

# BIOGEOGRAPHIC REALISM IN SPECIES DISTRIBUTION MODELS: PSEUDO-ABSENCE STRATEGIES AND SPATIAL AUTOCORRELATION IN *APODEMUS SYLVATICUS*

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## ABSTRACT

Species distribution models (SDMs) often extrapolate into regions that are ecologically and geographically unsuitable for the focal species. Using the Western Palearctic wood mouse (*Apodemus sylvaticus*) as a case study and data pre-filtering, we evaluated six pseudo-absence (PA) generation strategies and four variable selection protocols aimed at improving the accuracy of predicted distribution maps while minimising spatial autocorrelation of residuals. Models were fitted using an iterative Bayesian additive regression trees algorithm (bart.step) and evaluated based on AUC, TSS, false-negative rate, Moran's I, and Biogeographic Realism – the latter defined as the absence of predicted suitability in absolute dispersal barriers such as deserts, Arctic tundra, and northern islands.

Environmental-contrast filtering (SRE) produced only limited improvements in spatial autocorrelation and did not consistently enhance the realism of predicted distributions. Across the tested pseudo-absence strategies, several models achieved very high discriminatory performance (AUC  $\approx$  0.97–0.99), including EuGlobal with Range and Palearctic-based approaches. However, these models often produced spatial artefacts in barrier regions or showed reduced coverage of the species' peripheral range. In contrast, the Global+AC strategy (random PA selection combined with autocorrelation-guided variable selection) provided the most balanced performance, achieving high predictive accuracy (test AUC  $\approx$  0.98; TSS  $\approx$  0.86) along with enhanced Biogeographic Realism and reduced spatial artefacts. All four best models were obtained using residual autocorrelation-guided variable selection. The reproducible workflow, implemented in custom R functions, is transferable to other Palearctic terrestrial vertebrates.

**Keywords:** background conditions; Biogeographic Realism; macroecological heterogeneity; model transferability; pseudo-absence generation; spatial ecology; spatial ecological niche; surface range envelope.

## INTRODUCTION

Species distribution models (SDMs) are widely used in ecology to assess climate change impacts, inform conservation planning, and study biogeography (Guisan & Zimmermann,

2000; Austin, 2002; Guisan & Thuiller, 2005; Peterson, 2006; Guisan *et al.*, 2013; Gastón *et al.*, 2014; Tulloch *et al.*, 2016). Mechanistic models (MNM), which incorporate species physiology (e.g., for Australian lizards; Kearney & Porter, 2004), population dynamics (Cabral & Schurr, 2010), and local experiments (Alexander *et al.*, 2015), remain rarely used in large-scale biogeographic studies due to data complexity and scale mismatches, despite a growing trend (Wüest *et al.*, 2018). A large number of SDMs rely on species presence data complemented by pseudo-absences (PAs) (Barbet-Massin *et al.*, 2012). The choice of PA generation strategy critically influences model calibration, predictive accuracy, and ecological interpretation (Chefaoui & Lobo, 2008; Phillips *et al.*, 2009; Broussin *et al.*, 2024; Rausell-Moreno *et al.*, 2025). Despite numerous proposed approaches – ranging from random selection to methods based on ecological or geographic distance – no consensus exists on an optimal strategy (Gábor *et al.*, 2022; Da Re *et al.*, 2023; Wang *et al.*, 2023; Pili *et al.*, 2025). Addressing this issue in finer detail was beyond the scope of the present work, but comparison under identical conditions allows evaluation of alternative approaches.

A critical consideration in SDMs is the distinction between the potential niche (defined by physiological limits) and the realised niche (constrained by dispersal barriers, biotic interactions, and landscape structure), as this distinction informs methodological choices (Jiménez-Valverde *et al.*, 2008; Tytar, 2011; Zarzo-Arias *et al.*, 2023). The choice of PAs is related to this distinction: for the potential niche, PAs from a wide range of conditions are preferred (Araújo & New, 2007), while for the realised niche, finer tuning is required, mimicking biotic interactions (Fleishman *et al.*, 2001; Ferrier *et al.*, 2002). As noted by Broussin *et al.* (2024), generating PAs in ecological space, rather than just geographical space, can improve the biological relevance of response curves in SDM.

In landscape ecology, the spatial configuration and composition of environmental patches – mediated by corridors and matrix quality – fundamentally shape species' realised distributions (Forman, 1995; Urban, 1994). Ignoring landscape context at any scale confuses the fundamental and realised niches. Despite the increasing statistical sophistication of SDMs, many models still produce geographically implausible predictions (Elith & Leathwick, 2009; Zurell *et al.*, 2020), including high suitability in deserts, Arctic islands, or other absolute dispersal barriers – a problem that is rarely explicitly tested. Such artefacts reveal a fundamental limitation of purely statistical model evaluation.

The challenge of incorporating biological realism into SDM predictions has received growing attention (Record *et al.*, 2018), yet practical frameworks for assessing the ecological plausibility of model outputs remain underdeveloped. We introduce the concept of Biogeographic Realism as a general framework for evaluating the biological and geographical plausibility of species distribution models. While the concept can encompass multiple dimensions of biological and geographical credibility – including historical range dynamics, demographic connectivity, or phylogeographic structure – here we operationalise it through two complementary and readily quantifiable components: barrier realism, describing the avoidance of geographically implausible predictions across major dispersal barriers, and empirical range completeness, describing the extent to which predictions retain the known empirical distribution of the species (see Methods for operational definitions).

Spatial autocorrelation (statistical dependence of values at nearby points, SAC) represents a serious challenge in SDMs. Autocorrelation analysis is one way to account for spatial heterogeneity in environmental drivers (Zhao & Pu, 2025). Its presence in model residuals may indicate unaccounted factors, violation of observation independence, incorrect conclusions about predictors, and overestimated accuracy (Legendre, 1993; Dormann *et al.*, 2007; Araújo *et al.*, 2008; Veloz, 2009), but this is not confirmed by some authors (Thibaud *et al.*, 2014). Before the rise of citizen science and GPS technology in the 2000s, sampling

bias often arose from imprecise occurrence coordinates, typically recorded as settlement or mountain peak names (Wieczorek *et al.*, 2004). On the other hand, positional uncertainty has less impact on model quality when the spatial autocorrelation of variables is high. In landscapes with high SAC, a 2 km shift implies minimal environmental change. Conversely, in heterogeneous terrain, such a shift may cross steep ecological gradients (Naimi *et al.*, 2011). Predictor selection is also important for minimising autocorrelation (Elith & Leathwick, 2009). Spatial autocorrelation of residuals can be related to sampling bias (Phillips *et al.*, 2009).

We examined how PA selection influences residual SAC and whether reducing autocorrelation concurrently with PA selection enhances macroecological realism. Furthermore, we integrated core landscape-ecology principles into SDM methodology (Forman & Godron, 1986; Jongman *et al.*, 2004) by explicitly linking pseudo-absence generation to matrix permeability and major biogeographic barriers.

The wood mouse provides a useful example of a species whose distribution is shaped by landscape structure. In Europe, it occurs in permeable matrices of hedgerows, small woodlands, riparian zones, and agricultural fields. In contrast, deserts, arctic tundra, and large bodies of water serve as dispersal barriers (Umetsu & Pardini, 2007; Rusin, 2024).

