibited a similar proportion of convergence areas (in relative terms) with the European rabbit and the Iberian hare (70.7% vs 66.1% of locations; **Figure 6.2a**), suggesting that the importance of these two prey species may be quite similar for this predator. From these interspecific biogeographical relationships, it can be inferred that there are some convergence locations where the red fox seems to depend on these prey species, following their slightly increasing density trends. This finding suggests that lagomorphs play a pivotal role as a resource for this carnivore (Barbar & Lambertucci, 2023). Meanwhile, in other cases this could indicate the presence of alternative resources that a generalist species like the red fox might be exploiting (Delibes-Mateos et al., 2008; Díaz-Ruiz et al., 2013).

We have demonstrated that spatial dependence impacts the values obtained in GL' and LL'. Therefore, it is relevant to emphasize that the matrices should be ecologically meaningful to facilitate adequate interpretations for wildlife management and conservation (Knaap & Rey, 2024). In this regard, it is

essential to determine the spatial dependence contingent on the specific study case. For example, when dealing with livestock datasets, which are also delimited by irregular spatial units, it could be useful to calculate the connectivity matrix by implementing the distance from the border of the livestock farms or to consider weighted edges (Rey et al., 2025). Alternatives to the aforementioned distance-based approaches could be the transformation of the dataset from irregular locations into a regular grid. The application of regular grids has been recently recommended for characterizing wildlife-livestock interface in Spain (Ruiz-Rodríguez et al., 2024). To perform the connectivity matrix for regular grids the most popular method used is contiguity neighbors, which can be implemented under rook or queen adjacency, among others (Chi & Zhu, 2008). Alternatively, an ecological connectivity approach, which considers both distance and the variable difficulty that species face when moving through the landscape, could be employed to perform the connectivity matrix between locations (Unnithan Kumar & Cushman, 2022; Zeller et al., 2024).

The study of spatial association between species at a large scale is essential for effective wildlife management and conservation. The incorporation of species-specific connectivity matrices into the GL' and LL' bivariate indices ensures the flexibility needed for its broad application in wildlife studies. While previous studies employed simpler indices of spatial overlap, the enhanced flexibility and robustness offered by the bivariate GL' and LL' indices facilitate a more precise and realistic assessment of the spatial association between species.

Author contribution

Sonia Illanas: data curation, methodology, formal analysis, visualization, software, writing – original draft. **Virgilio Gómez-Rubio:** supervision, methodology, writing – review and editing. **Joaquín Vicente:** resources, writing – review and editing. Funding acquisition. **Pelayo Acevedo:** Conceptualization, supervision, writing – review and editing. Funding acquisition, project administration.

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S6 Supporting information

S6-1 lee() adapted function for computing global L index (GL') and local L index (LL')

```
lee <- function (x, y, listwx, listwy, n,
                S2 = NULL,
                zero.policy = attr(listwx, "zero.policy"), NAOK = FALSE) {
  if (is.null(zero.policy))
    zero.policy <- get("zeroPolicy", envir = .spdepOptions)
  stopifnot(is.logical(zero.policy))
  n1 <- length(listwx$neighbours)
  n2 <- length(listwy$neighbours)
  x <- c(x)
  y <- c(y)
  if (n1 != length(x) | n2 != length(y))
    stop("objects of different length")
  if (n1 != n2)
    stop("'listwx and listwy objects of different length'")
  xx <- mean(x, na.rm = NAOK)
  yy <- mean(y, na.rm = NAOK)
  zx <- x - xx
  zz <- sum(zx^2, na.rm = NAOK)
  zy <- y - yy
  zzy <- sum(zy^2, na.rm = NAOK)
  lzx <- lag.listw(listwx, zx, zero.policy = zero.policy, NAOK = NAOK)
  lzy <- lag.listw(listwy, zy, zero.policy = zero.policy, NAOK = NAOK)
  if (is.null(S2))
    S2 <- sqrt(sum((unlist(lapply(listwx$weights, sum)))^2)) *
              sqrt(sum((unlist(lapply(listwy$weights, sum)))^2)))
  L <- (n/S2) * (sum(lzx * lzy))/(sqrt(zz) * sqrt(zzy))
  localL <- n * lzx * lzy/(sqrt(zz) * sqrt(zzy))
  res <- list(L = L, localL = localL)
  return(res) }
```

S6-2 lee.mc() adapted function for computing global L index (GL') p-value

```
lee.mc<-function(x, y, listwx, listwy, nsim,
                 zero.policy = attr(listwx, "zero.policy"),
                 alternative = "greater", na.action = na.fail, spChk = NULL,
                 return_boot = FALSE) {
  alternative <- match.arg(alternative, c("greater", "less", "two.sided"))
  if (!inherits(listwx, "listw"))
    stop(paste(deparse(substitute(listwx)), "is not a listw object"))
  if (!inherits(listwy, "listy"))
    stop(paste(deparse(substitute(listwy)), "is not a listy object"))
  if (!is.numeric(x) | !is.numeric(y))
    stop(paste(deparse(substitute(x)), "is not a numeric vector"))
  if (is.null(zero.policy))
    zero.policy <- get("zeroPolicy", envir = .spdepOptions)
  stopifnot(is.logical(zero.policy))
  if (missing(nsim))
    stop("nsim must be given")
  if (is.null(spChk))
    spChk <- get.spChkOption()
  if (spChk && !chkIDs(x, listwx) && !chkIDs(y, listwy))
    stop("Check of data and weights ID integrity failed")
  cards.x <- card(listwx$neighbours)
  cards.y <- card(listwy$neighbours)
  if (!zero.policy && any(cards.x == 0))
    stop("regions with no neighbours found")
  if (!zero.policy && any(cards.y == 0))
    stop("regions with no neighbours found")
  xname <- deparse(substitute(x))
  yname <- deparse(substitute(y))
  wnamex <- deparse(substitute(listwx))
  wnamey <- deparse(substitute(listwy))
  if (deparse(substitute(na.action)) == "na.pass")
    stop("na.pass not permitted")
  na.act <- attr(na.action(cbind(x, y)), "na.action")
}
```



```

x[na.act] <- NA
y[na.act] <- NA
x <- na.action(x)
y <- na.action(y)
if (!is.null(na.act)) {
  subset.x <- !(1:length(listwx$neighbours) %in% na.act)
  subset.y <- !(1:length(listwy$neighbours) %in% na.act)
  listwx <- subset(listwx, subset, zero.policy = zero.policy)
  listwy <- subset(listwy, subset, zero.policy = zero.policy)
}
n1 <- length(listwx$neighbours)
n2 <- length(listwy$neighbours)
parallel <- p_setup$parallel
ncpus <- p_setup$ncpus
cl <- p_setup$cl
res <- boot(xy, statistic = lee_boot, R = nsim, sim = "permutation",
            listwx = listwx,
            listwy = listwy,
            n = n1, S2 = S2, zero.policy = zero.policy,
            parallel = parallel, ncpus = ncpus, cl = cl)
return(res) }
res <- numeric(length = nsim + 1)
for (i in 1:nsim) {
  idx <- sample(1:n1)
  res[i] <- lee(x[idx], y[idx], listwx, listwy, n1, S2, zero.policy)$L
}
res[nsim + 1] <- lee(x, y, listwx, listwy, n1, S2, zero.policy) $L
rankres <- rank(res)
xrank <- rankres[length(res)]
diff <- nsim - xrank
diff <- ifelse(diff > 0, diff, 0)
if (alternative == "less")
  pval <- punif((diff + 1)/(nsim + 1), lower.tail = FALSE)
else if (alternative == "greater")
  pval <- punif((diff + 1)/(nsim + 1))
else pval <- punif(abs(xrank - (nsim + 1) / 2) / (nsim + 1),

```

```
0, 0.5, lower.tail = FALSE)
if (!is.finite(pval) || pval < 0 || pval > 1)
  warning("Out-of-range p-value: reconsider test arguments")
statistic <- res[nsim + 1]
names(statistic) <- "statistic"
parameter <- xrank
names(parameter) <- "observed rank"
method <- "Monte-Carlo simulation of Lee's L"
data.name <- paste(xname, ", ", yname, "\nweights:", wnamex, namey,
  ifelse(is.null(na.act), "", paste("\nomitted:",
    paste(na.act, collapse = ", "))), "\nnumber of
  simulations + 1:", nsim + 1, "\n")
lres <- list(statistic = statistic, parameter = parameter, p.value = pval,
  alternative = alternative, method = method,
  data.name = data.name, res = res)
if(!is.null(na.act))
  attr(lres, "na.action") <- na.act
class(lres) <- c("htest", "mc.sim")
lres
}
```


7. Large-scale Modeling of Wild Ungulate Relative Abundance from a National Camera Trap Network



Illanas. S., Fernández-López, J., Vicente, J., Blanco-Aguilar, J.A., Sereno-Cadierno, J., Fassetta, E., Acevedo, P., Zipkin, E.F. (in prep.). Large-scale modeling of wild ungulate relative abundance from a camera trap network.

Abstract

Large-scale wildlife monitoring is essential for assessing species status and informing management, yet national estimates of ungulate abundance often rely on hunting statistics that can be spatially biased or unavailable where hunting is restricted. Using data from a standardized national camera-trap network deployed across 26 study areas in mainland Spain (2023) our objective was to model relative abundance (site-use intensity) for seven-species wild ungulate community.

We analyzed images from 817 camera-traps sites. Independent detection events were defined as all images of a species recorded within a 60-min window at a camera and aggregated to weekly counts (sampling occasion). We fitted a hierarchical multispecies N-mixture model that separates ecological variation in site-use intensity from imperfect detection. Relative abundance was modeled through a function of macro-scale covariates (elevation, precipitation, slope) and micro-habitat covariates (forest and shrub cover), while detection was modeled using sampling week, camera deployment duration, slope, and canopy height.

Species-specific intercepts indicated substantial heterogeneity in baseline relative abundance and detectability: red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) had the highest relative abundance, whereas fallow deer (*Dama dama*) showed the highest detection intercept, underscoring that abundance and detectability are distinct processes. Environmental effects were largely

species-specific and community-level responses were weak, consistent with heterogeneous habitat requirements across the assemblage. Macro-environmental gradients showed clearer signals than micro-habitat variables, while detectability was driven primarily by temporal sampling variables.

Comparisons with independent data of hunting yield density were generally positive but weak across spatial levels (within study areas and nearby buffers), with global slope credible intervals overlapping zero, suggesting that harvest intensity in our study areas and nearby zones primarily reflect interspecific differences and management/effort variation. Overall, standardized camera-trap networks coupled with multispecies hierarchical models can deliver spatially explicit, internally consistent indices of ungulate relative abundance for national monitoring and provide a complementary evidence base to existing management datasets.

Key words: camera-trap network; multispecies N-mixture models; ungulates; imperfect detection; relative abundance; Spain

Resumen

La monitorización de la fauna silvestre a gran escala es esencial para evaluar el estado de las especies e informar sobre su gestión, aunque las estimas nacionales de abundancia de ungulados suelen basarse en estadísticos cinegéticos que pueden estar espacialmente sesgados o no disponibles donde la actividad cinegética tiene restricciones. Utilizando datos de una red nacional de fototrampeo desplegada a lo largo de 26 áreas de estudio en España peninsular (2023) nuestro objetivo fue modelizar la abundancia relativa (intensidad de uso del sitio) para siete especies de la comunidad de ungulados silvestres.

Analizamos imágenes procedentes 817 estaciones de cámaras trampa. Los eventos de detección independiente se definieron como todas las imágenes de una especie registradas en un tiempo de 60 minutos en cada cámara y se agregaron en conteos semanales (ocasiones de muestreo). Ajustamos un modelo jerárquico N-mixture multiespecies que separa la variación ecológica en la intensidad de uso del sitio de la detección imperfecta. La abundancia relativa se modeló en función de covariables a macroescala (elevación, precipitación y pendiente) y de covariables de microhábitat (cobertura forestal y arbustiva), mientras que la detectabilidad se modeló utilizando la semana de muestreo, el tiempo de funcionamiento de la cámara, la pendiente y la altura del dosel vegetal.

Los interceptos específicos por especie indicaron una heterogeneidad sustancial en la abundancia relativa basal y en la detectabilidad: el ciervo (*Cervus elaphus*) y el jabalí (*Sus scrofa*) presentaron las mayores abundancias relativas, mientras que el gamo (*Dama dama*) mostró el mayor intercepto de detectabilidad, lo que pone de manifiesto que la abundancia y la detectabilidad son procesos distintos. Los efectos ambientales fueron en gran medida específicos de cada especie y las respuestas a nivel de comunidad fueron débiles, en consonancia con los requisitos heterogéneos de hábitat del conjunto de especies. Los gradientes ambientales a macroescala mostraron señales más claras que las variables de microhábitat, mientras que la detectabilidad estuvo impulsada principalmente por variables temporales del muestreo.

Las comparaciones con datos independientes de densidad de rendimientos de caza fueron en general positivas, aunque débiles, para distintas escalas espaciales (dentro de las áreas de estudio y en zonas buffer cercanas). Los intervalos de credibilidad de la pendiente global se solaparon con cero, lo que sugiere que la intensidad de caza en nuestras áreas de estudio, y zonas adyacentes, refleja principalmente diferencias interespecíficas y variación en la gestión y el esfuerzo. En conjunto, las redes estandarizadas de fototrampeo junto con los modelos jerárquicos multiespecie pueden proporcionar índices espaciales explícitos e internamente consistentes de abundancia relativa de ungulados para el monitoreo nacional y constituir una base de evidencia complementaria a los conjuntos de datos de gestión existentes.

7.1. Introduction

Wildlife monitoring underpins the assessment of species status and supports management and conservation decisions (Whittaker et al., 2005). Implementing long-term monitoring programs across broad spatial scales requires substantial financial investment, consistent sampling effort and institutional coordination to ensure standardized protocols and data continuity. In recent years, growing evidence that common species can decline rapidly while others become locally overabundant has highlighted the need to monitor entire communities, not only threatened taxa (Cerri et al., 2026; Delibes-Mateos et al., 2026; Dupont & Dobson, 2025; Leuenberger et al., 2025; Zipkin et al., 2023). This need is particularly acute for wild ungulates, whose population increases and range expansions can generate ecological impacts, conflicts and management challenges (Apollonio et al., 2010; Cerri et al., 2026).

Within the European Union, Member States are required to report the conservation status and abundance of species every six years under Article 17 of the Habitats Directive. However, the lack of standardized and structured national monitoring programs for many mammals has limited the availability of reliable abundance information (Moersberger et al., 2024). As a result, large-scale assessments often rely on hunting statistics as proxies for relative abundance and spatial patterns in common game species (Carvalho et al., 2024; Cerri et al., 2026; Illanas, Fernández-López, Vicente, et al., 2025; Moreno-Zarate et al., 2021).

Harvest data can provide valuable information over broad geographic extents, but hunting is prohibited for some species or in some areas, and reporting can be spatially biased, leading to gaps and uncertainty in the available information (Aubry et al., 2020).

Camera traps offer an alternative and complementary approach for monitoring mammal communities using a single, cost-efficient method that can be deployed consistently through time (Gilbert, Clare, et al., 2021; Wearn & Glover-Kapfer, 2019). Increasing automation in image processing and the availability of standardized sampling protocols have also enabled coordinated camera-trap networks that implement harmonized designs across large areas (ENETWILD-consortium, Guerrasio, et al., 2024; Rooney et al., 2025). Together, these developments create new opportunities for large-scale monitoring, yet most camera-trapping studies remain limited in spatial extent and duration (Bruce et al., 2025).

A central challenge is how to translate inherently local camera-trap detections collected at discrete sites into robust, comparable inference at broad spatial scales (Burton et al., 2015; Steenweg et al., 2017). Each camera trap samples only a small area, yet management questions typically operate at landscape to continental scales, requiring inference beyond the immediate area monitored by individual cameras (Kays et al., 2024; Townsend et al., 2021). This raises a fundamental issue of representativeness: detections from a limited set of camera locations may not reflect wildlife use across the wider landscape,

especially when habitats, human disturbance, or accessibility vary strongly within regions (Barton et al., 2025; Burton et al., 2015). These issues are further amplified in community-wide monitoring, where species differ in detectability and ecological traits (Hofmeester et al., 2019; Zipkin et al., 2010). Standardized camera-trap deployment protocols and sampling designs can help improve the comparability of relative abundance indices across sites, but robust large-scale inference still requires models that explicitly link local detections to broader patterns (Kays et al., 2024). Consequently, there is a growing need for models that leverage locally structured camera-trap data to make robust, large-scale inference across diverse landscapes (Steenweg et al., 2017).