This study is based on a comparative analysis of six PA selection methods using *A. sylvaticus* as an example. The objectives of the study were:

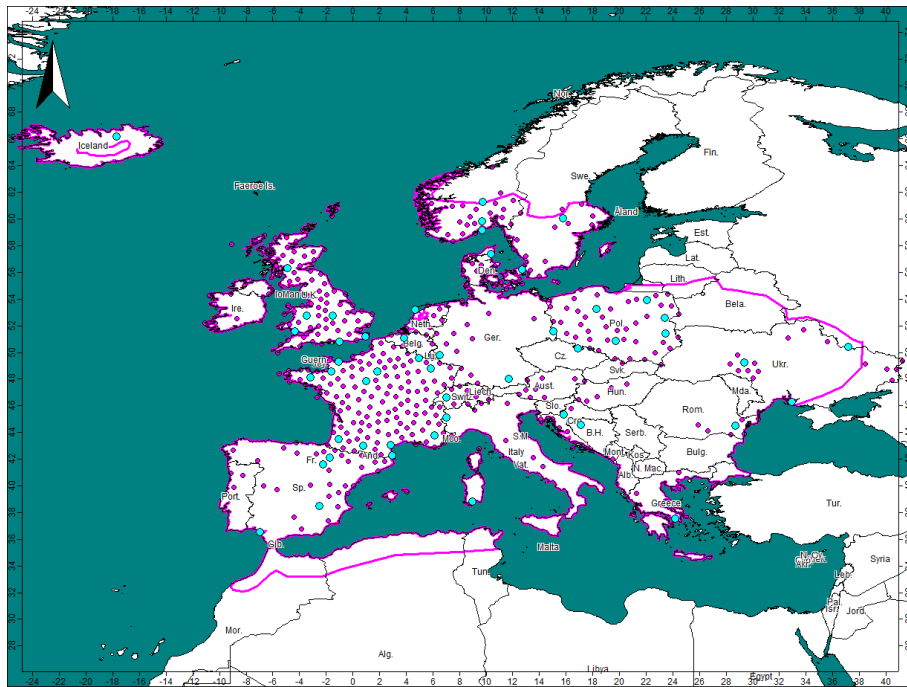
1. To assess the influence of various PA selection strategies on the Biogeographic Realism of predicted distribution maps (i.e., minimising implausible predictions).
2. To assess statistical indicators of model accuracy (Area Under the Curve, AUC; True Skill Statistic, TSS; False Negative Rate, FNR).
3. To investigate how PA selection affects the level of autocorrelation of model residuals (Moran's I index).
4. To study how variable selection, aimed at reducing the spatial autocorrelation of model residuals, affects the macroecological realism of the model prediction map.
5. To propose practical recommendations for choosing a PA selection strategy, emphasising Biogeographic Realism, SAC and degree of range coverage as key criteria, and to present algorithms for solving these problems.
6. To test whether variable selection guided by minimisation of residual Moran's I could simultaneously improve both statistical and macroecological performance.

## STUDY SPECIES AND PRESENCE DATA

The wood mouse *Apodemus sylvaticus* (Linnaeus, 1758), a member of the Muridae family, was selected for this study due to its well-documented distribution and abundance of occurrence records across the Western Palaearctic. The species is currently listed as Least Concern on the IUCN Red List. Its range extends latitudinally from North Africa to southern Scandinavia, and longitudinally from the British Isles and Iceland in the west to the borders of Ukraine, Belarus, and Russia in the east (Mezhzhherin & Lashkova, 1992). Notably, the eastern range limit, although relatively sharp, is not associated with obvious landscape or habitat barriers, suggesting that factors other than gross environmental discontinuities constrain the distribution. The species has been extensively studied using genetic and DNA markers, providing a wealth of reliable occurrence data (Michaux *et al.*, 1996, 2003, 2005) and making it a well-established model in phylogeographic research on post-glacial refugia (Herman *et al.*, 2017). These characteristics render *A. sylvaticus* particularly suitable for GIS-based species distribution modelling.

From a landscape ecology perspective, the wood mouse typifies species that persist in fragmented, human-dominated environments. Its distribution is maintained by dispersal corridors such as forest belts, hedgerows, and riparian zones. In agricultural landscapes, small woodlots and hedgerows form a permeable matrix that preserves structural connectivity, in contrast to intensively cultivated monocultures where connectivity is lost. The species avoids dense taiga forests and open tundra, confining its occurrence to landscapes where woody and herbaceous linear elements provide cover and food resources. These habitat requirements make *A. sylvaticus* an excellent umbrella species for assessing landscape permeability and the effectiveness of green infrastructure in European cultural landscapes.

**Fig. 1: The location of the training and test presence subsets used in all methods.**



Legend: Training (small purple circles) and test (large blue circles) presence points overlaid on the IUCN range polygon (purple line).

Occurrence records were downloaded from the Global Biodiversity Information Facility (GBIF, 2024). We retained only observations from 1970–2000 to align with the temporal coverage of the climatic layers, thereby minimising potential bias from temporal mismatch (Fithian *et al.*, 2015). Temporal autocorrelation was considered by including the “year” variable and assessing its importance only at the preliminary modelling stage. Spatial duplicates were removed to reduce sampling bias inherent to opportunistic biological recording (see Table A). All additional materials are uploaded to the repository [https://codeberg.org/reviewer12345/Supplementary\\_Information](https://codeberg.org/reviewer12345/Supplementary_Information).

The initial set of presence data underwent a spatial thinning procedure to reduce clustering and maintain spatial representativeness. Custom code with a function from the *spThin* package (Aiello-Lammens *et al.*, 2015) was used in the R environment, ensuring a minimum distance between points (30 km) for a specified total number of 500 points (Thibaud *et al.*,

2014). This approach adapts the principles described by Beck *et al.* (2014). The total sample of presence points was divided into training (90 %) and testing (10 %) subsets. A custom code was used for maximising intra-group and inter-group distances using k-means clustering (algorithm and results B, Fig. 1 (training/test points)).

Presence data with covariates are provided in Supplementary Tables C (training) and D (test), with the corresponding algorithm detailed in Appendix E.

Geospatial data of the wood mouse's range were obtained from the IUCN Red List in ESRI Shapefile format (Schlitter *et al.*, 2021 (amended version of 2016 assessment)). In zoogeographic studies, species ranges are usually displayed as continuous polygons without internal gaps, except in cases justified by natural hurdles such as large water bodies, deserts (points F), or high mountains.

## ENVIRONMENTAL VARIABLES

We used 19 bioclimatic variables from WorldClim v2.1 (1970–2000) and elevation data. The spatial resolution was set to 5 arc-minutes (~10 km) (algorithm G) to match the positional uncertainty of the historical occurrence records: 78.6 % of the records had an uncertainty of up to 5009 m, and following Moudrý *et al.* (2024), we set the resolution to approximately twice the uncertainty. This resolution also aligns with the broad spatial scale of our analysis, consistent with the hierarchical framework of Pearson & Dawson (2003), which advocates modelling macroclimatic suitability before incorporating finer-scale predictors. Finer resolutions (e.g., 2.5') were not considered, as they would exceed the spatial accuracy of most available observations. To maintain sample size, the remaining 21.4 % of points with higher positional uncertainty were retained, as boosted regression trees have been shown to be only slightly affected by such location errors (Graham *et al.*, 2008; Smith *et al.*, 2023). Data sampled from presence points and PAs were subsequently normalised (0–1). Future work could integrate finer-scale variables (e.g., land use, soil) to refine predictions at regional scales (Pearson & Dawson, 2003).

### Pseudo-absence generation

Six methods for generating PAs (see below) within six different-sized areas, but outside the species' default range or within it when specifying “with Range” (Varela *et al.*, 2014), were tested and compared. The radius-based method (random PAs within fixed distances from presence points) performed poorly in preliminary tests and was therefore excluded from further analysis (but see Fig. P.31 for comparison).

1. EuGlobal: PAs were randomly sampled across all global landmasses. This is a large area, including both climatically suitable but inaccessible regions (North America), and completely unsuitable ones (tundra and deserts).