Hierarchical models provide a framework for analyzing camera-trap data by separating ecological variation from observation processes while accounting for imperfect detection (Kéry & Royle, 2016; MacKenzie et al., 2002). This is important since animals are not always detected, even when they are present. In particular, N-mixture models link repeated counts to latent site-level state while estimating detection probability from repeated sampling; that is, repeated counts at the same site allow inference on how many individuals may be present while also estimating how likely they are to be detected (Royle, 2004). Camera traps have been used for estimating abundance or relative abundance indices for species that are not individually identifiable (Allen et al., 2025; Blount et al., 2025; Harris et al., 2024; Kays et al., 2024; Searle et al., 2020; Shamon et al., 2022). To reduce the risk of repeatedly recording the same individuals, study designs often

apply a species-dependent minimum distance between cameras and apply temporal rules (*e.g.*, minimum time between independent events) to ensure that detections are as independent as possible (Harris et al., 2024; Link et al., 2018; Royle, 2004).

At management-relevant scales, this motivates multispecies hierarchical models that estimate comparable, species-specific responses to environmental gradients from local camera-trap detections. Multispecies hierarchical models offer a unified framework for community-level inference across sites, explicitly accommodating interspecific differences in detectability and ecological strategies (Pacifi et al., 2014; Zipkin et al., 2010). Through partial pooling across taxa, these models stabilize estimates for less frequently detected or spatially restricted species and facilitate community-level inference of species-environment relationships (Ayebare et al., 2023; Tilker et al., 2020; Zipkin et al., 2009, 2010).

In this study, we use camera trap data from a standardized national network and multispecies hierarchical models to estimate wild ungulates relative abundance across Spain, where several species have experienced substantial range expansions and population increases (Apollonio et al., 2010; Cerri et al., 2026). The community includes highly generalist species such as the wild boar (*Sus scrofa*), three cervids with different feeding habits and social behaviors (*Cervus elaphus*, *Capreolus capreolus*, and *Dama dama*), mountain ungulates specialists (*Capra pyrenaica* and *Rupicapra pyrenaica*), and introduced species

(*Ovis aries* and *Ammotragus lervia*). We evaluate whether combining a standardized camera trap network with multispecies N-mixture models can capture species-environment relationships and produce robust indices of relative abundance for wild ungulates across Spain. Specifically, we assess whether camera-trap-based indices are consistent with independent large-scale datasets currently used in wildlife management.

7.2. Materials and methods

7.2.1. Study area, camera trap network and sampling design

Our study was conducted in mainland Spain, which covers 494,011 km². Its topography, characterized by six mountain systems, two plateaus and two depressions, and its geographic location produce three main climates: Atlantic, Mediterranean and Alpine (**Figure 7.1a**). Forest surface in Spain has increased in the last decades due to the abandonment of marginal agriculture crops and changing forestry management practices, as well as reforestation and afforestation (Vadell et al. 2016), currently covering approximately the 55% of the country (**Figure 7.1b**).

Wild ungulates were surveyed in forested environments, the primary habitat for wild ungulates (*e.g.*, Acevedo et al., 2011) using a standardized camera-trap network deployed during 2023. Sampling was organized in 26 study areas, representing four different environmental regions: the Atlantic region (north and northwest), the Continental Mediterranean region (plateaus), South

Large-scale modeling of wild ungulate relative abundance from a national camera trap network

Mediterranean region (south and east), and Mountain systems (**Figure 7.1c**).

Study areas encompassed a gradient of hunting and forestry management regimes, ranging from private estates to public national hunting reserves or protected areas such as National parks, where hunting is forbidden. Each study area consisted of a systematic grid with random origin, following the ENETWILD standardized protocol (**Figure 7.1d**; ENETWILD-consortium et al., 2021). We deployed a total of 883 camera traps across the 26 study areas (mean = 30 ; range 14-40), with inter-camera distances varying among study areas (432 m to 1555 m), yielding grid extents of 2.72 km² to 110.41 km² (**Table S7-1.1**). Individual cameras within each grid constitute sampling sites (site = camera).

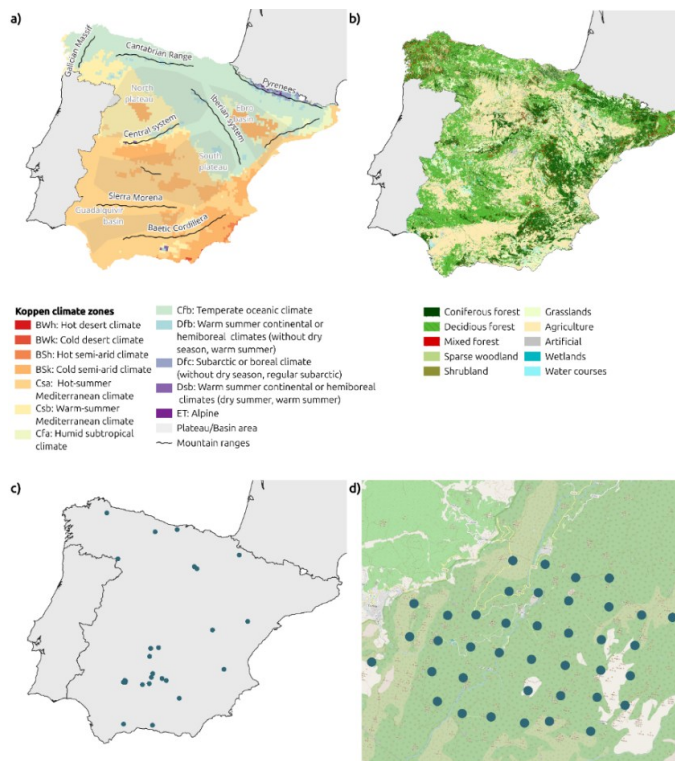


Figure 7.1. Study area and sampling design: climatic regions and main geographical features of mainland Spain (a); land cover classification based on Spanish Forest Map (MFE25; b); Spatial distribution of the 26 sampling locations (c) and schematic representation of the systematic grid design used for camera trap deployment within a sample location (d). Source: Adapted by the authors from Kriticos et al. (2012), topographic map (BCN500), and forest map (MFE25).

Due to logistical constraints, grids were not deployed simultaneously across study areas; however, all cameras within a given study area operated concurrently, ensuring synchronized sampling window within each grid. Deployments started between March and October, and cameras operated for a mean of 51 days (range: 5-114 days). Short deployments were mainly due to camera malfunctions, whereas longer deployments (>70 days) occurred in three study areas where adverse weather conditions delayed equipment retrieval. After data cleaning, 817 camera sites had ≥ 1 weekly sampling occasion with recorded effort that were retained for the analysis. Cameras were set at ~40 cm above ground, facing north and without bait (Sereno-Cadierno et al., 2026).

7.2.2. Species data

Camera-trap images were processed using the DeepFaune (France) v0.6 classification pipeline (Rigoudy et al., 2023) in order to determine species and remove blank images. All classifications with detections were subsequently manually validated by trained observers, with corrections applied when needed.

We defined an independent detection event as all images of a given species recorded within a 60-minute time window at the same camera (Tobler et al., 2008). Detection exceeding this interval were treated as independent events. For each camera and species, we summarized the number of independent events within weekly sampling occasions (Goldstein et al., 2024). Because individual identification of ungulates was not feasible, these weekly event counts were used

as an index of relative abundance (see above). This approach assumes that, at fixed stations, higher local abundance leads to higher detection events (Palencia et al., 2021). For each weekly occasion, we recorded 0 when camera was active and the species was not detected, and NA when the camera was inactive for that week (*e.g.*, due to technical failure or extended periods). To ensure reliable estimation, we excluded species with extremely sparse detections. Accordingly, aoudad (*Ammotragus lervia*) was excluded because it was detected only once across the entire dataset; the final community analyzed included seven species.

7.2.3. Modeling framework

Species-specific relative abundance was estimated using a hierarchical multispecies N-mixture model (Dorazio et al., 2006; Royle, 2004). This framework accounts for imperfect detection by explicitly partitioning the latent ecological process from the observation process. We assumed closure within each camera deployment period; because N is interpreted as a relative abundance index derived from weekly event counts, estimates reflect site-use intensity during the sampling window rather than absolute abundance.

7.2.3.1. Ecological process (relative abundance)

Latent abundance $N_{s,i}$ for species s ($s = 1$ to 7) at camera site i ($i = 1$ to 817) was modeled as a Poisson distribution $N_{s,i} \sim \text{Poisson}(\lambda_{s,i})$, where $\lambda_{s,i}$ is the expected relative abundance value that varies in space according to covariates defined as a function with log link:

$$\log(\lambda_{s,i}) = \beta_s * \mathbf{X}_i$$

where β_s is a vector of species-specific regression coefficients and $\mathbf{X}_i$ is a vector of standardized site-level covariates measured at camera i . All ecological covariates were extracted at the camera site level within a 500m buffer surrounding the x , y coordinates of each deployment. Macro scale variables described broad-scale abiotic conditions and included elevation (meters above sea level) and squared elevation, annual precipitation (mm) and squared precipitation, and slope (percentage degrees). Micro scale covariates described local habitat structure and included shrub cover (percentage) and forest cover (percentage). All ecological covariates were standardized (mean = 0, SD = 1) prior to model fitting. Alternative reduced specifications (macro-only and micro-only) and coefficient-comparison diagnostics are reported in [supplementary information S7-2](#).

7.2.3.2. Observation process (detection)

We accounted for imperfect detection by modeling the observation process during sampling conditional on the number of weekly events present at each camera trap. We assumed that the observed counts, $y_{s,i,k}$, for a species s at a site i during occasion k ($k = 1$ to 18) followed a binomial distribution conditional to the latent relative abundance:

$$y_{s,i,k} \sim \text{Binomial}(N_{s,i}, p_{s,i,k})$$

where $p_{s,i,k}$ represents the detection probability. We model the factors that influence the probability of detecting an individual using a logit link function:

$$\text{logit}(p_{s,i,k}) = \alpha_s * \mathbf{X}_{i,k}$$

where α_s is a vector of species-specific detection regression coefficients and $\mathbf{X}_{i,k}$ is a vector of standardized detection covariates (occasion and site level). At the occasion level, we considered week of detection, to account for seasonal variation in species' behavior that may influence activity patterns and, consequently, detection. We incorporated an effect of sampling effort (operational hours per week) to account for variation in camera performance. At the site level, we included slope (%) and canopy height (m), calculated within a 25 m buffer around each camera trap, to account for local conditions that may affect the effective detection zone. All detection covariates were standardized (mean = 0, sd = 1). Detailed information regarding data sources and spatial resolution of these covariates is provided in [supplementary information S7-3](#).

7.2.3.3. Community-level structure

We employed a community-level approach where species-specific coefficients for the ecological process (β_s) and the detection process (α_s) were modeled as random effects drawn from common, community-level distributions, enabling partial pooling across species (Kéry & Royle, 2016; Royle & Dorazio, 2008). This partial pooling structure allows information to be shared across taxa and stabilizes estimation for less frequent detected species while retaining species-specific responses to environmental gradients. We used weakly informative priors for community-level means and among-species variance components (see [S7-4](#) for full prior specifications).

Models were implemented using Markov Chain Monte Carlo (MCMC) algorithms in the spAbundance 0.2.2 R package (Doser, Finley, et al., 2024), with three chains, 250,000 iterations, 100,000 burn-in iterations, and a thinning parameter set to 10, resulting in 45,000 total posterior samples. Model convergence was assessed through visual inspection of traceplots, the Gelman & Rubin Rhat ($0.9 < \text{Rhat} < 1.1$; Gelman & Rubin, 1992) and the Effective Sample Size ($\text{ESS} > 200$; (Gelman et al., 2025; Vehtari et al., 2021). Further details on convergence are provided in [supplementary information S7-4](#).

7.2.4. Benchmarking between model prediction and an independent dataset

Model predictive ability was evaluated through a comparative analysis against official hunting statistics (hunting yields) as a proxy of relative abundance (*e.g.*, Imperio et al., 2010). These comparisons were conducted at three distinct levels of spatial representativeness: within the study areas, and in surrounding areas within 20 km and 50 km buffer distances. For the within study areas comparison, predicted values were calculated for the specific sampling study areas where camera trap grids were deployed. For the buffer-based comparisons, predicted values were generated for a random subset (30%) of areas within each buffer distance. Buffer distances were chosen to capture nearby areas with broadly comparable environmental conditions to those sampled, while extending inference to a management-relevant spatial scale.

Environmental covariates for both within study areas and nearby zones were standardized using the mean and standard deviation values from the original dataset. We verified that all standardized values remained within a range -3 to 3. This threshold ensured that environmental conditions in the validation localities were represented in the sampled study areas; locations falling outside were excluded from the comparison.

For each species, we derived model predictions relative abundance at the three levels of spatial representativeness, within each study area or nearby study areas. Specifically, we used the posterior median of predicted values (λ_{pred}) and their associated standard errors. For each level of spatial representativeness, we calculated the maximum number of animals harvested per species during the period 2014-2023. Given that locations differ by area size and in order to standardize the number of animals harvested, we transformed it to log hunting yield density (individuals per km²).

At each spatial representativeness, we evaluated the relationship between multispecies model predictions and hunting yield density using a Bayesian linear mixed model fitted with brms R package (v2.23.0; Bürkner, 2017). Species-specific intercepts and slopes were included to allow the relationship to vary among species while partially pooling information across taxa. Random-effects of intercepts and slopes were defined as independent (*i.e.*, uncorrelated) to improve model stability given the small number of species. Uncertainty from the multispecies camera-trap model was propagated into the comparison by

incorporating the standard error of the predicted values as a known observation-level uncertainty in the likelihood via the `se()` argument in `brms` (with `sigma = TRUE`). Fixed effects were assigned Normal (mean = 0, sd = 2) priors. Standard deviations of the species-level random effects were assigned exponential (1) priors. Convergence was assessed using standard diagnostic criteria. Further details on model fitting and convergence are provided in [supplementary information S7-5](#).

7.3. Results

From the deployed camera traps, we obtained 59,022 independent detection events (60-minute threshold). These events comprised 89 species, mainly mammals and birds. Camera traps recorded all eight wild ungulates species present in mainland Spain; however, aoudad was only detected once and therefore excluded from further analyses (**Figure 7.2**). Ungulate accounted for 70.57% of all events ($n = 41,649$), and detection frequency varied markedly among species (**Figure 7.2**).

The multispecies model convergence successfully (see [S7-4](#)). Species-specific intercepts revealed substantial variation among ungulates in both baseline relative abundance and detection probability (**Figure 7.3**). Red deer and wild boar were the most abundant species in the community, with higher values than the remaining ones. However, higher relative abundance values did not necessarily translate into higher detection probability, where fallow deer exhibited the highest

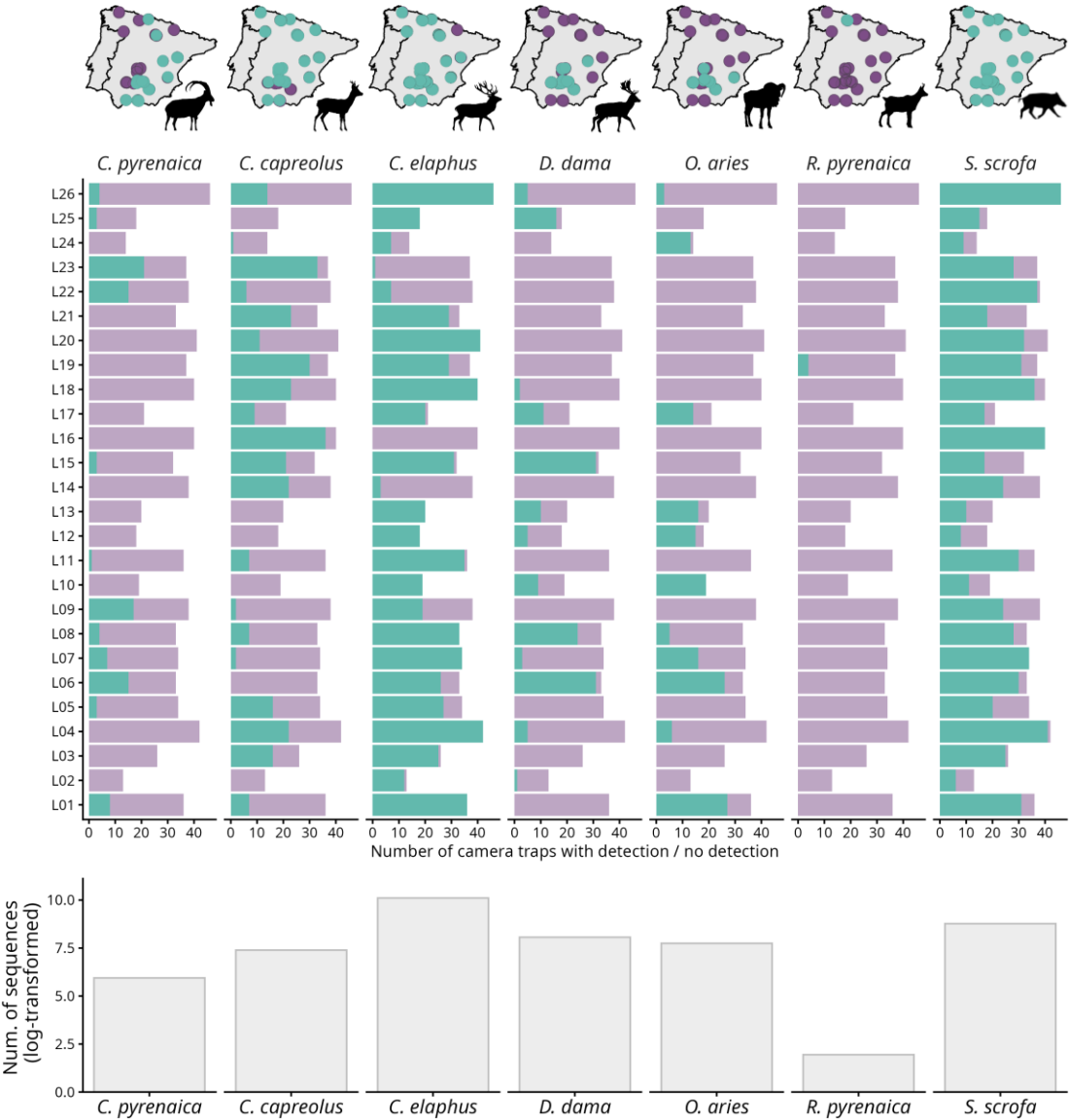


Figure 7.2. Camera trap detection summary by species and study area (L01-L26). Colors indicate detections (teal) and non-detections (purple). The top panel shows the spatial distribution across localities, the middle panel number of camera traps detecting each species per site, and the bottom panel the total number of sequences recorded for each species.

detection intercept. Overall, estimated detection probabilities were low, with all species falling below 0.5 values, and uncertainty increased for the less frequently detected species (**Figure 7.3**).

Environmental covariates explained variation in relative abundance primarily through species-specific responses, with wide credible intervals for several species, while community-level effects were generally weak (**Figure 7.4a**). Macro-environmental covariates tended to show clearer signals than micro-environmental covariates. For example, red deer showed a tendency toward decreasing relative abundance with increasing elevation and precipitation,

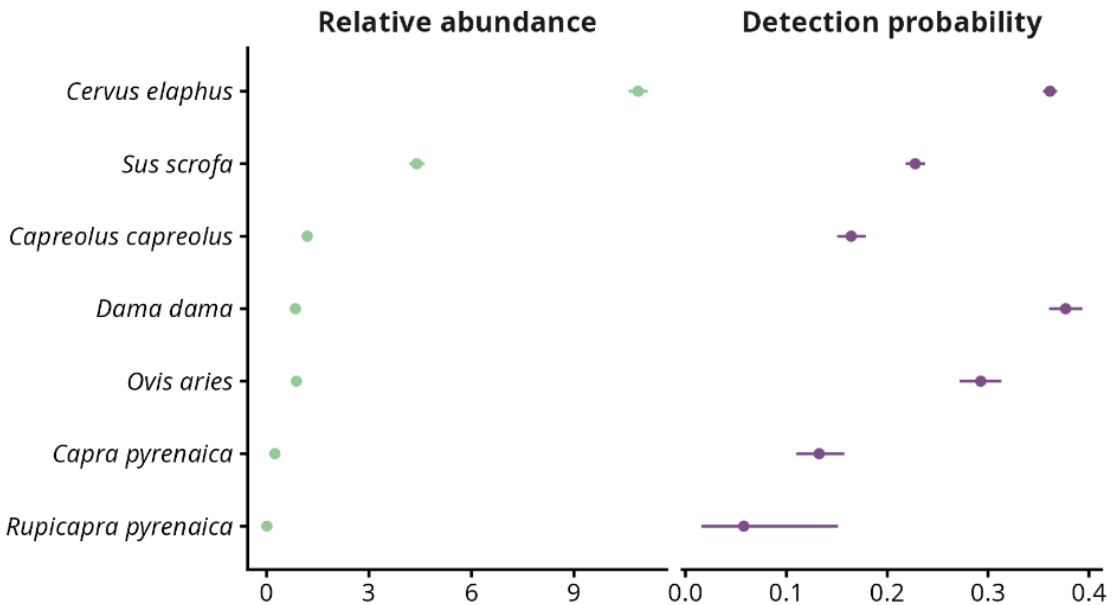


Figure 7.3. Species-specific intercepts for relative abundance (left) and detection probability (right). Points represent posterior medians, and bars represent 95% Bayesian credible intervals (BCI). Species are ranked by their median relative abundance.

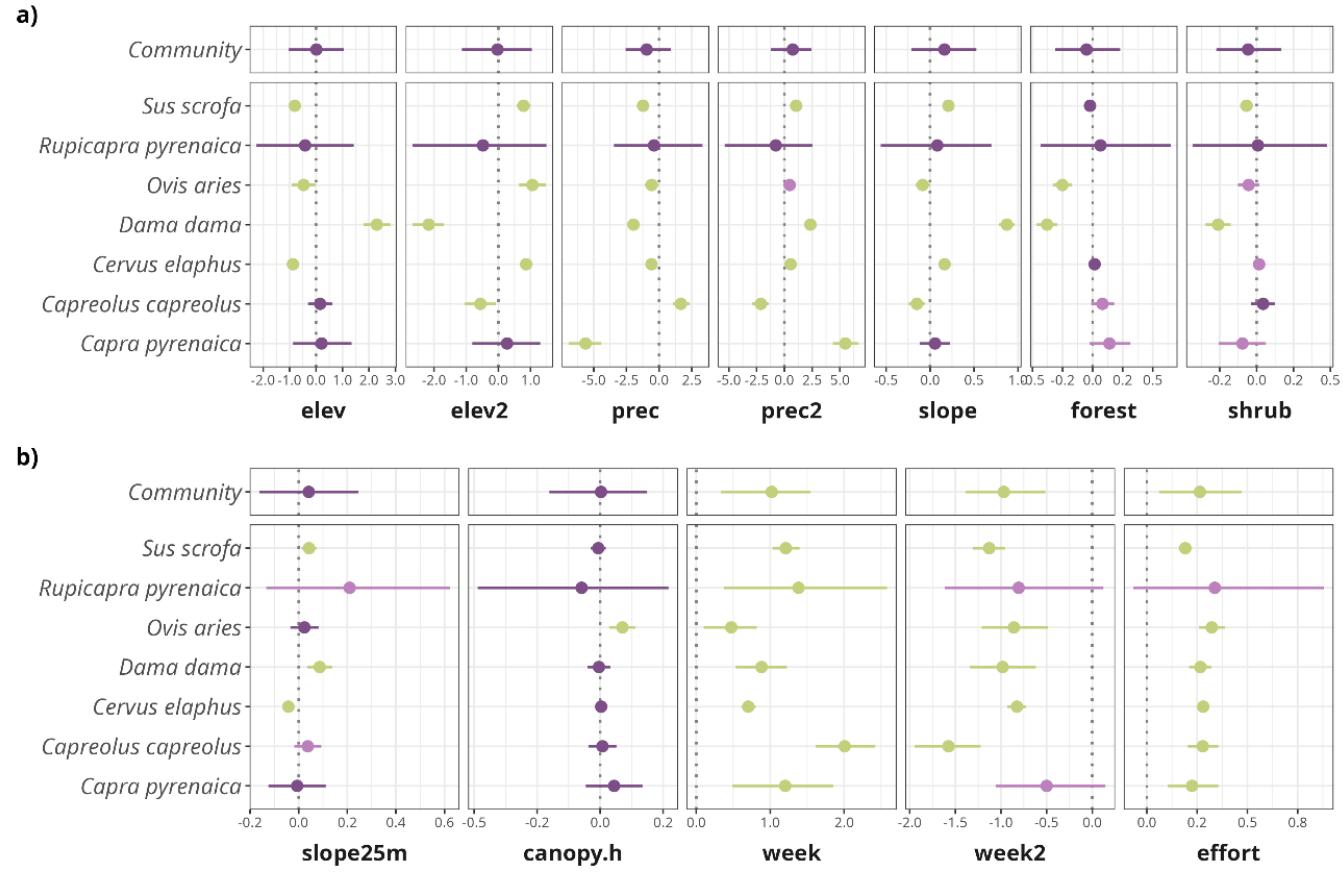


Figure 7.4. Top panel shows beta coefficients (median, 95% Bayesian credible interval (BCI), 75% BCI on the log scale) showing covariates effects on species relative abundance (A). Bottom panel shows alpha coefficients (median, 95% BCI, 75% BCI on the logit scale) showing covariates effects on species detectability. Dark purple bars show relationship in which the 75% BCI overlaps zero, light purple indicates that the 75% BCI does not overlap zero but the 95% BCI does, and green bars indicates that 95% BCI does not overlap zero. The community response is shown in the upper panel of each plot.

whereas wild boar displayed broadly similar responses across environmental gradients with generally modest effect sizes. Iberian wild goat and roe deer showed their clearest associations with macro-environmental covariates, notably precipitation. Southern chamois, the least frequently detected species, exhibited the greatest uncertainty in parameter estimates, with credible intervals overlapping zero for all covariates. Detection probabilities varied among species and were primarily influenced by temporal sampling variables (**Figure 7.4b**). At the community level, detectability increased with sampling effort and week of detection, although the magnitude of these effects differed among species. In contrast, local habitat covariates generally showed weaker and less consistent effects on detectability.

All models used for prediction comparisons achieved satisfactory convergence. Hunting yield data showed a positive association with multispecies model predictions for most species (**Figure 7.5**); however, these relationships were weak. Credible intervals around the estimates included zero, indicating that the strength of the relationship could be small (**Table 7.1**). Results were consistent across levels of spatial representativeness. Most variation was explained by species-level random effects rather than fixed effects, with large variability in intercepts ($SD = 1.37 - 2.56$), and smaller variation in slopes ($SD = 0.08 - 0.20$; **Table 7.1**). Conditional R^2 values were high and consistent across models ($0.607 - 0.871$), whereas marginal R^2 values were negligible ($0.001 - 0.004$).

Table 7.1. Summary of models relating predicted relative abundance estimates (λ_{pred}) to hunting yield density independent datasets across different levels of spatial representativeness. β (mean) represents the fixed effect slope with its corresponding 95% Confidence Interval (CI). Random effects are shown as the standard deviation (SD) for the species-level intercept and slope. Model performance is indicated by the residual standard deviation (σ), along with Conditional R^2 (variance explained by both fixed and random effects) and Marginal R^2 (variance explained by fixed effects only).

Model	Spatial extent	β (mean)	β 95% CI	SD		σ	R2 conditional	R2 marginal
				intercept (species)	SD slope (species)			
H1	Within	0.10	-0.13 – 0.45	1.37	0.20	0.46	0.607	0.004
H2	Nearby (20 km)	0.03	-0.04 – 0.10	2.50	0.08	0.38	0.871	0.001
H3	Nearby (50 km)	0.02	-0.08 – 0.11	2.56	0.10	0.38	0.850	0.001

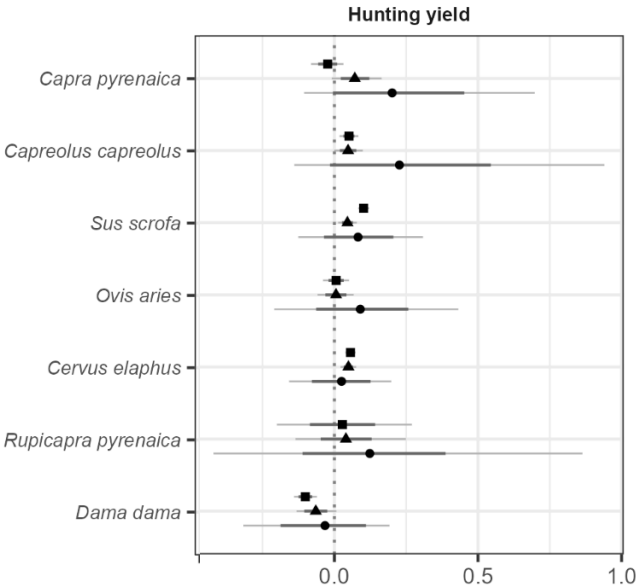


Figure 7.5. Species-specific slopes describing the relationship between hunting yields and the predicted relative abundance (λ_{pred}) from the N-mixture model across the three levels of spatial representativeness: within (circles), nearby at 20km (triangles) and 50km (squares) buffers. Slopes correspond to species-level coefficients from the hierarchical model, combining fixed and species-specific effects. Estimates account for uncertainty in λ_{pred} through their associated standard errors. Points are posterior means, black bars indicate the 75% BCI and grey bars the 95% BCI.

7.4. Discussion

Our results show that standardized camera-trap networks analyzed with multispecies N-mixture models can generate spatially explicit and internally consistent indices of relative abundance (site-use intensity), together with species-environment relationships, for wild ungulate communities at broad spatial scales. By explicitly accounting for imperfect detection and borrowing strength across taxa through partial pooling, this framework stabilizes inference for infrequently detected species, that would otherwise be difficult to analyze with single-species models, while preserving species-level inference for common taxa (M. T. Farr et al., 2022; Pacifici et al., 2014; Zipkin et al., 2010). In our dataset, several species were recorded infrequently and exploratory single-species N-mixture models failed to converge (*e.g.*, southern chamois, Iberian wild goat; data not shown). Because standardized camera-trap deployments inherently collect community data and species differ in ecology traits, detectability, and habitat associations, imbalanced information across taxa is expected, making multispecies models a natural analytical match. This capacity to analyze multiple species simultaneously makes multispecies models particularly valuable in camera-trap networks and large-scale biodiversity monitoring programs aiming to assess entire communities using standardized sampling designs (Moersberger et al., 2024; Sandercock et al., 2015).

Ungulate monitoring at national scales often relies on indirect proxies (*e.g.*, harvest statistics) that provide broad coverage but are spatially biased and

incomplete where hunting is restricted, resulting in gaps and uncertainty (Aubry et al., 2020). By combining standardized camera-trap sampling with a community-level hierarchical model, we provide a unified framework that yields three practical points for large-scale monitoring: (i) baseline relative abundance and detectability are not interchangeable, and (ii) macro-scale environmental gradients can provide a robust signal across broad extents, whereas local habitat effects may be harder to estimate consistently at the spatial grain of individual cameras, and (iii) management-relevant benchmarking of model-based indices against hunting yields across multiple spatial supports.

7.4.1. Relative abundance and detectability are distinct processes

The hierarchical community model revealed differences among species in both relative abundance and detection probability, highlighting that abundance and detectability represent distinct processes. Consistent with previous studies, red deer and wild boar reached the highest predicted relative abundance values (**Figure 7.3**; Cerri et al., 2026; Fernández-López et al., 2025). In contrast, they did not exhibit the highest detection probabilities, which were most closely associated with species gregariousness (*e.g.*, fallow deer and mouflon), suggesting that detection may be influenced by species social organization (D. Wang et al., 2025). This decoupling is important for inference and management: interpreting raw camera detections without accounting for detection can lead to misleading conclusions when

comparing species or regions (Guillera-Arroita et al., 2014; Hofmeester et al., 2021; Kéry & Royle, 2016; Royle, 2004; Ruiz-Gutiérrez & Zipkin, 2011).

7.4.2. Drivers of ungulate communities

Effects at community-level were generally weak, reflected by posterior distribution overlapping zero, due to contrasting species-specific responses (**Figure 7.4**). This is due to the fact that wild ungulate community in Spain is highly heterogeneous in terms of habitat requirements and ecological niches (Apollonio et al., 2010). Grouping species with similar habitat preferences may provide a way to obtain stronger community effects, although grouping species in the ecological process has been found to increase estimate uncertainty compared with considering the community as a whole (Pacifi et al., 2014).