2. Global selection (Global): PAs were selected within the extent from the equator to the North Pole 0–90°N (mask of the land) and from 25°W to 180°E. This method selected pseudo-absences in areas that were largely inaccessible or ecologically poorly compatible with the species. This extent was deliberately restricted to the Euro-Afro-Asian extent to intentionally exclude North and South America, whose temperate climates are highly analogous to Europe but historically inaccessible to *A. sylvaticus* due to post-Pleistocene dispersal barriers and competitive exclusion. Our 'Global' method corrects this by focussing on truly unsuitable habitats (e.g., Arctic tundra, Sahara) within a sufficiently broad climate zone of the species, ensuring that the model learns from absence conditions rather than analogous but unreachable ones.

3. Selection within the Palaearctic (Palaearctic): PAs were selected within a Palaearctic-bounded polygon (I), excluding islands. The idea was similar to the previous one, but taking into account zoogeography.

4. Western Palaearctic: The selection space comprised two zoogeographic regions of the Western Palaearctic (Holt *et al.*, 2013) (polygon J) where the species range is located.

5. Radii around presence points (Radii): PAs were generated in an annular zone around presence points: at a distance of at least 30 km and no more than 500 km (BCCVL (2020), algorithm K).

6. Buffer zone around the range (Buffer): PAs were selected randomly in a 500 km zone around the known species range, but not closer than 30 km to presence points. This method assumes that the species, for some reasons, has not occupied adjacent territories despite their potential suitability (algorithm L).

Essentially, these methods are a combination of background sampling of the target group and random sampling at a distance, interacting factors “M” and “A” (according to Barve *et al.*, 2011). The question of how many of these PAs actually fall in the climatically suitable but inaccessible zone, or in the accessible but unsuitable zone, is addressed in this study by modelling biogeographic suitability conditions.

For each method, the same number of PAs and presence points were obtained in the end (900 points for the training set and 100 for the test set, representing both classes), based on Carlson (2020), Rausell-Moreno *et al.* (2025) for optimal performance and to minimise suitability bias towards any class.

PAs were generated in two ways: by random sampling or by using the Surface Range Envelope (SRE) method (Hutchinson, 1957). The SRE method aimed to select PAs from conditions significantly different from those where the species is present. We tested three quantile thresholds – 0.025 (95 % confidence interval) based on BCCVL recommendations (2020), 0.1, and 0.25–0.75 (Lobo *et al.*, 2010) – in cross-validation experiments that balanced two objectives: reduction of spurious suitability in known dispersal-barrier biomes and maintaining range cover. Preliminary testing indicated that a 0.1 quantile provided the optimal trade-off: it excluded core suitable habitats more effectively than the 0.025 quantile (which was too conservative) while maintaining a broader representation of background conditions than the 0.25 quantile (which overly restricted the pseudo-absence space) (for example algorithm M.1 for Global method). Creating a SRE mask based on quantiles of selected layers and generating PAs used spatSample (algorithms H) limited the amount of data processed simultaneously. The environmental space for SRE was defined by the principal components from a principal component analysis (PCA) of environmental information extracted from presence and PA (Varela *et al.*, 2014).

### Predictor Selection

Where species distribution is largely determined by environmental factors, a correctly specified model fitted using an adequate set of predictors should exhibit minimal SAC in its residuals (Elith & Leathwick, 2009). Minimising Moran's I is not only a statistical goal but also reflects the elimination of spatial artefacts associated with hurdles and matrix structure. For each pseudo-absence method, we applied four variable-selection algorithms aimed at retaining ecologically relevant predictors while minimising residual spatial autocorrelation. All algorithms followed three core steps:

1. Correlation filtering: Variables with Pearson correlation  $> 0.85$  were removed using the `findCorrelation()` function from the caret package.

2. Variable importance: Remaining predictors were ranked using the Bayesian Additive Regression Trees (BART) algorithm (`bartMachine` package), with a threshold determined via the elbow method on sorted importance scores.

3. Residual SAC was evaluated using Moran's I thresholds in the range 0.5–0.85, chosen to retain macroecologically important predictors (see model reports for details). Variables were iteratively removed until Moran's I approached a target range (0.5–0.85) or reached a plateau, ensuring that at least three predictors (including BIO3 and BIO9) were retained for ecological interpretability.

This multi-algorithm approach allowed derivation of alternative predictor subsets tailored to sampling and regional contexts, enabling evaluation of trade-offs in model performance and spatial bias. By integrating correlation filtering, importance ranking, and residual autocorrelation checks, the selected variables maximised ecological representativeness while minimising spatial artefacts (Phillips *et al.*, 2009). A more detailed logic of the algorithmic steps (M.2–M.5) is given in M.7; here we summarise only the main principles. Detailed outputs, including selected variables, Moran's I values, and comparisons between exploratory and final subsets, are provided in method-specific reports (e.g., report M.6 for the best method).

### Model calibration

The BART algorithm was used for modelling species' occurrence probability, chosen for its flexibility and resistance to overfitting in SDM, outperforming Generalised Linear Model (GLM) in identifying non-linear dependencies (Carlson, 2020; Chipman *et al.*, 2010) and methods like `randomForest` that require intensive hyperparameter tuning (not used in this study). The main model was trained on the training sample (Table C) using `bart.step` (`embarcadero` package), which implemented modified algorithms from Chipman *et al.* (2010) for ecological modelling. Because `bart.step` does not natively support prediction on test data (a requirement for assessing model quality), we employed an alternative procedure using `wbart` and `dbart` models (for more details, see text N.1 and algorithm N.2).

For comparison, we also fitted a GLM with a spatial lag to assess whether a simpler linear model could adequately account for spatial autocorrelation (Dormann *et al.*, 2007). We selected BART over MaxEnt to strictly control the prevalence ratio (1:1 presence-absence) within an iterative Bayesian framework, which offers robust handling of non-linearities and spatial autocorrelation without the need for the specific background sampling parameter tuning required to adapt MaxEnt to equal-prevalence designs (Barbet-Massin *et al.*, 2012; EcoCommons, 2025).

### Evaluation metrics

Model quality was assessed using the following metrics:

1. AUC: area under the receiver operating characteristic (ROC) curve, characterising the overall discriminatory ability of the model.
2. TSS: true skill statistic.
3. Kolmogorov-Smirnov test to compare predicted probabilities and residuals.

Overfitting analysis included comparing AUC and TSS on training and test samples. The difference ( $\Delta$ ) of AUC and TSS served to diagnose overfitting with the following thresholds (target:  $\Delta\text{AUC} < 0.05$  normal, 0.05–0.1 possible overfitting,  $> 0.1$  overfitting;  $\Delta\text{TSS} < 0.1$  normal, 0.1–0.2 possible overfitting,  $> 0.2$  overfitting). AUC and TSS thresholds for assessing overfitting were taken from Muscarella *et al.* (2014) and Allouche *et al.* (2006) respectively.

4. FNR: false negative rate. Evaluation was performed on both training and test samples.
5. FPR: False Positive Rate.
6. Biogeographic Realism: While visual inspection of predicted distributions is a common diagnostic tool in SDM studies (Alvarado-Serrano & Knowles, 2014), here it was not based on subjective judgment, but was operationalised through two complementary components. First, barrier realism was evaluated as the absence of predicted suitability in three predefined barrier categories: (1) Sahara and Libyan Desert, (2) Arctic islands (Greenland, Svalbard, Novaya Zemlya), and (3) Central Asian deserts (Karakum, Thar). Second, empirical range completeness was evaluated as the proportion of the species' IUCN range polygon covered by the predicted suitability surface, with minimisation of omission (FNR) as the primary target. Models with high scores on both components were considered to exhibit strong Biogeographic Realism. Formal quantitative definitions of the Biogeographic Realism components are provided in Supplementary Appendix P immediately below Table P.1.