Using a standardized camera-trap network and multispecies hierarchical models, we provide, to our knowledge, the first community-wide national assessment of wild ungulates for Spain. Our results indicate that relative abundance across Spain is jointly structured by broad environmental conditions (macro) and local habitat composition (micro), where macro-scale predictors show stronger effects for all species at this extent (**Figure 7.4a**). Although macro-covariates effects varied across taxa, elevation and precipitation emerged as the most consistent species-specific drivers, suggesting that macro-environmental gradients, such as climatic variables and topographic covariates, act as primary constraints on ungulate distributions at the spatial scale considered in this study (Illanas et al.,

under review – see [Chapter 4](#); King et al., 2021). In contrast, local habitat variables showed moderate effects on relative abundance, suggesting that habitat conditions may vary substantially among nearby sites, potentially limiting the ability of the model to detect consistent responses to habitat covariates (Kays et al., 2021). In our dataset, forest and shrub cover varied more within study areas than among them, potentially reducing the model's ability to detect strong responses along the full environmental gradient (**Figure S7-3.3**). Increasing local replication (*e.g.*, multiple cameras per sampling point) may help to obtain more representative value of relative abundance (Palencia et al., 2024).

7.4.3. Interpretation of the predicted relative abundance indices

Relationships between predicted relative abundance estimates and hunting yields were generally weak and varied among species, suggesting that there is not a consistent global relationship across the community (**Figure 7.5**; **Table 7.1**). Most variation was attributable to species-level differences, indicating that this external dataset primarily reflect broad interspecific differences according to differences in abundance between species (Cerri et al., 2026). The relatively weak relationships observed here do not necessarily indicate poor model performance but rather highlight differences in how abundance information is represented across data sources, especially when comparison are made with hunting harvest data, as it may be influenced by management decisions, hunting effort, and regulatory

frameworks. These factors may weaken direct quantitative relationships with model derived abundance indices, even when broad ecological patterns are consistent.

From a monitoring perspective, the similarity of benchmarking outcomes across spatial supports suggests that the camera-trap-based indices retain a coherent signal when summarized at management-relevant spatial scales within the environmental domain represented by the sampling network. However, extending site-level indices beyond the sampled grids remains challenging and warrant explicit evaluation through dedicated scale-sensitivity analyses and additional replications.

7.4.4. Limitations and methodological considerations

In this study, we used a systematic grid design similar to those commonly implemented in camera trap surveys aimed at estimating population densities of unmarked species (*e.g.*, the Random Encounter Model; Rowcliffe et al., 2008). Our results suggest that this type of camera trap grid performs well for relatively common species but may be less effective for detecting less frequent ones, making detectability of elusive species a critical factor. Inference for these taxa may be improved by strategically placing cameras in habitats where the species is more likely to occur. For multispecies monitoring, prioritizing spatial coverage across the landscape and subsequently increasing camera deployment in selected study areas to improve detection of more difficult to detect species may represent a practical compromise (Curveira-Santos et al., 2026; Fuller et al., 2022). Understanding how different sampling designs commonly used for deploying camera-traps influence

estimates of abundance and detection probability in N-mixture models therefore remains an important area for further research.

Data processing decisions can influence inference in camera-trap N-mixture models analysis because continuous detections must be converted into discrete counts by defining independent events and sampling occasions (Blount et al., 2025; Goldstein et al., 2024; Harris et al., 2024; Koetke et al., 2024). These choices may affect detectability, the resulting count distribution and, consequently, parameter estimates (*e.g.*, zero-inflated counts; (Kéry, 2018). Here we used an a priori event definition and weekly occasions aligned with common practice; exploring alternative definitions is beyond the scope of this study but represents an important avenue for future work (Kays et al., 2020)

Taken together, our results indicate that multispecies N-mixture models applied to standardized camera-trap networks can translate local detections into spatially explicit, model-based indices of ungulate relative abundance. Comparing these model predictions with hunting yield density provides an independent check on how closely camera-trap-based predictions align with harvest-based proxies across spatial levels. Although associations were generally positive, they were weak, suggesting that concordance may be driven mainly by broad interspecific differences. These results also suggest that the two data sources capture partially different components of abundance-related variation and therefore provide complementary information for monitoring and management. Future work should

focus on improving spatial transferability and on integrating these data sources, or additional independent monitoring datasets, to improve the robustness and spatially continuity of predictions of wildlife abundance and distribution for large-scale biodiversity monitoring.

Authors contribution

SI: camera traps deployment (supporting), image processing (lead), conceptualization (lead); data curation (lead); data analysis (lead); writing – original draft (lead). EFZ: conceptualization (lead); data analysis (supporting); writing – original draft (supporting). PA: conceptualization (lead); data curation (lead); data analysis (supporting); writing – original draft (supporting); funding acquisition (lead). JFL: conceptualization (lead); data analysis (supporting); writing – review and editing (supporting). JV: writing – review and editing (supporting), funding acquisition (lead). JABA: camera traps deployment (supporting); writing – review and editing (supporting). JSC: camera traps deployment (supporting); writing – review and editing (supporting). EF: image processing (supporting); writing – review and editing (supporting).

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Conflict of interest statement

The authors report no conflict of interests.

Data accessibility statement

Data and code used for modeling are open and available at [github](#).

S7 Supporting Information

S7-1 Sampling design information

In this section, we summarize the spatial sampling effort, including the number of camera traps, the mean grid spacing and the total area sampled per study area (**Table S7-1.1**). The reported grid spacing represents the actual mean distance between the nearest neighbor camera traps deployment in each study area, which may show minor deviation from the theoretical grid design due to field constraints.

The sample area (km²) for each locality was estimated using the minimum convex hull around the camera traps coordinates using the `st_convex_hull` function from the `sf` package (Pebesma, 2018).

Table S7-1.1. Total number of camera traps installed (CT deployed), total number of camera trap used for the analysis (CT analyzed), grid spacing (m) and area (km²) covered within each locality.

Study area	CT deployed	CT analyzed	Grid spacing (m)	Area (km ²)
L01	40	36	620.60	18.42
L02	19	13	532.28	4.49
L03	40	26	1,064.47	46.59
L04	42	42	1,476.35	47.11
L05	34	34	846.66	31.41
L06	39	33	1,301.16	66.10
L07	39	34	1,054.91	54.29
L08	35	33	646.88	7.94
L09	40	38	1,555.19	110.41
L10	19	19	648.84	8.85
L11	40	36	948.93	33.35
L12	18	18	485.23	4.31
L13	20	20	760.16	11.76
L14	40	38	1,203.60	51.23
L15	40	32	577.25	14.89
L16	40	40	849.71	34.49
L17	21	21	696.79	11.04

Study area	CT deployed	CT analyzed	Grid spacing (m)	Area (km ²)
L18	40	40	1,242.14	26.15
L19	38	37	925.05	52.61
L20	41	41	858.95	13.70
L21	40	33	1,193.60	54.67
L22	40	38	515.92	15.12
L23	40	37	942.01	38.14
L24	14	14	432.21	2.72
L25	18	18	698.83	8.54
L26	46	46	1,079.92	24.63

Table S7-1.2. Number of sites where species were detected or not detected. The proportion is also given in teal color.

Species	Detected	No detected
<i>Capra pyrenaica</i>	102 (0.125)	715 (0.875)
<i>Capreolus capreolus</i>	315 (0.386)	502 (0.614)
<i>Cervus elaphus</i>	622 (0.761)	195 (0.239)
<i>Dama dama</i>	154 (0.188)	663 (0.812)
<i>Ovis aries</i>	164 (0.201)	653 (0.799)
<i>Rupicapra pyrenaica</i>	5 (0.006)	812 (0.994)
<i>Sus scrofa</i>	653 (0.799)	164 (0.201)

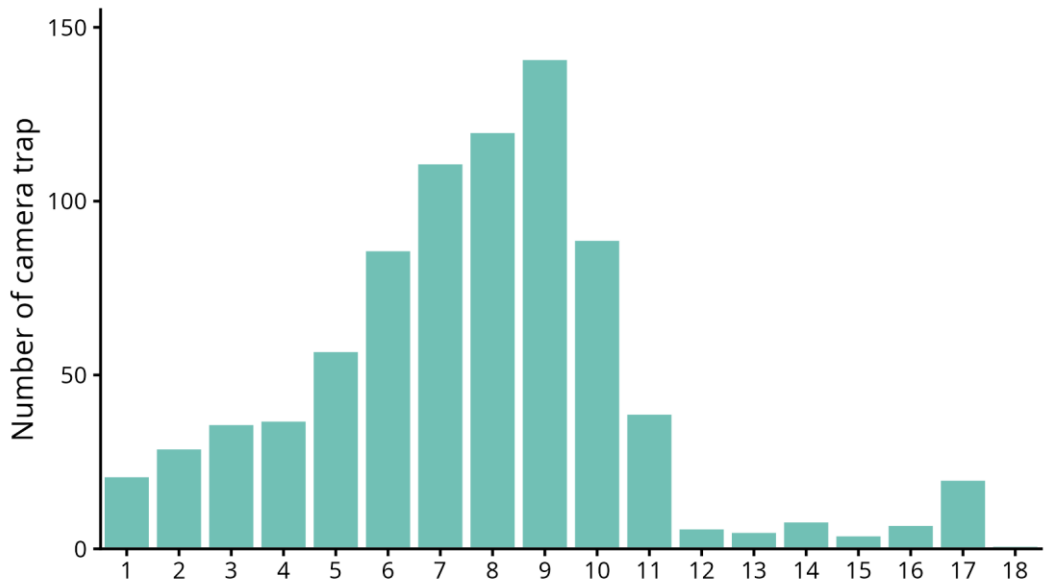


Figure S7-1.1. Number of sites with k sampling occasions (1 to 18). The mean number of sampling occasion per site was 6.8.

S7-2 Alternative ecological covariate specifications for latent site-level

To assess whether inferred species-environment relationships depend strongly on the choice of ecological covariates, we fitted two reduced ecological specifications in addition to the a priori combined model presented in the main text. These reduced models were used as a qualitative sensitivity check and were not intended for formal model selection. Inference in the main manuscript is based on the combined specification.

All three models share the same multispecies N-mixture structure fitted with msNmix (package spAbundance; Doser et al., 2024). Models differ only in the set of covariates included in the ecological (latent-state) component. The detection component is identical across specifications. We considered three alternative covariate sets for the latent site-level state N (interpreted as relative abundance):

1. Macro-only model (broad-scale abiotic conditions). Included elevation, elevation², annual precipitation, precipitation², and slope.
2. Micro-only model (local habitat structure). Included shrub cover (%) and forest cover (%).
3. Combined model (main analysis; “comb”). Included the full set of macro- and micro-scale covariates: elevation, elevation², annual precipitation, precipitation², slope, shrub cover, and forest cover.

All ecological covariates were calculated within a 500 m buffer around each camera site and standardized (mean = 0, SD = 1) prior to model fitting.

Detection probability was modeled using the same covariates in all three specifications. At the sampling-occasion level, we included week and week² (seasonality) and weekly effort (camera operational hours). At the site level, we included slope (25 m buffer) and canopy height (25 m buffer) to account for local factors affecting detectability. All detection covariates were standardized (mean = 0, SD = 1).

We compared species-specific posterior summaries of standardized ecological coefficients from the combined model to those obtained under reduced macro-only and micro-only specifications. This comparison evaluates whether the magnitude and direction of estimated effects are broadly consistent when macro- or micro-scale predictors are modeled in isolation.

Posterior median coefficients for macro-scale covariates were highly consistent between the combined and macro-only specifications (**Figure S7-2.1**). In contrast, micro-scale effects showed greater dispersion relative to the 1:1 line when comparing the combined and micro-only models (**Figure S7-2.1**); however, these differences are shown on a narrower coefficient range, so visual deviations should be interpreted accordingly.

Taken together, this scale-covariates check indicates that macro-scale coefficient estimates are highly stable when modeled with or without local habitat covariates, whereas micro-scale effects are more sensitive when modeled in isolation (**Figure S7-2.1**). Because the micro-scale panel spans a narrower

coefficient range, visual deviations from the 1:1 line should be interpreted cautiously. This pattern suggests that local habitat effects may be more difficult to identify robustly at this extent and grain, either because (i) habitat structure varies at finer scales than captured by the covariates used here, (ii) camera placement and micro-topography influence local encounter rates, or (iii) local habitat effects are partly confounded with broad gradients in ways that become more apparent when modeled alone.

These results support focusing inference on the combined a priori model (described in the main text), because macro-scale gradients and local habitat composition may jointly shape ungulate relative abundance, and estimating them simultaneously provides a coherent basis for inference at broad spatial scales. Reduced macro-only and micro-only specifications are therefore interpreted as a qualitative sensitivity check to assess coefficient stability, rather than as competing models for selection

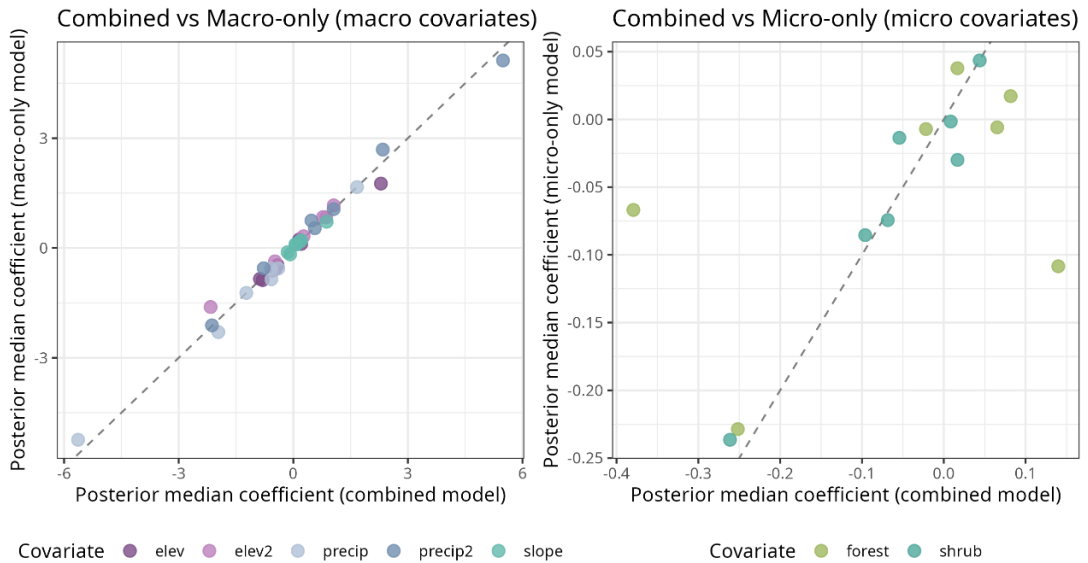


Figure S7-2.1. Sensitivity of species-specific ecological effects to covariate specification. Each point represents the posterior median standardized coefficient for a species-covariate combination. Left panel compares coefficients from the combined model versus the macro-only model for broad-scale covariates; right panel compares coefficients from the combined model versus the micro-only model for local habitat covariates. The dashed line indicates equality (1:1).

S7-3 Source of information of environmental covariates

In this section, we describe the primary source of information and the pre-processing workflows for the environmental covariates used in this study (**Table S7-3.1**). Several covariates required extensive processing prior to analysis. Specifically, three datasets were not available as a single continuous raster and required merging or mosaicking, while two others were derived as boolean variables from original cartographic sources.

Canopy height data were accessed and downloaded via Google Earth Engine. Since a single-file download for the entire Spanish territory is currently unavailable, we implemented a custom JavaScript within the GEE Code Editor using multiple bounding boxes to cover the full national extent. The script used for this procedure is provided [here](#). Note that users must adjust the bounding box according to their specific study area. Download limits per window are subject to the storage capacity of the user's Google account (standard or premium). Following the download, the individual tiles were mosaicked into a single raster covering the study area.

The Spanish National Geographic Institute provides elevation data in discrete tiles. Consequently, these spatial datasets were homogenized by reprojecting them into a common coordinate reference system (EPSG:25830), addressing inconsistencies between the various UTM zones of the source files. Individual tiles of the MDT25 were mosaicked to create a continuous elevation

surface for the entire study area. Finally, from this continuous layer, secondary topographic variables, slope, was derived. The script used for this procedure is provided [here](#).

Vegetation cover variables were derived from CLCplus Backbone (European Environment Agency (EEA), 2024). We generated two primary binary Boolean layers: forest, created by aggregation pixels classified as needle-leaved trees (value 2), broad-leaved deciduous trees (value = 3) and broad-leaved evergreen trees (value = 4); and shrubs extracted directly from the shrubland category (value = 5). The script used for this procedure is provided [here](#).

Prior to model analysis, correlation between covariates was assessed in order to identify potential multicollinearity and better understand the underlying data structure (**Figure S7-3.1**) and spatial patterns were visually inspected (**Figure S7-3.2**) and plotted (**Figure S7-3.3**).

Table S7-3.1. Source of information from which site covariates were downloaded as well as their resolution is provided.

Covariate	Spatial resolution	Source
Elevation (m)	25m	MDT25m (Instituto Geográfico Nacional, 2024)
Annual precipitation (mm; bio12)	~1 km ²	Worldclim (Fick & Hijmans, 2017)
Forest cover (%)	10m	CLCplus Backbone 2021 (European Environment Agency (EEA), 2024)
Shrub cover (%)	10m	CLCplus Backbone 2021 (European Environment Agency (EEA), 2024)
Slope (%; calculated from elevation)	25m	MDT25m (Instituto Geográfico Nacional, 2024)
Canopy height (m)	1m	High Resolution 1m Global Canopy Height (Tolan et al., 2024)

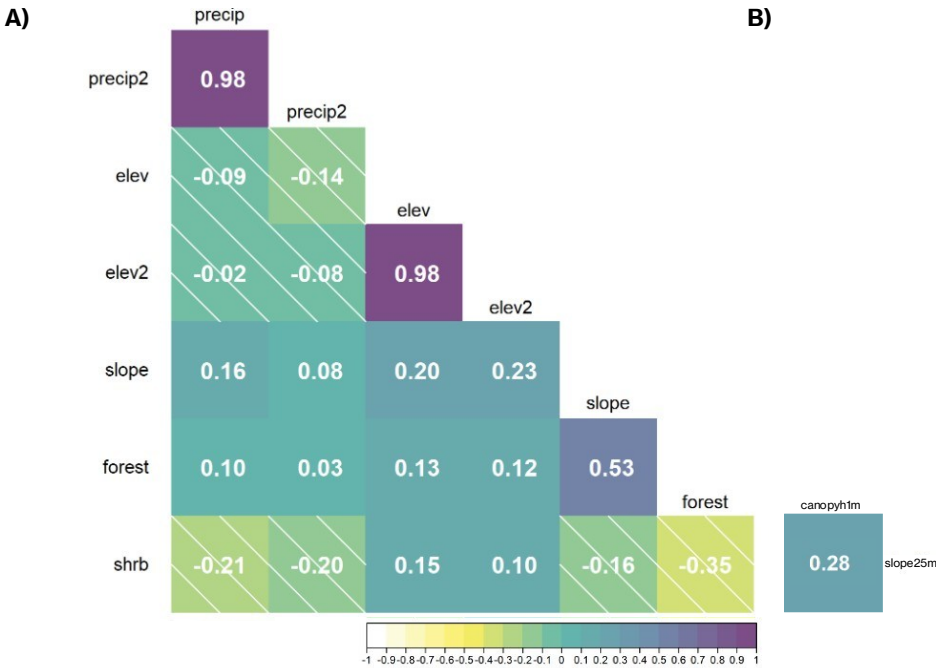


Figure S7-3.1. Correlation plot of site covariates used for the ecological process (A) and site covariates of the observation process (B).

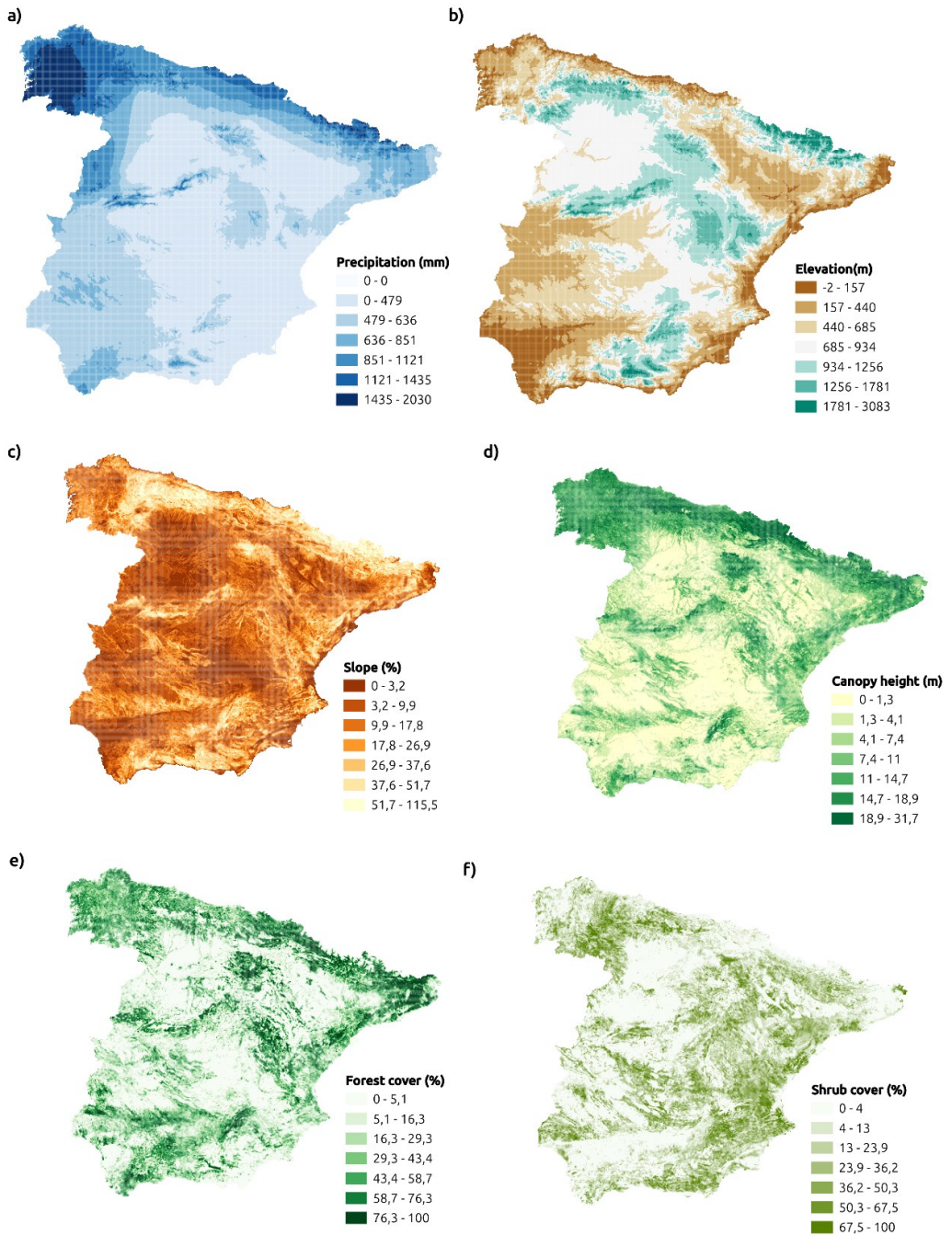


Figure S7-3.2. Spatial distribution of covariates, Individual panels show the spatial patterns and local gradients for precipitation (a), elevation (b), slope (c), canopy height (d), forest cover (e) and shrub cover (f), allowing for a visual assessment of spatial overlap and potential collinearity.

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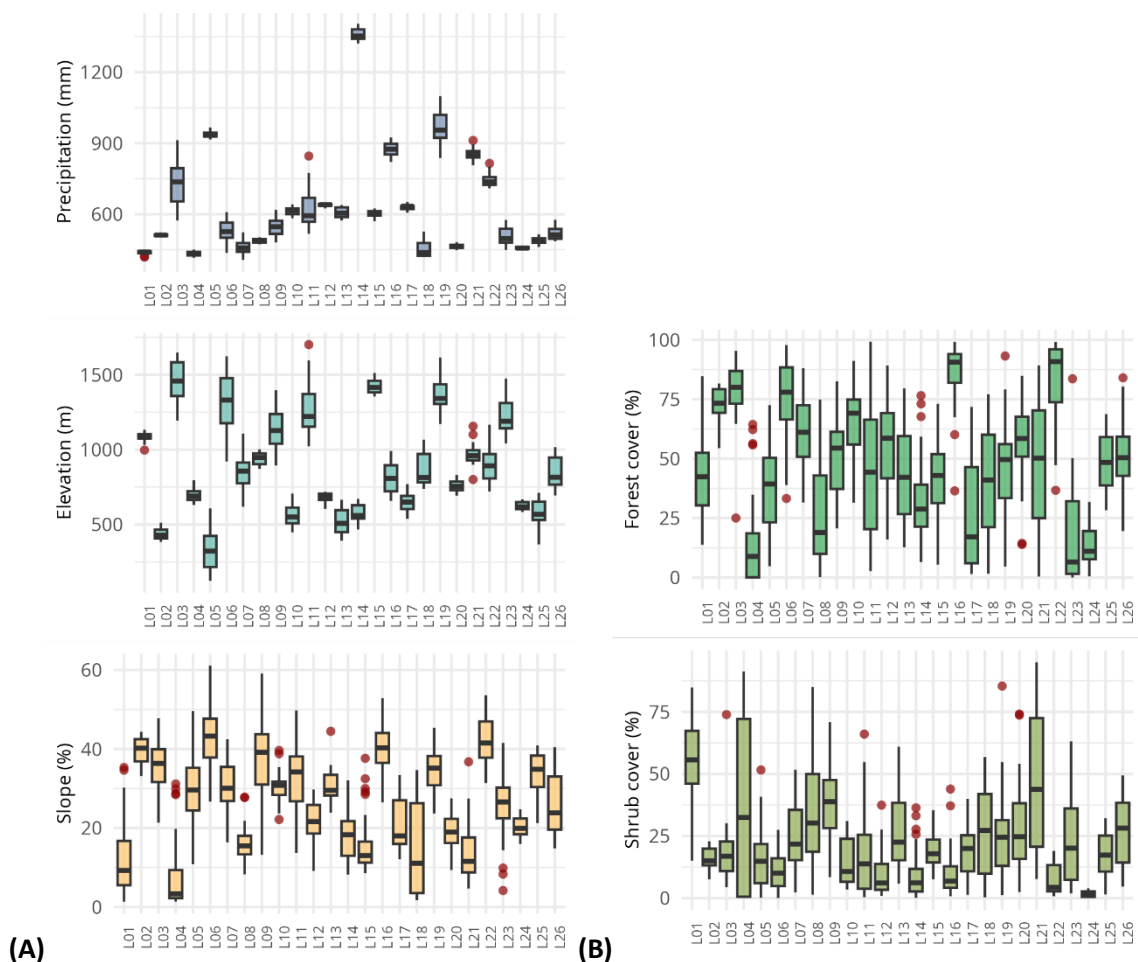


Figure S7-3.3. Environmental characterization of the 26 sampling study areas (L01–L26). Box plots illustrate the distribution within camera traps of the macro covariates (A): annual precipitation (mm), elevation (m), terrain slope (%), and micro covariates (B) forest cover (%), and shrub cover (%). Red circles denote statistical outliers.

S7-4 Model implementation details (priors, MCMC settings, diagnostics)

We used a community-level hierarchical formulation in which species-specific coefficients for the ecological and detection components were modeled as random effects drawn from common community distributions, enabling partial pooling across species (Royle & Dorazio, 2008; Kéry & Royle, 2016).

For the ecological component, species-specific regression coefficients $\beta_{s,i}$ were modeled as $\beta_{s,i} \sim \text{Normal}(\mu_{\beta,i}, \sigma_{\beta,i})$ and for the detection component, coefficients $\alpha_{s,i,k}$ were modeled as $\alpha_{s,i,k} \sim \text{Normal}(\mu_{\alpha,i,k}, \sigma_{\alpha,i,k})$ where $\mu_{\beta,i}$ and $\mu_{\alpha,i}$ are community-level means and $\sigma_{\beta,i}$ and $\sigma_{\alpha,i}$ represent among-species variation (community-level SD) for each covariate effect. We assigned weakly informative priors to the community-level means $\mu_{\beta,i} \sim \text{Normal}(0, 2.72)$ and detection mean effects $\mu_{\alpha,i} \sim \text{Normal}(-1.5, 1.5)$. Among-species variation in covariate effects was modeled using an Inverse-Gamma prior on the community-level variance as $\sigma^2 \sim \text{Inverse-Gamma}(0.1, 0.1)$, where σ^2 denotes the variance of the corresponding community distribution (*i.e.*, $\sigma = \sqrt{\sigma^2}$). Models were implemented using Markov Chain Monte Carlo (MCMC) algorithms in the spAbundance package (v0.2.2; Doser et al., 2024). Each model was run for 250,000 iterations with three chains. The first 100,000 iterations were discarded as burn-in and chains were thinned every 10 iterations, yielding 45,000 posterior samples. The models required approximately

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280 min to complete the run on a computer equipped with 64 GB of RAM and 2.90GHz processor.

We evaluated convergence using visual inspection of traceplots, R-hat, and effective sample size (ESS). Summary diagnostics for key parameters are provided in

Figure S7-4.1 and **Figure S7-4.2**.



Figure S7-4.1. Traceplots, Rhat and ESS of ecological observational process.

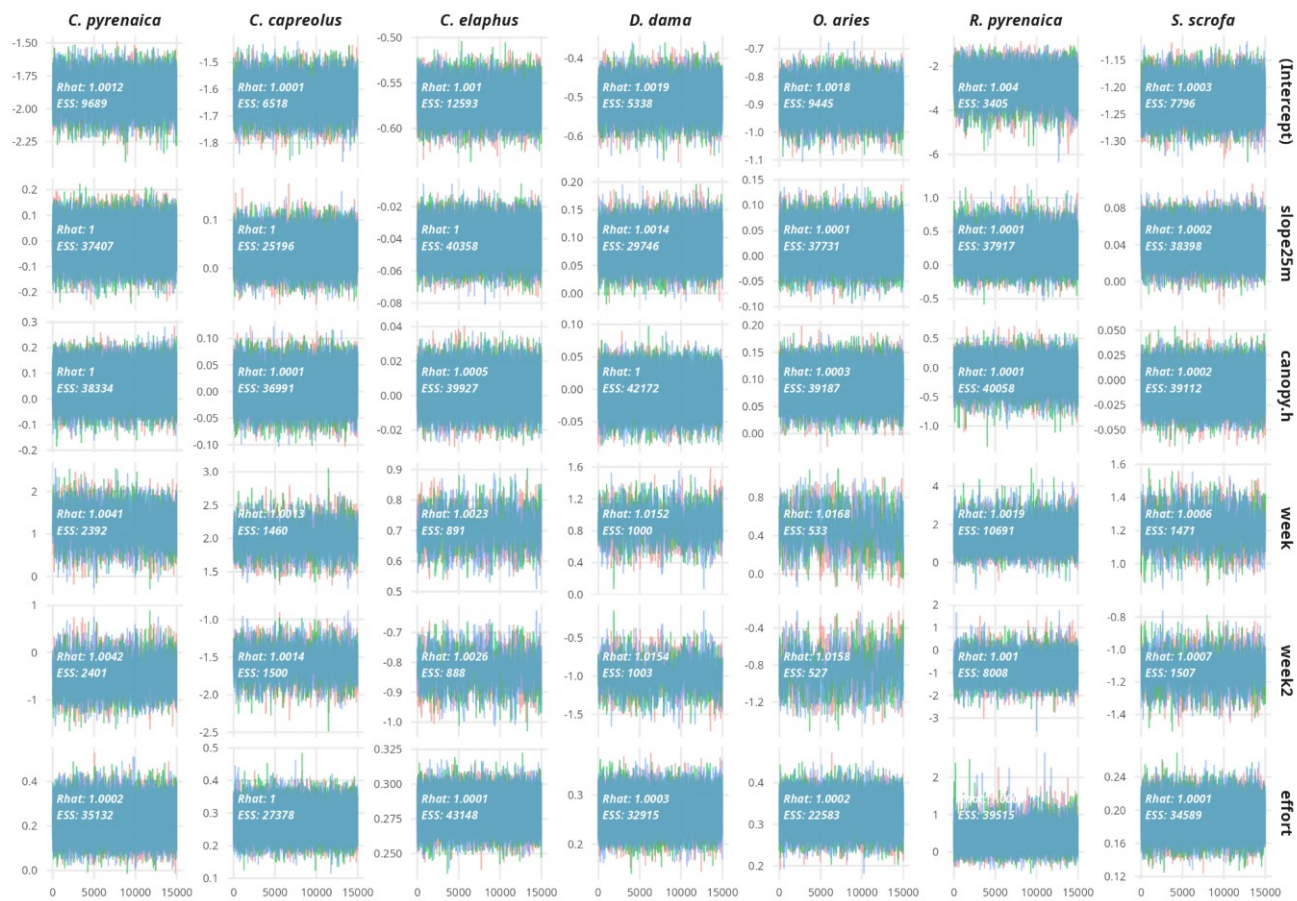


Figure S7-4.2. Traceplots, Rhat and ESS of detection process.