A model with excellent statistical performance but producing geographically implausible predictions has limited ecological value; conversely, visual inspection alone without statistical grounding is insufficient. Therefore, statistical metrics were used in the first stage to detect overfitting (and ultimately for the final comparison of the best methods). The absence of overfitting is a necessary but not sufficient condition. In the second stage, the cutoff threshold on the prediction map was adjusted (the target FNR had to be less than 0.06, corresponding to three test skip points). In the third stage, the model's likelihood was visually assessed by examining the spatial consistency of the predicted distributions.

To assess the transferability and stability of the best BART models, we performed spatial cross-validation and bootstrap uncertainty estimation. Cross-validation was conducted on the training set using five spatially structured folds defined by latitudinal bands. We adopted latitudinal band partitioning rather than a standard checkerboard or random block scheme for the following structural reason. All 450 presence records are confined to Europe (37–63°N), while pseudo-absences are observed throughout the entire Euro-Afro-Asian extent. Applying a checkerboard or random spatial block design to this strongly asymmetric distribution routinely produces folds that contain zero presences or zero absences, rendering fold-level metrics undefined. Roberts *et al.* (2017) explicitly advocate partitioning schemes that reflect the geographic structure of the data rather than a single standard implementation; latitudinal bands defined by quantiles of presence-record latitude satisfy this requirement by guaranteeing approximately equal numbers of presences per fold while allocating absences by geographic position. Band boundaries were therefore determined by quantiles of presence-record latitude, and absences were allocated to bands by their latitude, so that each fold contained both classes. For each fold, the remaining four bands served as the training set and the held-out band as the test set; a BART model was fitted using `dbarts::bart` with reduced parameters (`ntree = 100`, `nskip = 100`, `ndpost = 200`) to ensure stability on smaller subsets. Posterior predictive probabilities were obtained by applying the logistic transformation to the column means of the posterior sample matrix and clipped to the [0, 1] interval. Fold-level discrimination was assessed by AUC (`pROC` package). Classification thresholds were determined in two ways:

- a) the "best" threshold according to the ROC curve, yielding maximum TSS and associated FNR and FPR;
- b) a threshold approximating a target false-negative rate of 0.04, from which TSS, FNR, and FPR were recorded.

To complement per-fold statistics, we also evaluated pooled predictions obtained by combining the outputs of all cross-validation folds, providing a single overall estimate that accounts for the full heterogeneity of the spatial design. Summary statistics were reported as mean  $\pm$  standard deviation across folds alongside the pooled estimate.

To quantify uncertainty in test-set predictions, we applied non-parametric bootstrap resampling (1000 replicates) to the test predictions of the selected best models and derived 95 % percentile confidence intervals for all metrics. Agreement between CV means and bootstrap confidence intervals of the corresponding test estimates was used as a consistency check for model generalisation. All random seeds (set.seed(123) for CV fold assignment, set.seed(456) for bootstrap), per-fold results, pooled metrics, bootstrap summaries, and the complete R scripts are provided in the Supplementary Information.

Post-hoc validation of the final model was conducted on independent data from the same 1970–2000 training period in North Africa, but obtained after our access to the modelling data (GBIF, 2025).

To test the robustness of the final BART-step model obtained over the 1970–2000 training period to temporal variability over the 2001–2025 test period (which accounts for interannual climate variations based on ERA5-Land data (Muñoz-Sabater *et al.*, 2021)), we also performed point, cv, bootstrap, and visual inspections of gaps in the predicted suitability conditions (see the scripts and results in GlobAut.zip (Supplementary Information)).

### Threshold Calibration and Bias Correction

The initial calibration of models based on a combination of BART and auxiliary regressions (GLM, LM) sometimes resulted in a systematic bias in the predicted probabilities: the distributions for the test set were shifted relative to the training set, which had a particularly strong impact on the threshold metrics (TSS, FPR) at a fixed FNR of 0.04. It was necessary to manually set the cutoff threshold on the macrodistribution folds, trying to achieve a FNR of less than 0.06, which corresponded to three missed test points. Since the primary goal of this study was to construct potential distribution maps with a minimal risk of missing true locations (FNR = 0), we applied a conservative post-hoc calibration: a uniform additive shift to predicted probabilities was chosen to ensure no test presences fell below the operational threshold (target FNR  $\leq$  0.06). This preserves rank order (AUC unchanged) while aligning absolute probabilities with the empirical threshold used for mapping (Fig. P.38). All final indicators in the tables are presented after this calibration; the original values (before the shift) are available in the Supplementary Information.

### SAC analysis

Calculations were performed using Moran's I for training and test residuals, and Cross-Moran's I between them according to Dormann *et al.* (2007) recommendations for SDM (algorithm N.2). We considered Moran's I values  $\leq$  0.2 as low, indicating successful accommodation of spatial structure; values between 0.2 and 0.3 as moderate; and values  $>$  0.3 as high, suggesting either unaccounted autocorrelation (training set) or potential overfitting to spatial noise (test set). Cross-Moran's I between residuals on the training and test subsets was also assessed to identify potential transfer of spatial patterns ( $>$  0.2 possible overfitting).

Residual spatial autocorrelation was quantified using Moran's I calculated on model residuals extracted at the 500 presence and 500 pseudo-absence locations (1000 points total). Although the number of evaluation points is modest relative to the vast study extent, it nevertheless provides sufficient power to detect large-scale residual autocorrelation and allows consistent comparison across models (cf. Veloz, 2009). To assess residual spatial

autocorrelation, we calculated the Moran's I index on the residuals of each model for neighbourhood values  $k = 1-10$  to test the sensitivity of the results to neighbourhood scale. For each model, we additionally calculated the corresponding Moran's I p-values for each  $k$ , which allowed us to track how the strength and statistical significance of the autocorrelation changes. The reports provide the full range of Moran's I values for  $k = 1-10$  and indicate the selected value for each model at the  $k$  value that yielded the minimum p-value (the most statistically significant autocorrelation) for that model. All reported Moran's I values were highly significant ( $p < 0.0001$ ), indicating the presence of spatial autocorrelation.

Given the study's focus on macroecological validity, detailed statistical comparisons were limited to core performance metrics. A detailed summary of all modelling results and diagnostic plots is provided in the Supplementary Information. The analyses were executed in the R statistical computing environment (R Core Team, 2023, version 4.3.0). The modelling workflow relied on several specialised packages: *terra* (v1.7.65; Hijmans, 2024) for spatial data manipulation, *caret* (v6.0.94; Kuhn, 2008) for model training and optimisation, *spdep* (v1.3.3; Bivand & Wong, 2018) for spatial dependency analysis, *bartMachine* (v1.3.4.1; Kapelner & Bleich, 2016) for BART modelling, *spThin* (Aiello-Lammens *et al.*, 2015) for spatial thinning of occurrence records, and *embarcadero* v. 1.2.0.1003 (Carlson, 2020). SAGA GIS (v. 9.7.1 17, Conrad *et al.* (2015)) was used to obtain predicted distribution maps.