S7-5 Traceplots, Rhat and ESS of prediction comparisons

We evaluated the relationship between multispecies model predictions and hunting yield density using a Bayesian linear mixed model fitted with the R package *brms* (v2.23.0; Bürkner, 2017), which interfaces with Stan for Bayesian inference.

The response variable was log-transformed hunting yield density (individuals per km²) and the predictor was the posterior median of predicted relative abundance (λ_{pred}) derived from the multispecies camera-trap model. The model included species-specific varying intercepts and slopes, specified as independent (*i.e.*, uncorrelated) random effects to improve parameter identifiability given the small number of species. Observation-level uncertainty in λ_{pred} was incorporated using the `se()` function in *brms* (with `sigma = TRUE`), allowing uncertainty from the camera-trap model to propagate into the comparison analysis.

Fixed-effect regression coefficients were assigned weakly informative Normal(mean = 0, sd = 2) priors, reflecting plausible effect sizes on the log scale while providing regularization. Standard deviations of species-level random effects were assigned Exponential(1) priors to constrain variance estimates to positive values while remaining weakly informative.

Posterior samples were obtained using Hamiltonian Monte Carlo implemented via the No-U-Turn Sampler (NUTS; Hoffman & Gelman, 2014). To improve sampling efficiency and reduce the risk of divergent transitions, the target acceptance rate (`adapt_delta`) was set to 0.99. Models were run with three independent Markov chains, each with 5,000 iterations, including a burn-in of 1,000 iterations per chain, resulting in a total of 12,000 posterior samples. Chains were initialized with dispersed initial values automatically generated by Stan. Model convergence was assessed through visual inspection of traceplots for all fixed and random-effect parameters. Convergence was further evaluated using the Gelman–Rubin diagnostic ($\hat{R}$), and effective sample sizes (ESS), which were sufficiently large for reliable posterior inference (**Figure S7-5.1, Figure S7-5.2Figure S7-5.3**).

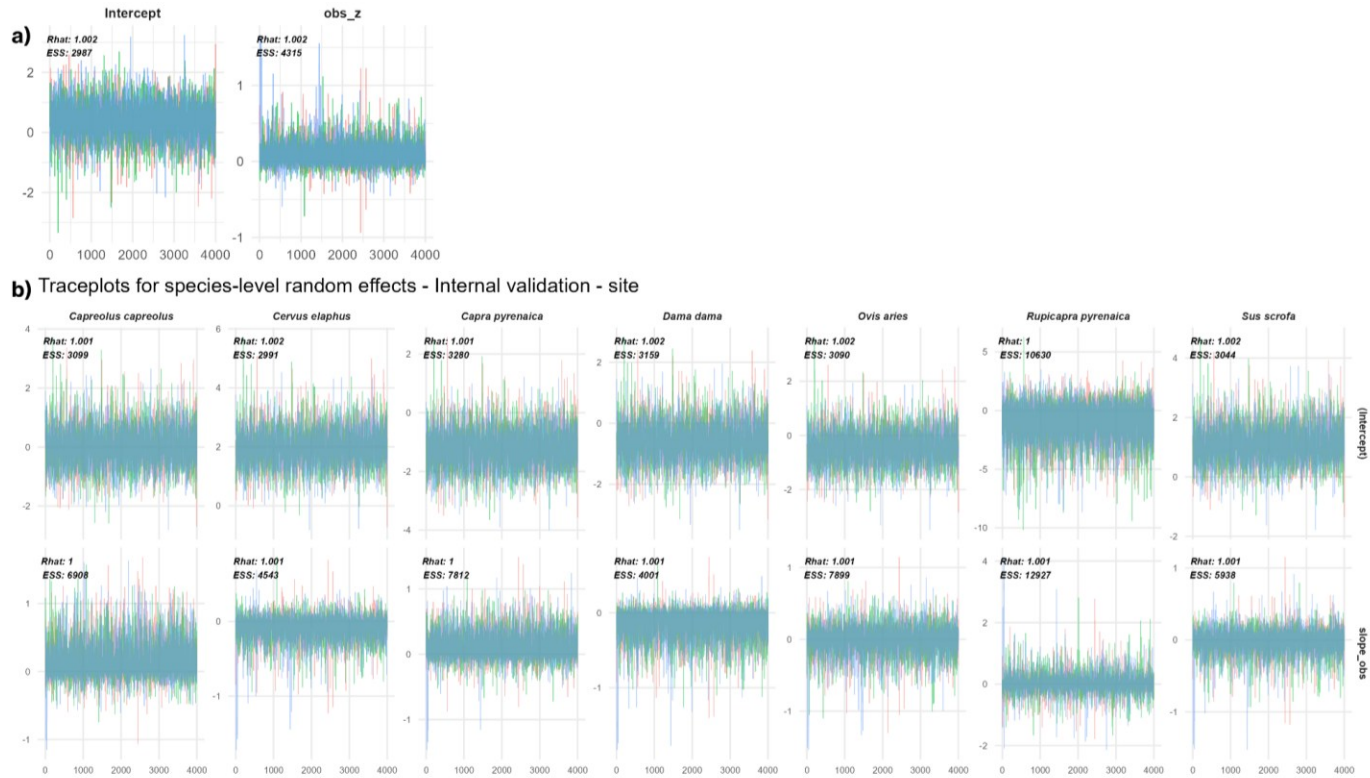


Figure S7-5.1. Traceplots for species fixed effects (a) and species-level random effects (b) obtained from the internal validation - site for hunting yields data source.

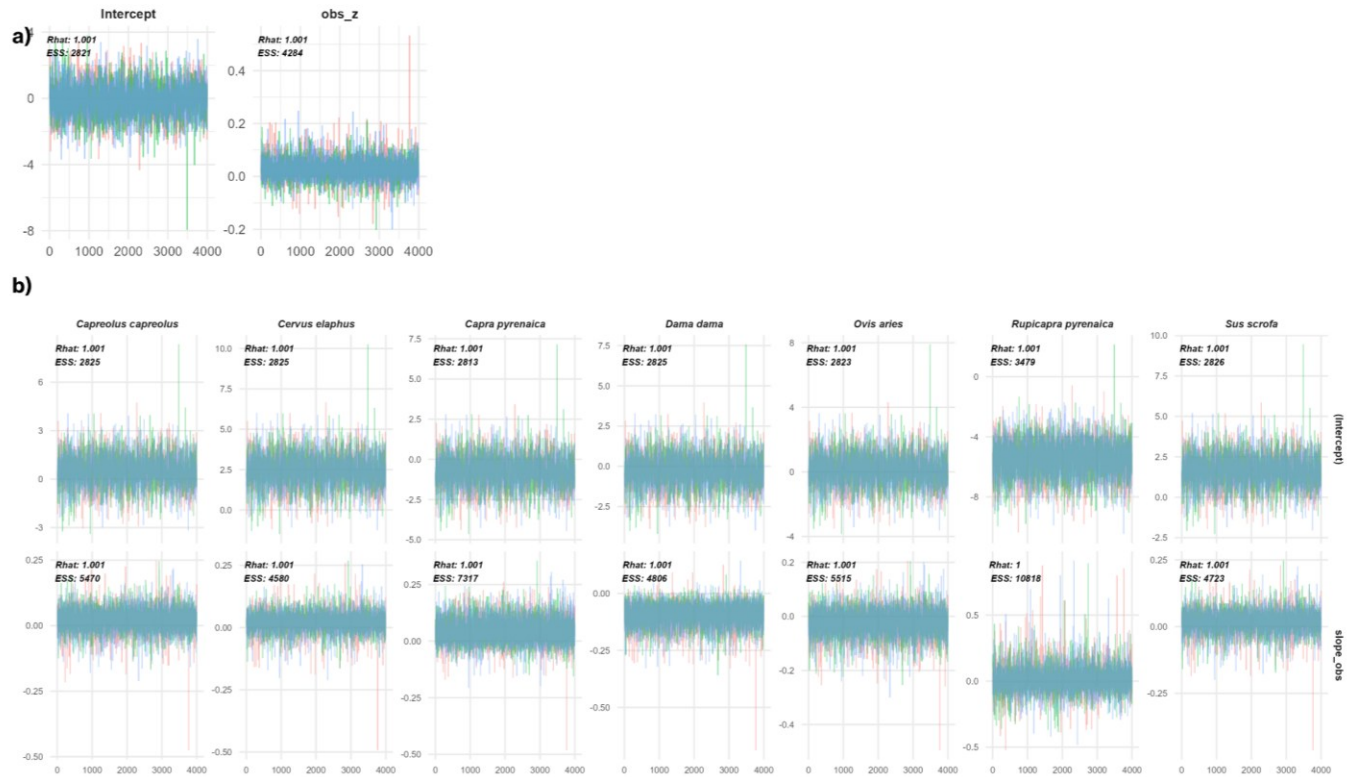


Figure S7-5.2. Traceplots for species fixed effects (a) and species-level random effects (b) obtained from the nearby area sites - 20 km buffer for hunting yields data source.

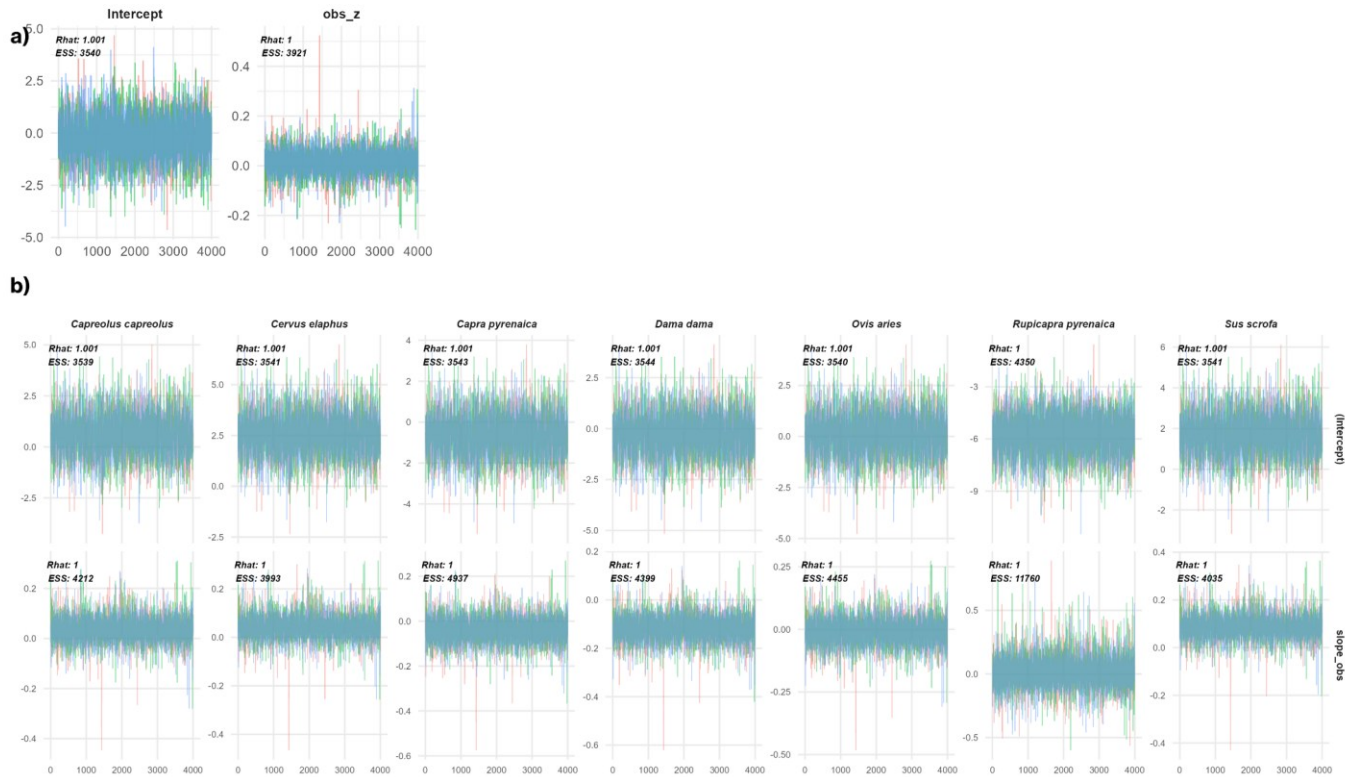


Figure S7-5.3. Traceplots for species fixed effects (a) and species-level random effects (b) obtained from the nearby area sites - 50 km buffer for hunting yields data source.

8. General Discussion & Conclusions



This section aims to bring together the main results, ideas, and contributions of each chapter, contextualizing and integrating them in a broader picture. It is not the purpose of this section to enter into a detailed discussion of results, as this task has already been addressed within each chapter.

During the 20th century a wide set of statistical tools was developed for the quantification and prediction in ecology (Gilbert et al., 2024). However, in recent decades, inferring wildlife abundance patterns has come to require increasingly specific knowledge of data characteristics (Koldasbayeva et al., 2024), modeling frameworks (Iijima, 2020; McCrea et al., 2023), spatial units for making predictions (Gotway & Young, 2002; Pacifici et al., 2019), the ecology of the species themselves and the aim of inference (Guillera-Aroita et al., 2015; Pollock et al., 2002). These components are intrinsically linked and cannot be considered in isolation when applying models to wildlife data (**Figure 8.1**; Zipkin et al., 2021).

In this thesis, we addressed the challenge of estimating mammal abundance at large spatial scales using heterogeneous data sources and flexible modeling approaches across multiple spatial and ecological contexts. Building on this framework (**Figure 8.1**), the following subsections focus on the main drivers of ecological inference identified: data availability, data pre-processing, modeling decisions, spatial scale and structure and species-specific ecological complexity. Together, these components illustrate how different aspects of the data, models and ecological systems interact to shape the estimation of species distribution and abundance and, consequently, inform wildlife management and conservation.

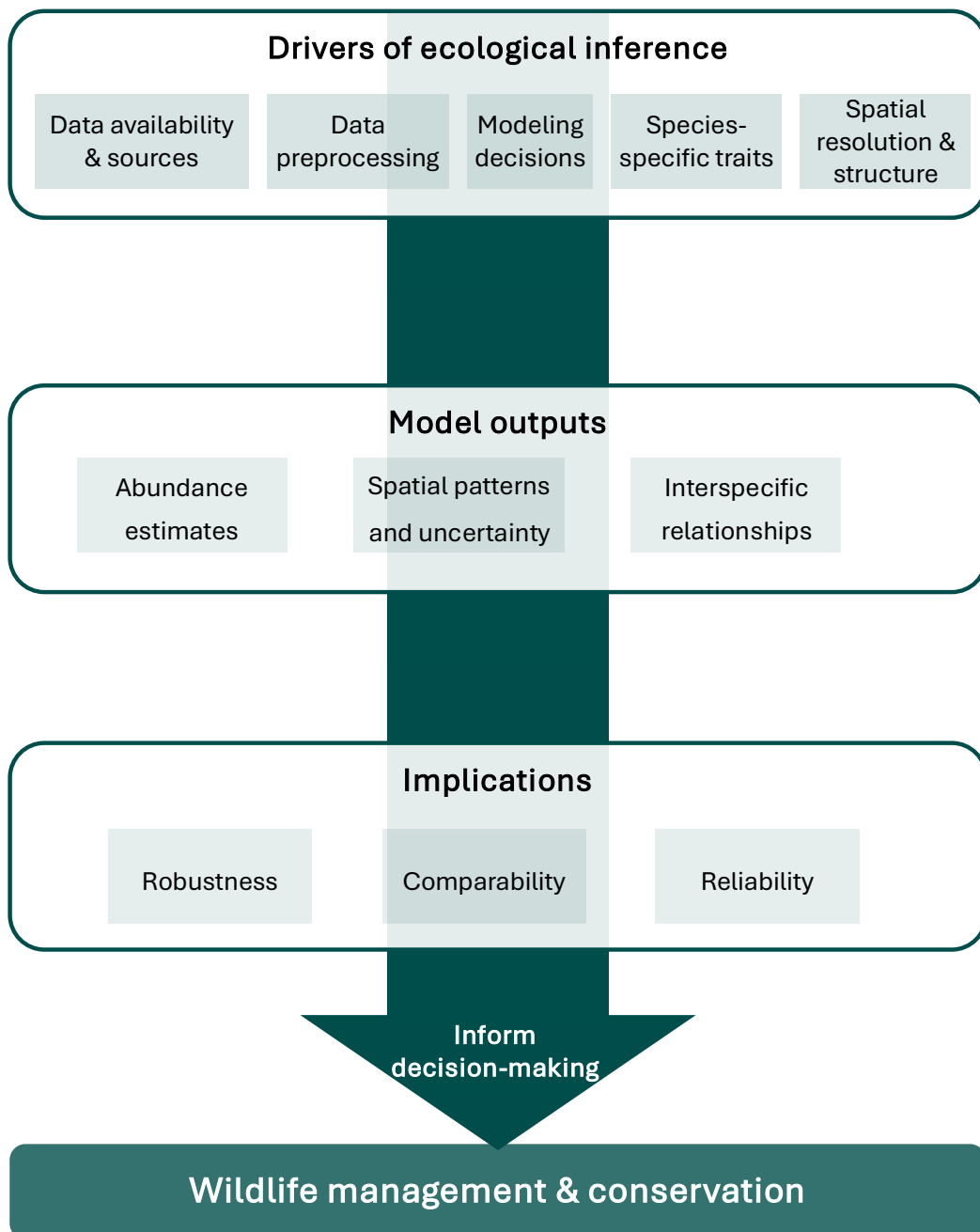


Figure 8.1. Conceptual framework linking data characteristics and modeling decisions to model outputs and their implications for ecological inference and wildlife management and conservation.

8.1. Public data availability

Data availability and accessibility represent the first critical step in enabling large-scale ecological inference. The lack of consistent, standardized, and accessible biodiversity and population data remains a major limitation for monitoring ecological patterns and trends, particularly at large spatial scales (Valdez et al., 2023). This limitation is especially relevant in Europe, where biodiversity monitoring is characterized by fragmented and heterogeneous systems, which hinder data integration at continental scale and their effective use for ecological inference and policy applications (Kissling et al., 2026; Moersberger et al., 2022, 2024). In this context, [Chapter 2](#) highlights the fundamental role of data availability and accessibility in large-scale ecological domains. The chapter shows that unstructured datasets, such as hunting yields, can be transformed into valuable sources of occurrence information, even for common and widespread species whose distribution data are often not systematically available at national scales and provide useful long-time series information (Carvalho et al., 2025; Croft et al., 2025; Jiménez Pérez & Clavero, 2026). In the case of Spain, the collection of hunting yield data at hunting ground level for multiple species over a decade represents an unprecedented source of information, which had not previously been compiled at centralized level. This effort was made possible through the HAWIPO I+D+i project, which enabled the collection and harmonization of these data across regions (ENETWILD-consortium et al., 2018;

Ruiz-Rodríguez et al., 2023). At a pan-European scale, the ENETWILD project (www.enetwild.com) has improved European capacities to monitor wildlife population by developing standards for the collection of information and by compiling and harmonizing data on the geographical distribution and abundance of wild ungulates and carnivores across Europe, constituting the first project at the European scale to assemble such comprehensive information (ENETWILD-consortium, 2025; ENETWILD-consortium, Acevedo, et al., 2021, 2023; ENETWILD-consortium, Plis, et al., 2024). However, data-sharing restriction associated with count data at fine-spatial resolution required transforming the dataset into an open access format. The resulting dataset provides one of the most complete spatial representations of ungulate species and red fox occurrence over 2013-2022 period, offering a consistent basis for monitoring, reporting distribution patterns and enabling the evaluation of shifts in their ranges (**Figure 2.3**, p. 59 and **Figure 2.4**, p. 66).

Beyond its specific application, **Chapter 2** illustrates how datasets with access or sharing restrictions can be transformed into standardized and openly available occurrence records following FAIR principles (Wilkinson et al., 2016). This approach represents a practical step forward in making large-scale biodiversity data more accessible, reproducible, and usable for ecological applications (Jantzen & Vriend, 2026). Importantly, the proposed workflow to data transformation is not restricted to hunting yield data but can be applied to other count-based datasets with similar constraints, including those derived from

different monitoring programs and taxa. Furthermore, the open and reproducible workflow developed here contributes to enhancing transparency in data preprocessing, a step that is often underreported but that may critically influence downstream analyses. The availability of both data and code enables reuse by other researchers and institutions, promoting consistency across studies and facilitating the development of large-scale monitoring initiatives.

At broader spatial scales, this transformation has important implications for biodiversity monitoring in Europe. Hunting-derived data may represent one of the most widespread and consistently collected sources of information on many game species; their harmonization into standardized formats can facilitate data reporting under European frameworks, such as the Habitat Directive, as well as the assessment of IUCN Red List criteria (Aubry et al., 2020; Nichols et al., 2001; Ruiz-Rodríguez et al., 2023). By improving the availability of standardized large-scale biodiversity data, these efforts support consistent assessments across regions and species, thereby strengthening evidence-based environmental policies in Europe and bridging gaps in wildlife information distribution, and linking ecological monitoring with policy needs (**Figure 1.1**, p. 14 ; Kissling et al., 2026; Santana et al., 2025). In this context, the publication of data papers following standardized protocols becomes increasingly relevant, supporting data mobilization, reducing the burden on national administrations, and improving timelines and quality of biodiversity reporting (Kissling et al., 2026). Within this framework, [Chapter 2](#) also highlights the value of decentralized data collection

systems, such as those based on stakeholder contributions (*e.g.*, hunters and local managers), which play a key role in supporting large-scale ecological inference (Crum et al., 2017). While such datasets are often considered unstructured and subject to biases (Moreno-Zarate et al., 2021; Ruiz-Rodríguez et al., 2023), their large-scale availability makes them a valuable component of wildlife monitoring systems for game species (Carvalho et al., 2025; Nichols et al., 2001). The published dataset has already contributed to subsequent monitoring efforts, such as the [MOMAT project](#) (Rodríguez-Rodríguez et al., 2025), and can support future applications at both national and continental scales.

In addition, these systems may provide information beyond targeted species and harvested individuals, as hunters can record observations of all individuals encountered during hunting activities, not only those that are harvested (ENETWILD-consortium, 2025; ENETWILD-consortium, Plis, et al., 2024; Ruiz-Rodríguez et al., 2023). This creates opportunities to improve the representation of species distribution and abundance (**Figure 8.2**). However, these benefits are closely linked to hunter commitment and reporting practices (**Figure 1.3**, p. 22), as the quality, quantity and information completeness ultimately depend on stakeholders (Bauder et al., 2021). These factors directly influence subsequent steps in the modeling process, as both the quantity and reliability of the available data determine how data should be modeled and inferred patterns of species distribution and abundance should be interpreted (Yates et al., 2018).

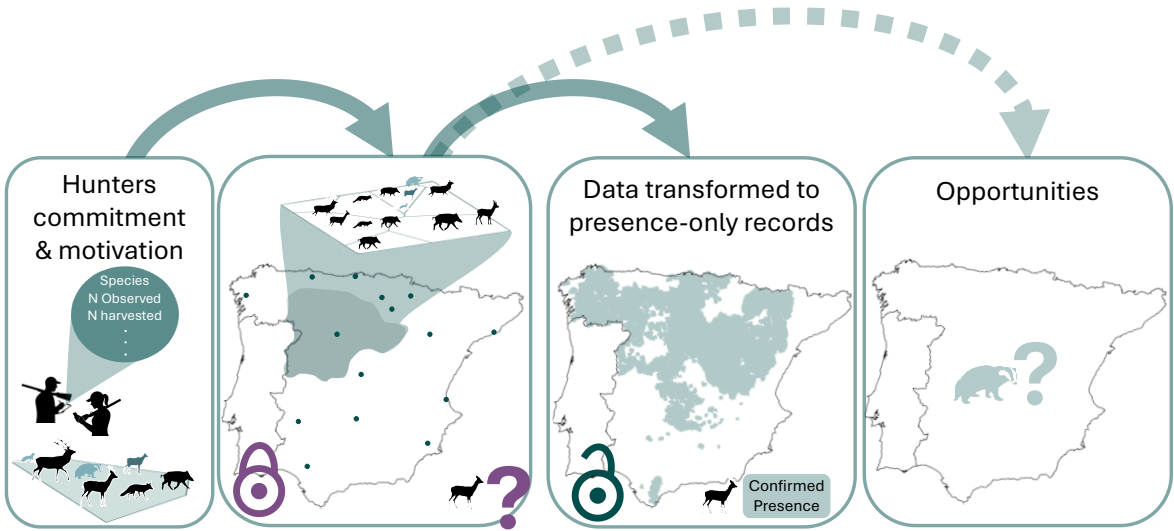


Figure 8.2. Overview of how hunting activity generates wildlife observation data and how these data can be transformed into presence-only records. The process highlights the role of hunter participation, spatial aggregation, and data transformation in large-scale mammal monitoring and further opportunities for the observation of non-targeted hunting species.

8.2. Role of data preprocessing

Data preprocessing and engineering decisions play a central role in the development of ecological models, as they directly determine the structure and content of the input data. These decisions affect not only the quantity and quality of available information, but also the spatial structure of the datasets, which is particularly relevant for modeling wildlife distribution and abundance at large scales. These decisions are fundamental when there is structural heterogeneity in wildlife data collected, digitized, aggregated, and documented across jurisdictions (ENETWILD-consortium, 2025; Guillemain et al., 2026; Ruiz-Rodríguez et al., 2023). Adopting shared data standards and submission-time validation workflows (including automated checks) can reduce downstream ad

hoc decisions by enforcing consistent identifiers and core metadata aligned with Darwin Core, as illustrated by the ENETWILD Wildlife Data Model and validation pipeline (Body, de Mousset, et al., 2020). However, standardization does not eliminate preprocessing: heterogeneous reporting can still lead to incomplete datasets or ambiguously defined records, introducing uncertainty about how observations should be interpreted and used (ENETWILD-consortium, 2025). Consequently, decisions related to data inclusion, exclusion, and transformation require careful consideration, as they directly influence subsequent modeling steps.

In the use of hunting yield data, it is common practice to remove missing values and zero observations without explicitly documenting or discussing their origin or ecological meaning in the published literature (*e.g.*, Klich et al., 2024; Marin-Sáez et al., 2025). [Chapter 3](#) demonstrates that data characteristics, such as the prevalence of zero values, spatial coverage, species distribution range, and management regulations across Europe strongly influence model formulation and, therefore, ecological inferences, but this effect is species dependent. In particular, widespread and spatially constrained species require different decisions, as zero values may reflect either ecological absence or limitations in data reporting. This highlights the importance of interpreting raw data within their ecological and observational context, rather than applying uniform preprocessing criteria.

Important analytical decisions made prior to model fitting are often underreported in the literature (Goldstein et al., 2026). In [Chapter 4](#), we specifically explored how specific preprocessing decisions, particularly the treatment of missing and zero values for species with different distribution range, affected abundance estimates and patterns. The results showed that these choices can substantially alter the magnitude of the predicted patterns and the associated uncertainty, even when resulting spatial patterns appear broadly consistent (**Figure 4.3**, p. 154). This is likely because these decisions can disrupt the spatial structure of the dataset (further discussed in [section 8.4](#)). Moreover, these decisions may also differ between species, as imputing zero values to NAs may be informative for some species, such as red deer and roe deer, while may add noise to widespread species such as red fox and wild boar. In this sense, results from [Chapter 4](#) support the preprocessing framework applied in [Chapter 3](#).

Rather than supporting universal rules, these findings highlight that preprocessing decisions must be tailored to species ecology, data context, and study objectives. Overall, these results demonstrate that preprocessing is not a purely technical step, but a fundamental component of ecological inference that directly shapes the resulting patterns of species distribution and abundance.

8.3. Modeling decisions and inference

Modeling decisions represent a central component of ecological inference, as they determine how data are translated into ecological patterns (Guillera-Arroita et al., 2015; Muscatello et al., 2021). Results from [Chapter 4](#) demonstrate that choices related to the representation of area, and the treatment of regional variation have first-order effects on abundance estimates, uncertainty, and spatial patterns (**Figure 4.3**, p. 154 and **Figure 4.4**, p. 155; Keil et al., 2014; Mäkinen et al., 2022; Paciorek, 2010). Importantly, different modeling strategies may lead to similar or contrasting spatial patterns while producing estimates of abundance that may be more or less consistent, highlighting that model outputs are not uniquely defined by the data alone (**Figure 4.3**, p. 154 and **Figure 4.4**, p. 155; S4-3; Viana et al., 2022; Waldock et al., 2022). These findings emphasize that modeling decisions must be aligned with the specific objectives of the study, whether the aim is to estimate total abundance, characterize species–environment relationships, or describe spatial patterns. Even though all models rely on the same principles and can infer across these three key aspects, the modeling process lets us make choices that emphasize the one we care about most. In this sense, there is no universally optimal modeling framework; rather, different approaches involve trade-offs between bias, uncertainty, and interpretability.

More broadly, these results highlight that ecological inference is inherently model-dependent, and that transparency in modeling choices is essential for ensuring robust and reproducible conclusions (Cooper et al., 2026; Kellner et al., 2025). This is particularly critical when working with heterogeneous data sources at large spatial scales. To this end, data, code, and R workflows associated with this thesis are openly available through public repositories (Zenodo and Github), ensuring fully transparent and reproducible analytical procedures.

8.4. Spatial scale and structure in ecological inference

Spatial structure of data sources plays a central role in ecological processes, particularly at large spatial extents (Cressie, 1993). In this thesis, hunting yield data are highly heterogeneous in the size of the observation units across Europe and within national (Spain) and regional (Castilla-La Mancha) scales, with important implications for large-scale abundance modeling and for the analysis of interspecific spatial relationships.

Results from [Chapter 5](#) show that this variability in spatial resolution (**Figure 3.3**, p. 90) may exacerbate the Modifiable Areal Unit Problem (MAUP; Openshaw, 1983) and may lead to the coexistence of multiple ecological processes within the same dataset (Rollinson et al., 2021). This can lead to a mixing of scale-dependent effects, where relationships between abundance and environmental variables are not directly comparable across units (Bauder et al.,

2021; Paciorek, 2010). In contrast, analysis based on more homogeneous spatial units ([Chapter 4](#)) have more consistent patterns, despite remaining spatial misalignment (Gotway & Young, 2002; Pacifici et al., 2019).

Spatially explicit models that account for spatial dependence produced smoother and more continuous spatial patterns (see S4-3 and **Figure 5.1**, p. 206), improving the ecological coherence of predictions. Nonetheless, model performance is strongly influenced by the size and distribution of observation units. In particular, countries with coarse spatial units (*e.g.*, France or Russia) showed spatial patterns that were difficult to interpret (**Figure 5.1**, p. 206), reflecting change-of-support effects in the use of centroid-based representations of aggregated data. This representation can affect the estimation and propagation of spatial dependence when observation units are highly variable in size. As a result, mismatches between the scale at which ecological processes operate and the way they are represented in the model can limit the interpretability and reliability of spatial predictions (Bauder et al., 2021; Paciorek, 2010). In addition, the unequal distribution of data across spatial resolutions (**Figure 3.1**, p. 84) may further influence the estimation of spatial dependence, such that areas represented by a larger number of fine-resolution units exert a disproportionate influence on the inferred spatial structure (Koldasbayeva et al., 2024; Yates et al., 2018). This arises both from their smaller support and higher sampling density, whereas regions characterized by fewer, coarser units may be comparatively underrepresented. Furthermore, this accounting for spatial

dependence produced confounded effects with the covariates (**Figure 4.2**, p. 151; Mäkinen et al., 2022) and showed the highest uncertainty in predictions (**Figure 4.3**, p.154 and **Figure 5.2**, p. 208).