## RESULTS

The following modelling results were calibrated using primary procedures (Table 1):

**Table 1: Results for all pseudo-absence generation methods.**

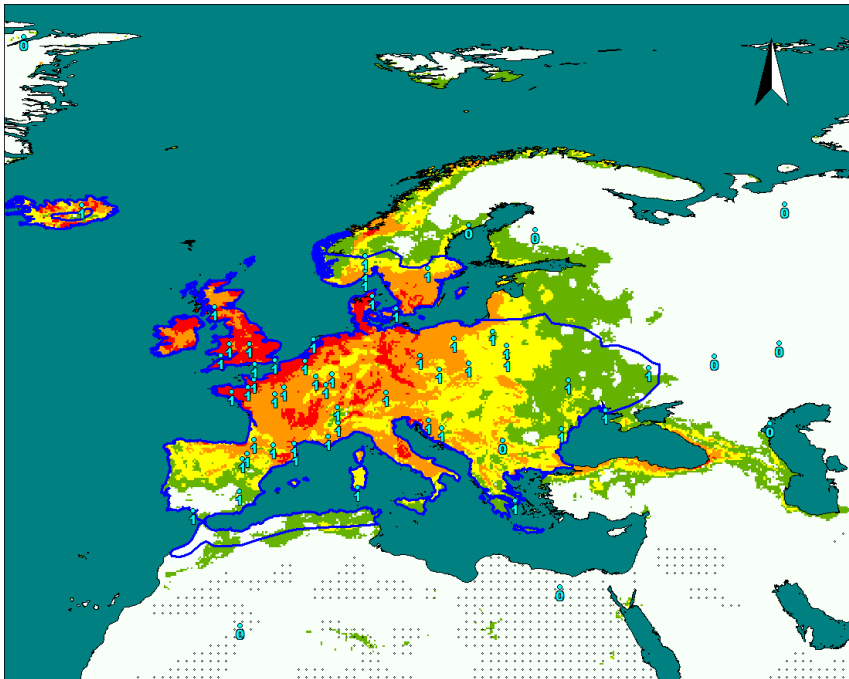
| Method             | Names of reports | Fig. reference |
|--------------------|------------------|----------------|
| EuGlobal           | O                | 2,3,P.1–P.8    |
| Global             | Q                | 4,P.9–20       |
| Palaeartic         | R                | 5,P.21–28      |
| Western Palaeartic | S                | P.29,30        |
| Radii              | T                | P.31           |
| Buffer             | U                | P.32–P.35      |

Model performance differed markedly among PA strategies. The Western Palaeartic and Radii methods produced the least biogeographically plausible predictions, with spurious suitability in known barrier regions; these models are shown only in the Supplementary Information. Across the 15 variable selection procedures tested, residual correlation was not consistently reduced. However, biogeographic plausibility improved in five cases (see comments on Figs. P.2, P.6, P.10, P.18, P.20), two of which corresponded to the best-performing models; decreased in three cases (Fig. P.28, P.33, P.34); and showed ambiguous effects in seven cases (Fig. P.4, P.12, P.14, P.16, P.22, P.24, P.26), two of which also ranked among the best models. Model deviations were most pronounced in distinct landscape units and potential biogeographic transition zones, including the northern islands, the northeastern and southwestern edges of the range, and the Libyan Desert, highlighting the challenge of projecting distributions across sharp macroecological gradients and barriers.

Surface Range Envelope (SRE) filtering at quantile 0.1 did not consistently improve model performance across the tested pseudo-absence strategies. Paired comparisons between SRE-filtered and random-selection models for EuGlobal, Global, and Palaeartic methods showed no statistically significant differences in AUC, TSS, or Moran's I (all  $p > 0.05$ ; Tables P.5–P.8). Reductions in training residual autocorrelation were marginal and often offset by increases in test-set or cross-Moran's I values. Detailed metrics for the Western Palaeartic method (Table P.6) illustrate this pattern. Visual assessment of prediction maps (Figs. P.11–P.18, P.25–P.28) confirmed that SRE filtering occasionally reduced overprediction in barrier regions but frequently introduced underprediction at range margins, particularly in southwestern Iberia and North Africa.

Four models demonstrated superior and statistically robust performance (Table P.1, Figs. 2–6, P.4, P.6, P.10, P.22): EuGlobal with Range, EuGlobal+SRE (0.1 quantile) with Range, Global, and Palaeartic methods—all using residual autocorrelation-guided selection.

**Fig. 2: Map of potential distribution of *A. sylvaticus* (EuGlobal method with Range) after residual autocorrelation-guided selection.**



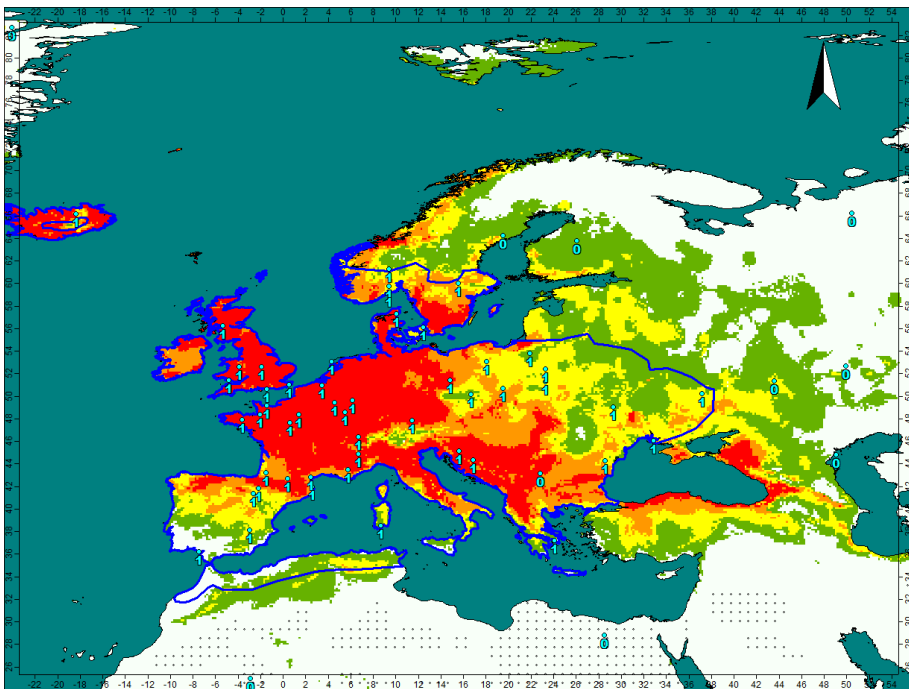
General legend for Figs. 2–5.

Test set: presence points = 1, pseudo-absences = 0. Small grey dots indicate major desert biomes. Blue line outlines the habitat. Colours from green to red indicate increasing probability of presence. Thresholds were selected by aligning the predicted probability scale so that the omission penalty matched the empirical rule used throughout the study (one omitted test presence  $\approx 0.02$  FNR). Because test presences rarely fall exactly on the classification boundary, threshold optimisation was performed by small uniform shifts that ensured consistent FNR accounting across all models ( $\leq 6\%$ ). Whenever model performance allowed, the threshold was adjusted to achieve FNR = 0 % (e.g. Global+AC method).

Threshold optimisation was guided by minimising false negatives (FNR), while false positive rates (FPR) were not the main focus, as the practical goal was to avoid omission of potentially suitable areas. For intermediate comparison maps, only binary thresholds are shown, because the purpose of these figures is to contrast spatial patterns rather than visualise continuous probabilities. Calibration is used only for mapping purposes to avoid missing known hotspots and is not used to select the best models. The final continuous map with a unified colour scale is presented in Fig. 9. To save space, only regions exhibiting implausible predictions (artefacts) are shown. The legend for Figs. 3–5, P.1–20 is identical to that for Fig. 2.

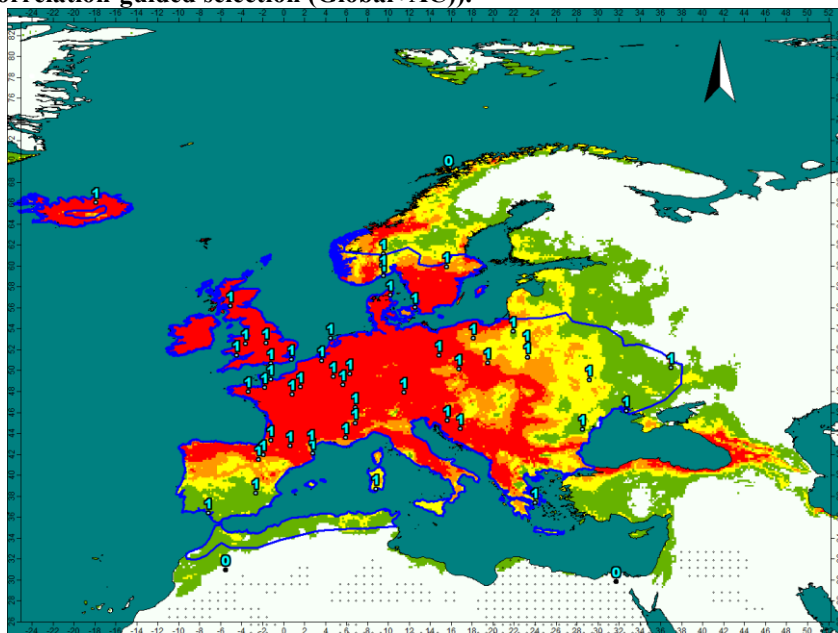
Minor under-prediction occurs in the east (FNR +2 %), southwestern Iberia and northwest Africa (FNR +3 %). Performance metrics (Figs. 2–5) are shown in Tables P.1–P.11.