The scale-related issues extend beyond abundance modeling and also influence how spatial relationships between species are characterized ([Chapter 6](#)). The connectivity matrix is derived from the spatial configuration of observation units and therefore reflects differences in their size and distribution. Defining connectivity based on distance provides a consistent criterion to represent spatial relationships across these heterogeneous units. The reformulation of the GL and LL index developed in this thesis, allowing for species-specific connectivity matrices, enhanced the reliability of bivariate spatial associations, particularly for species with different movement behaviors. This approach enabled the detection of spatial patterns such as divergence and convergence areas (**Figure 6.4**, p. 239) that cannot be captured by overlap-based metrics. This has important implications for applied contexts, as it can lead to different prioritization of areas for multi-species management and conservation.

These findings highlight that spatial structure and scale are not merely properties of the observed data, but fundamental components that shape both abundance patterns and interspecific relationships across large spatial scales (Bauder et al., 2021; Gotway & Young, 2002; Pacifici et al., 2019; Paciorek, 2010). Consequently, failing to account for differences in data resolution can lead to

inconsistent or misleading inferences, requiring modeling strategies to be aligned with the scale of the underlying ecological processes and the specific aims of the study (Guillera-Arroita et al., 2015; Norberg et al., 2019). Rather than pooling heterogeneous datasets into a single modeling framework, hierarchical or resolution-specific approaches could offer a promising alternative (Gotway & Young, 2002; Isaac et al., 2020).

8.5. Species differences and ecological complexity

At large spatial scales, monitoring entire mammal communities is often motivated by the need to scale up local observations to assess biodiversity patterns (Nichols & Williams, 2006; Yoccoz et al., 2001), trends and changes over time and space, particularly in Europe where policies are defined at continental level (**Figure 1.1**, p. 14; Kissling et al., 2026; Moersberger et al., 2024; Sandercock et al., 2015). Differences in species distribution, ecological traits, data availability and management regulations introduce important challenges for sampling design and data collection, as they influence how species are captured by monitoring schemes (Aubry et al., 2020; Kissling et al., 2026). These sources of variability translate into distinct modeling requirements and response patterns across species, reinforcing the need for flexible, species-informed approaches when working across large spatial and taxonomic scales, particularly in the absence of a formal and standardized sampling design (Elith & Leathwick, 2009; Guillera-Arroita et al., 2015; Kays et al., 2024; Norberg et al., 2019).

Results from [Chapter 3](#) and [4](#) demonstrate that species with contrasting distribution ranges and data structures require tailored modeling strategies (Norberg et al., 2019; Yates et al., 2018). In particular, widespread and spatially constrained species differed in both data preprocessing and modeling formulation. These findings emphasize that both data handling and model specification must be adapted to species ecology and data characteristics (Doser & Pacifici, 2025; Guillera-Arroita et al., 2015).

As shown in [Chapter 7](#), the systematic deployment of camera traps on a spatial grid within a national scale network captured consistent large-scale characterization of specific species-environment relationships and revealed species-specific abundance patterns that were consistent with those detected in unstructured datasets (**Figure 7.5**, p. 274). Nevertheless, species with constrained distribution or lower detectability exhibited higher uncertainty in the estimates (**Figure 7.3**, p. 271; **Figure 7.4**, p. 272; and **Figure 7.5**, p. 274), highlighting potential limitations of purely systematic non-stratified designs for these taxa. For such species, stratified or targeted sampling strategies can play a complementary role by enhancing detectability in suitable habitats or regions (Curveira-Santos et al., 2026; Fuller et al., 2022; Kays et al., 2021). This is particularly relevant for elusive species, whose low detection probability can bias estimates (MacKenzie et al., 2002; Tobler et al., 2015).

Beyond sampling design, careful consideration must also be given to the modeling framework applied to the data. Each modeling approach relies on specific assumptions, and the validity of their underlying assumptions critically depends on how the data are collected. For instance, models derived from N-mixture framework assume independence among sampling sites (Royle, 2004; Royle & Dorazio, 2008). Although the focus of this thesis was on site use index rather than absolute abundance, both quantities remain conditional on the detection process and are therefore sensitive to sampling design. The implementation of systematic grids with varying inter-camera distances across study areas may influence detection processes and therefore bias ecological inference if not properly accounted for. These effects may be particularly pronounced for gregarious species, for which smaller inter-camera distances can increase the probability of repeated detections whereas larger distances may lead to under-sampling (D. Wang et al., 2025). Consequently, differences in grid spacing between study areas may introduce systematic differences in the effective sampling unit and detection process, potentially compromising comparability of site use intensity, activity, or abundance proxies among regions (Dupont et al., 2021; Sun et al., 2014). Explicitly evaluating how sample design choices influence estimates in N-mixture models is therefore essential for improving the effectiveness of camera-trap-based monitoring programs aimed at the entire mammal community (Barton et al., 2025; Rowcliffe et al., 2026; Sun et

al., 2014). This highlights that differences in sampling design are not only a logistical issue, but a fundamental component shaping ecological inference.

Building on these findings, an important implication concerns the choice between species-specific and community-level frameworks. While species-specific models are more appropriate when ecological differences among species dominate and require tailored representation, community-level models provide a complementary framework when the objective is to infer shared patterns or jointly account for observation processes across species (Zipkin et al., 2010). Rather than representing a single model for all species, community approaches allow the integration of both shared and species-specific components, offering a coherent way to capture ecological complexity across taxa (Zipkin et al., 2023). In this sense, extending these approaches to jointly model species across heterogeneous data sources represents a promising direction for future research (Isaac et al., 2020; Zipkin et al., 2021). Multi-species integrated models could provide a unified framework to account for both species-specific ecological processes and data-specific observation processes (Doser et al., 2025; Isaac et al., 2020; Leuenberger et al., 2025). The implementation remains challenging due to differences in spatial resolution, sampling design and detectability across datasets (Goldstein et al., 2026; Isaac et al., 2020; Pacifici et al., 2019; Zipkin et al., 2021). Advancing this field will therefore require the development of flexible hierarchical frameworks capable of integrating heterogeneous data sources while

explicitly accounting for differences in sampling design, spatial resolution, and detection processes, without compromising ecological interpretability across species.

8.6. From ecological inference to decision support in wildlife management and conservation

This thesis shows that the contribution of large-scale wildlife research extends beyond ecological interpretation by producing analytical outputs that support operational decisions in wildlife management, animal health, and conservation policy. Its added value lies not only in describing wildlife populations and their spatial structure, but in transforming heterogeneous monitoring records into analytical outputs that can support concrete management decisions under real institutional settings.

The datasets, indices and modeling approaches developed throughout this thesis have already been used in decision-support contexts in Europe, including African swine fever risk assessment through EFSA at the European level (EFSA et al., 2025; ENETWILD-consortium, Illanas, Acevedo, et al., 2021; ENETWILD-consortium, Illanas, Fernández-López, et al., 2021), and outbreak-response decision-making in Spain by the Ministry of Agriculture, Fisheries and Food (MAPA). In Spain, these tools provided spatially explicit estimates of wild boar numbers in affected areas to support control measures aimed to limiting disease outbreak. These applications demonstrate that the thesis generates not

only ecological knowledge but also operational evidence relevant to wildlife management.

A further lesson is that decision-relevant wildlife evidence depends not only on model performance but also on data infrastructures that enable timely, transparent, and scalable workflows. ENETWILD experience indicates that the increasing volume of data mobilized across Europe is exposing important organizational and technical bottlenecks (*e.g.*, heterogeneous national reporting systems, delays in submission and validation, inconsistent metadata, repeated clarification cycles, and limited feedback to data providers), as well as downstream constraints in managing large spatial datasets for continental-scale applications. (ENETWILD-consortium, 2025). However, moving towards a more integrated European data system is neither trivial nor cost-free: it requires investment, technical expertise, transition costs, long-term maintenance, and coordination among administrations and data providers operating under different legal and institutional frameworks.

This policy relevance matters because methodological choices have tangible consequences for decision-making. More consistent harmonization, preprocessing, and modeling of wildlife data can improve sanitary risk assessment, strengthen the evidence base for European reporting obligations, and support adaptive management by enabling decisions to be updated as new information becomes available. Viewed this way, methodological improvements are not simple technical refinements; they influence the spatial patterns that are

inferred, how uncertainty is quantified, which areas or species become management priorities, and the extent to which evidence can be compared across countries and administrative contexts (ENETWILD-consortium, Illanas, Croft, Acevedo, et al., 2022; ENETWILD-consortium, Illanas, Croft, et al., 2021; ENETWILD-consortium, Illanas, Croft, Smith, et al., 2022; ENETWILD-consortium, Illanas, et al., 2023).

This thesis also shows that no single source of information is sufficient on its own. Hunting-derived data offer broad coverage and long time series, whereas camera-trap networks provide standardized observation process for multi-species coverage. Integrating these evidence streams, along with other standardized monitoring sources, within a hierarchical likelihood framework can help address limitations of harvest statistics, improve predictions and ecological interpretability, and provide a pathway toward more robust, policy-relevant wildlife monitoring systems (Gilbert, Pease, et al., 2021; Yoccoz et al., 2001; Zipkin et al., 2021).

Taken together, this thesis frames wildlife monitoring as an iterative policy-relevant process that links data collection, harmonization, modeling, validation, and implementation to management needs (**Figure 1.2**, p.15). Ecological modeling does not fully eliminate uncertainty; instead, it makes uncertainty explicit and organizes evidence, so decisions are more informed, comparable, and defensible.

Conclusions / Conclusiones

1. Large-scale wildlife inference becomes more reproducible when heterogeneous monitoring data (e.g., hunting yields) are harmonized under a shared standard, documented with explicit data-handling rules, and released as a public open-source product.

La inferencia de fauna silvestre a gran escala se vuelve más reproducible cuando datos heterogéneos de monitorización (e.g., bolsas de caza) se armonizan bajo el uso de estándares comunes, documentados explícitamente bajo protocolos de gestión de datos y se publican como un producto público de acceso abierto.

2. Unstructured wildlife data can be converted into consistent national-scale spatial evidence by treating records as “presence” vs. “unknown” (rather than presence–absence) when zeros and missing values cannot be always interpreted as true absences.

Datos no estructurados de fauna silvestre pueden convertirse en una evidencia consistente de información espacial a escala nacional si los registros se tratan como “presencia” vs. “desconocido” (en lugar de presencia-ausencia), cuando los ceros y los valores faltantes no pueden interpretarse siempre como ausencias reales.

3. Large-scale mammal monitoring becomes analytically usable for spatial modeling only after data harmonization and standardization, because the raw inputs (especially hunting yields) are intrinsically heterogeneous in reporting, spatial units, and meaning of zeros and missing values.

El seguimiento de mamíferos a gran escala se vuelve analíticamente utilizable sólo después de que se hayan armonizado y estandarizado los

datos, dado que éstos (especialmente las bolsas de caza) son intrínsecamente heterogéneos en la forma de reporte, el tamaño de las unidades espaciales y el significado de los valores cero y faltantes.

- 4.** Zeros and missing values are not interchangeable across large-scale datasets; treating them as the same can change ecological conclusions, bias estimates, and distort spatial patterns. Decisions about them must be formalized and reported as part of the modeling protocol.

Los ceros y los valores faltantes no son intercambiables en conjuntos de datos a gran escala; tratarlos de igual manera puede cambiar las conclusiones ecológicas, introducir sesgos en las estimas y distorsionar los patrones espaciales. Las decisiones sobre ellos deben formalizarse y reportarse como parte del protocolo de modelización

- 5.** From unstructured wildlife data a single modeling framework is unlikely to perform well across all mammal species at continental scale; models should be tailored to species ecology and to data structure (distribution range, species regulation and management, reporting completeness, and zero structure).

A partir de datos no estructurados de fauna silvestre es poco probable que un único marco de modelización funcione adecuadamente para todas las especies de mamíferos a escala continental; los modelos deben adaptarse a la ecología de cada especie y a la estructura de los datos (rango de distribución, regulación y gestión de la especie, grado de completitud de los datos y la estructura de los ceros).

- 6.** How area is handled strongly controls both totals and spatial patterns; ignoring area inflates uncertainty and can distort maps, whereas using area

as an offset often provides a stable compromise across prediction resolutions and reduces change-of-support bias.

La forma en la que se trata el área influye decisivamente tanto en las estimaciones totales de abundancia como en los patrones espaciales; ignorar el efecto del área aumenta la incertidumbre y puede distorsionar los resultados predictivos, mientras que utilizar el área como offset suele ofrecer un compromiso estable entre distintas resoluciones predictivas y reduce el riesgo asociado al cambio de soporte.

- 7.** Regionalization is an effective operational solution to non-stationarity in abundance-environment relationship, but it tends to create artificial discontinuities at region borders, leading to abrupt jumps in predicted abundance.

La regionalización es una solución efectiva operacional frente a la no estacionariedad en la relación abundancia-ambiente, pero tiende a generar discontinuidades artificiales en los bordes regionales que se manifiestan como cambios abruptos en la abundancia predicha.

- 8.** Models that incorporate spatial dependence can smooth those artificial regional boundaries in predicted abundance, producing more continuous gradients, but they are not a universal solution, and their reliability depends critically on the homogeneity and resolution of the observation units.

Los modelos que incorporan explícitamente la dependencia espacial pueden suavizar los bordes regionales abruptos y producir gradientes más continuos, pero no son una solución universal ya que su fiabilidad depende críticamente de la homogeneidad y la resolución de las unidades observacionales.

- 9.** When observation units vary by orders of magnitude in size, spatial covariance estimation becomes unstable and can yield implausible patterns

in coarse-data regions, representing an explicit manifestation of the modifiable area unit problem at a continental scale.

Cuando las unidades observacionales varían en tamaño en órdenes de magnitud, la estimación de la covarianza espacial se vuelve inestable y puede generar patrones implausibles en regiones con datos a baja resolución, siendo una manifestación explícita del problema de la unidad del área modificable a escala continental.

- 10.** Meaningful spatial relationships between species cannot be reliably assessed using overlap-only co-location metrics when ecological processes operate beyond the observation unit; incorporating species-relevant spatial connectivity is therefore necessary to infer ecological associations.

No es posible evaluar de manera fiable las relaciones espaciales entre especies utilizando sólo métricas de solapamiento espacial si los procesos ecológicos exceden los límites de las unidades de observación. En consecuencia, incorporar la conectividad espacial de cada especie es imprescindible para inferir sus asociaciones ecológicas.

- 11.** Applying species-informed connectivity to real data reveals ecological spatial associations (e.g., convergence vs. divergence zones) that differ systematically from overlap-based interpretations, thereby changing prioritization of areas for multi-species management and conservation.

La aplicación de conectividad informada por la especie a datos reales revela asociaciones ecológicas espaciales (e.g., zonas de divergencia frente a zonas de convergencia) que difieren sistemáticamente de las interpretaciones basadas en el solapamiento, lo que modifica la priorización de áreas para la gestión y conservación de múltiples especies.

12. Standardized structured data from camera trap networks coupled with multispecies N-mixture models provide consistent abundance-environment relationships across broad spatial extents, while revealing species-specific variation in detectability.

Los datos estructurados y estandarizados provenientes de redes de fototrampeo combinados con modelos N-mixture multiespecie permiten obtener índices consistentes entre la abundancia y el ambiente a lo largo de amplias extensiones espaciales, al tiempo que ponen de manifiesto variaciones específicas en la detectabilidad entre especies.

13. Camera-trap–based relative abundance indices from multispecies N-mixture models align only weakly with hunting-yield–derived abundance proxies across spatial scales, highlighting fundamental differences in observation processes.

Los índices de abundancia relativa obtenidos a partir de información de cámaras trampa mediante modelos N-mixture multiespecies presentan una baja concordancia con los proxies derivados de bolsas de caza a diferentes escalas espaciales, evidenciando diferencias fundamentales en los procesos de observación.

Continued progress in large-scale ecological inference will depend not only on improved data collection and more sophisticated statistical models, but also on a deeper understanding of how methodological choices interact with ecological complexity to shape the patterns we seek to describe. Recognizing and embracing this interplay is essential for developing approaches that are not only analytically rigorous but genuinely useful for ecological research. As famously stated by George Box, “*all models are wrong, but some are useful*”.

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*You will probably have people tell you
to pace yourself, try not to rush (...)
and that might be the right advice.*

*But I also want you to consider
where being young and unknown
could be an advantage.*

*Go fast when you need to go fast. (...)
I've found that once you start fast,
you can go further than you think you can.*

Listen to your coaches.

Listen to your family members.

Listen to your mentors and bosses.

But also listen to yourself. Don't be afraid.

*Sometimes you just have to go for it
and find out what you're capable of.*

—Katie Ledecky

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*Gracias por venir a donde alguien os quiere,
sin querer – Robe Iniesta*

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