**Fig. 3: Map of potential distribution of *A. sylvaticus* (EuGlobal and SRE (quantile 0.1) method with Range) after residual autocorrelation-guided selection.**



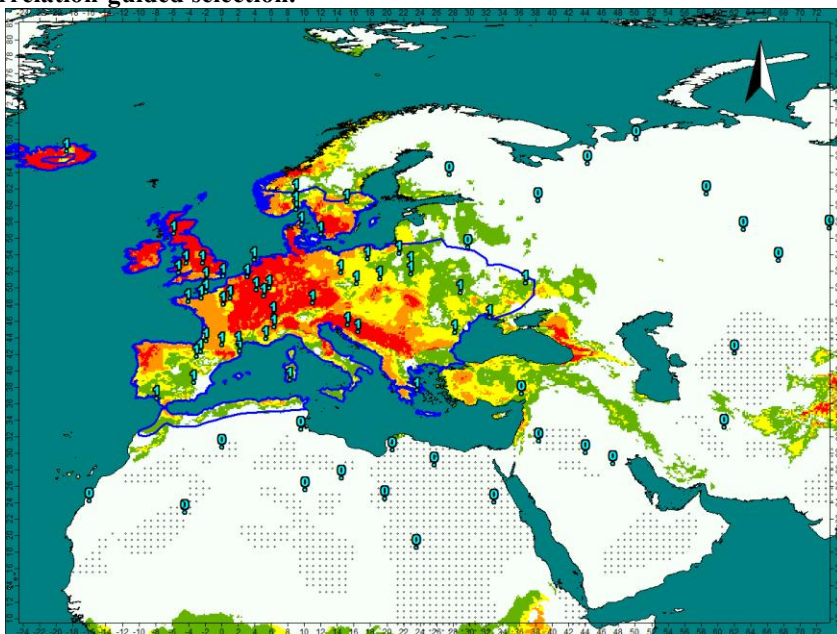
Suitability for southern Svalbard is realistic due to warm currents.

**Fig. 4: Potential distribution map of *A. sylvaticus* (Global method after residual autocorrelation-guided selection (Global+AC)).**



The model achieved high predictive accuracy with minimal omission error.

**Fig. 5: Potential distribution map of *A. sylvaticus* (Palearctic method) after residual autocorrelation-guided selection.**

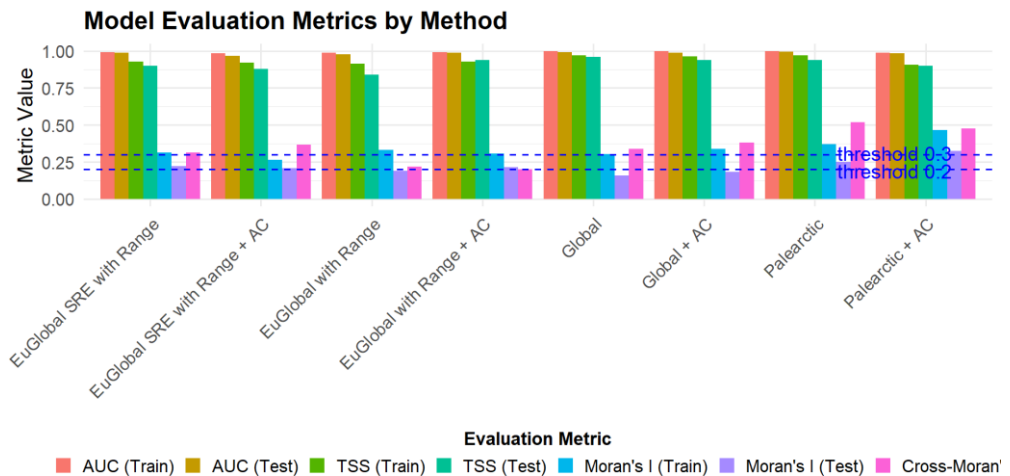


No artefacts are visible on northern islands, but predictive coverage is limited in the northeastern and southwestern parts of the range.

Among the four BART models, Global+AC performed best, with minimal differences between training and test metrics (AUC, TSS, FPR) and spatial generalisability (Moran's I for residuals) (Fig. 6, P.37), disregarding the KS-test as a calibration quality proxy, which often fails due to systemic artefacts (bart.step lacks native test predictions, necessitating an alternative procedure: wbart/dbarts + GLM/LM/Quantile). Training–test divergence was negligible across all key metrics, and test residuals showed low spatial autocorrelation (Moran's I = 0.1834 at k=6), while residual SAC in training predictions remained substantial (Moran's I  $\approx$  0.34; cross-Moran's I  $\approx$  0.38), reflecting large-scale spatial structure not fully captured by the predictors.

The Global+AC model achieved a test AUC of 0.987 and TSS of 0.940 (optimal threshold) and 0.900 (FNR  $\approx$  0.04 threshold), with bootstrap resampling (1000 replicates) confirming the stability and precision of all estimates (Table P.9). Spatial cross-validation (k = 5 latitudinal bands) produced a mean performance consistent with the test estimates (CV AUC =  $0.969 \pm 0.058$ ; CV TSS =  $0.908 \pm 0.167$ ), though with elevated standard deviation – particularly for TSS – reflecting the deliberately heterogeneous fold design. Folds covering the core European range produced near-perfect discrimination, while the southernmost fold (extrapolation to subtropical and tropical background points) and the boreal fold yielded lower values, as expected for a species with a European distribution. Pooled CV metrics were accordingly more conservative than the per-fold means, driven primarily by the extrapolation fold. Critically, all CV means fell within the 95 % bootstrap confidence intervals of the corresponding test metrics, confirming agreement between the two independent evaluation frameworks and the robustness of the model.

**Fig. 6: Comparative performance of PA generation methods with and without residual autocorrelation-guided selection.**



Legend: Based on Table P.1. AUC, TSS: 0–1; Moran's I: -1–1

The Palearctic+AC model achieved a test AUC of 0.982 and TSS of 0.900 (optimal threshold) and 0.840 (FNR  $\approx$  0.04 threshold), confirmed by bootstrap resampling (Table P.9). Spatial cross-validation (k = 5 latitudinal bands) yielded results consistent with the test estimates, with all CV means falling within the 95 % bootstrap confidence intervals. Notably, fold 1 (18°–45°N, subtropical and Mediterranean background points) produced substantially

better discrimination than the equivalent fold in the Global+AC model (AUC = 0.945 vs 0.866), suggesting that the Palearctic training extent better captures the southern boundary of the species range. Folds 2–5 showed uniformly high performance (AUC = 0.995–0.998), confirming stable discrimination within and above the core range.

The EuGlobal SRE with Range +AC model achieved a test AUC of 0.970 and TSS of 0.880 (optimal threshold) and 0.740 (FNR  $\approx$  0.04 threshold), confirmed by bootstrap resampling (Table P.9). Spatial cross-validation yielded substantially lower mean values (CV AUC =  $0.925 \pm 0.051$ ; CV TSS =  $0.782 \pm 0.118$ ), which fell below the lower bounds of the corresponding bootstrap confidence intervals – the only model in the comparison where this occurred. This divergence is explained by the global training extent: fold 1 spans  $-90^\circ$  to  $45^\circ\text{N}$ , encompassing the entire Southern Hemisphere and tropical regions, where background points are climatically very different from the European range core, resulting in weaker discrimination (AUC = 0.867, TSS = 0.680). Folds 2–4 contained very few absences (10–17 per fold), making per-fold TSS estimates unstable. Fold 5 (boreal zone) performed strongly (AUC = 0.987, TSS = 0.950), consistent with the other models.

The EuGlobal with Range +AC model achieved the highest bootstrap test AUC among all four models (0.988) and TSS of 0.940 (optimal threshold) and 0.900 (FNR  $\approx$  0.04 threshold), with narrow confidence intervals confirming stable predictions (Table P.9). However, spatial cross-validation yielded substantially lower mean values (CV AUC =  $0.921 \pm 0.082$ ; CV TSS =  $0.795 \pm 0.144$ ), which fell below the lower bounds of the bootstrap confidence intervals. This matches the pattern observed for EuGlobal SRE and is attributed to the same factor: fold 1 ( $-90^\circ$  to  $45^\circ\text{N}$ ) results in the weakest performance (AUC = 0.802, TSS = 0.598) due to the background-extent mismatch. Folds 2–4 also suffered from low absence counts (13–20 per fold). Fold 5 (boreal zone) again performed strongly (AUC = 0.989, TSS = 0.940). The CV–test divergence for this model thus reflects the challenge of global background sampling for a restricted European species rather than model instability.

At the same time, Biogeographic Realism scores revealed noticeable differences in spatial plausibility among the approaches, indicating that similar statistical performance does not necessarily translate into equally realistic spatial predictions.

A specialist in this genus, blinded to the PA selection method, assessed the Biogeographic Realism of the predictions, confirming the quantitative findings. The Global+AC model was identified as the most biologically plausible because it minimised suitability artefacts in barrier zones and provided the most comprehensive coverage of the species' range.

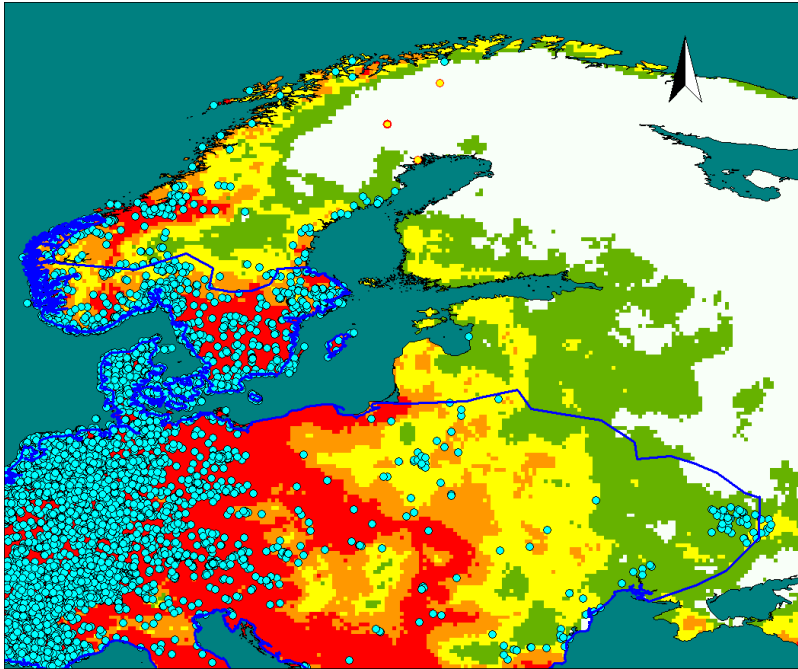
The proportion of desert cells ( $n = 1,761$ ) with suitability  $> 0.36$  was 0.2 % for Global+AC, compared to 3.1–17 % for the Western Palearctic and Radii models.

### Calibration of the best model

Post-hoc validation on 61 independent records collected between 1912 and 2025 (GBIF, 2025) from Morocco, Tunisia and Algeria (Table A) retrieved after model training showed 96.7 % of these points fall into cells with predictive suitability  $> 0.36$  (59/61 above threshold, Global+AC model).

Among 30,639 sightings of the species from 2001 to 2025 (GBIF, 2026), only four (0.013 %) were misclassified as absent. Notably, all four occurred in northern Fennoscandia ( $65\text{--}69^\circ\text{N}$ ), including winter records (January–February) and repeat observations at the same location (Tunastigen, Sweden) (see Fig. 7 and GlobAut.zip for details).

**Fig. 7: Test sample for 2001–2025 on the suitability map of macroecological conditions for 1970–2000, obtained using the Global+AC method.**



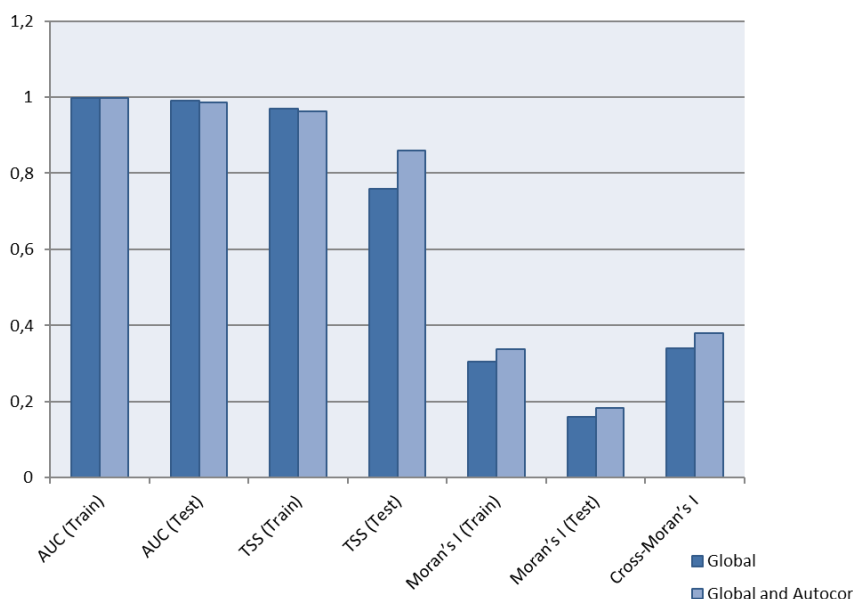
Legend: Blue circles indicate presence points for 2001–2025; four yellow points (two of which are located close to each other) indicate presences from Fennoscandia not included in the prediction.

Bootstrap results confirmed near-perfect performance:  $AUC = 1.00$  (CI: 1.00–1.00),  $TSS_{max} = 1.00$  (CI: 1.00–1.00),  $TSS_{fnr05} = 0.957$  (CI: 0.954–0.959), with  $FNR_{fnr05} = 0.043$  (CI: 0.041–0.046) and no NAs in replicates. CI collapsed to a point due to near-perfect separation; this result reflects the extreme class imbalance (30,635 correct/4 incorrect) rather than model robustness in a strict statistical sense. For *A. sylvaticus*, low-FNR thresholds support proactive monitoring of northward shifts under warming.

### Threshold shifting

A post-hoc calibration was conducted to test the robustness of predictions, confirming that the main conclusions remained stable under test threshold adjustments. The results of the secondary calibration of the metrics of the Global (Fig. P.9) and Global+AC (Fig. 5, P.10) methods, related to the approximation of the test distributions of the primary calibration, are shown in Fig. 8.

**Fig. 8: Graph of secondary calibration of the «Global» and «Global+AC» metrics.**



Legend: based on Table P.11 and preceding explanations. AUC, TSS: 0–1; Moran's I: -1–1.

In the recalibrated summary (Table P.11, focussed on FNR=0 scenarios), the “Global+AC” method demonstrated a moderate  $\Delta$ TSS of approximately 0.102 (calculated as  $TSS(Train) = 0.962$  minus  $TSS(Test) \approx 0.86$ ), placing it within the «possible overfitting» threshold range (0.1–0.2). Considering the limitations of both calibration procedures, such a slight excess can be considered insignificant. This represents a tangible improvement over the baseline “Global” method's more pronounced  $\Delta$ TSS of  $\sim 0.209$  ( $0.969 \sim 0.76$ ), which exceeds 0.2 and signals clear overfitting under the diagnostic criteria.

The residuals of the training model for both true classes in the Global+AC based variable selection are concentrated around zero, but the distributions are not perfectly symmetrical or bell-shaped (Fig. P.36).

Results for GLM: When adding a spatial lag to GLM (global method), most variables lost predictive significance; the model with BIO9 yielded a fragmented and narrowed distribution. Therefore, subsequent analyses focussed on the BART models.

The most common predictor across all models for *A. sylvaticus* was BIO3 (Isothermality, mean value 33.7 %), characteristic of a temperate continental climate. BIO9 (Mean Temperature of Driest Quarter, 8.2 °C) also indicated moderately warm conditions during the dry season. In the best-performing Global method with residual-SAC-guided variable selection, the baseline predictors were BIO14 (Precipitation of Driest Month), BIO19 (Precipitation of Coldest Quarter), BIO3 (Isothermality), BIO4 (Temperature Seasonality), BIO8 (Mean Temperature of Wettest Quarter), and BIO9 (Mean Temperature of Driest Quarter) (see Supplementary Information Q).

## DISCUSSION

### Ecological interpretation of predictors

*A. sylvaticus* shows a preference for mild temperature stability. Ecologically important predictors included:

- BIO3 (Isothermality) – representing temperature stability, which is critical for small mammals with limited thermoregulatory capacity during inactive periods (Dallas & Kramer, 2022). Higher isothermality reduces physiological stress associated with daily and seasonal temperature fluctuations (Korslund & Steen, 2006).
- BIO9 (Mean temperature of the driest quarter) – representing thermal conditions during the dry season (typically late summer in Mediterranean systems), a period characterised by food scarcity and increased energetic demands that strongly influence survival and reproductive success.

Several studies also highlight temperature as a limiting factor. Heat tolerance evolves slowly, so climatic limits are rigid (Araújo *et al.*, 2013). Nater *et al.* (2018) demonstrated its role in seasonal food availability in the African striped mouse, whereas Cerezer *et al.* (2021) showed its influence on vegetation and soil cover. Temperature has a predominantly positive effect on the biodiversity of small rodents (Jiang *et al.*, 2013). Other variables, such as anthropogenic pressure and land use, may increase temperature influence (Wan *et al.*, 2022) or show instability depending on the selected background (Castillo & Higa, 2025).

### Geographic constraints of the species range

In the northern part of the range, expansion appears constrained by biotic or temporal factors (Svenning & Skov, 2007a, 2007b), since no clear geographic barriers are observed. In contrast, southeastern expansion is constrained primarily by geographic barriers. In the southwest, the range is limited by coastal climatic conditions, whereas in the northwest (Greenland) expansion is hindered both by the sea strait and by harsh climatic conditions.

### Generality and transferability of the results

An important consideration concerns the generality of our results. *Apodemus sylvaticus* is a widespread generalist species with numerous occurrence records and a well-documented range, which enabled a robust comparison of PA generation methods. Generalist species therefore provide a statistically stable test case but should not be considered a universal benchmark (Stewart, 2008).

The performance and suitability of the tested PA strategies may differ for specialist species, rare taxa with few records, or species with poorly defined geographic ranges (McPherson *et al.*, 2004; Hernandez *et al.*, 2006; Hernandez *et al.*, 2008; Austrich *et al.*, 2021; Bazzichetto *et al.*, 2023). For narrow-range endemics, sampling pseudo-absences across the Euro-Afro-Asian extent may introduce excessive environmental contrast, potentially inflating model performance or producing misleading response curves (Lobo *et al.*, 2010). In such situations, more localised background sampling or alternative PA strategies among the six evaluated here may be more appropriate. Da Re *et al.* (2023) emphasise that PA strategies often depend on species-specific characteristics, and ignoring this dependence can lead to overly general recommendations. Under-sampled taxa may also exhibit stronger sensitivity to sampling bias and may require bias-correction approaches (Fithian *et al.*, 2015).

And conversely, for species with limited data availability, the Global+AC approach may be particularly useful because it does not require precise parameterisation of the background range, which is often difficult when species distributions are poorly known. In a study by Mezhzherin & Kozlov (2026) (see also the repository link in Appendix

<https://codeberg.org/reviewer12345/MURINAE>), the recommended workflow was applied to 25 Murinae species representing diverse ecological strategies, range sizes and data availability, producing promising results. Future studies should evaluate the transferability of the Global+AC method using simulation frameworks that systematically vary species-specific attributes (Barbet-Massin *et al.*, 2012; Pili *et al.*, 2025).

### **Niche interpretation and spatial scale**

Because only abiotic predictors were included, the predicted suitability surfaces approximate the Grinnell niche (Soberón, 2007; Jiménez-Valverde *et al.*, 2008; Peterson *et al.*, 2011) rather than the Eltonian or Hutchinsonian fundamental niche. Edaphic properties, vegetation structure and biotic interactions were not included because they primarily operate at finer spatial scales (Whittaker *et al.*, 2001) and are beyond the spatial resolution of the present modelling framework. Therefore, the model outputs should be interpreted as macroclimatic suitability zones in geographic space.

Ignoring fine-scale constraints can lead to local under- or overestimation of suitability (Bean *et al.*, 2014). A comprehensive literature review of 885 range boundaries (Paquette & Hargreaves, 2021) showed that biotic interactions influence more than 60 % of boundaries, especially on warm range edges, whereas abiotic factors more frequently determine cold boundaries. Temperature often affects both types of boundaries, which is consistent with our results.

Consequently, factors operating at different spatial scales influence the realised distribution of species. Because these factors are inferred from the realised distribution itself, modelling introduces a degree of circularity. To address this issue, we interpret our background selection spaces, which include the range, within the concept of actual ecological space (in the terms of Jackson & Overpeck, 2000) as its geographical representation. Our resulting potential macrodistributions of species map their “potential niche space” onto a geographic map. Following the hierarchy of spatial scales proposed by Pearson & Dawson (2003), including land-use and soil property variables with pixel dimensions of approximately 5 km to 500 m will approximate the potential distribution and fundamental niche (the Grinnell fundamental niche  $N_f$  in the concept of Soberón, (2007)), whereas including more detailed biotic interactions (ideally to less than 10 m) can approximate the potential microdistribution. The positional uncertainty of most data should be no more than half the pixel dimension. This perspective is consistent with the emergence principle of landscape ecology: patterns of species distribution arise from ecological filters operating at multiple spatial scales. Biogeographic realism emerges when SDMs correctly represent ecological filters operating at the scale of the modelled system. Fractal theory provides a formal framework for understanding such scale-dependent patterns, as ecological systems often exhibit self-similar properties across limited ranges of spatial scales (Li, 2000; Halley *et al.*, 2004; Zarzo-Arias *et al.*, 2023). The hierarchical structure of patchiness – from local habitat elements to interregional barriers – is consistent with fractal representations of landscape heterogeneity (Milne, 1992; Seuront, 2009; Guisan *et al.*, 2025).

### **Performance of pseudo-absence strategies**

From a landscape-ecology perspective, the Global+AC method expands the sampling domain to a continental scale, deliberately targeting geographically unsuitable matrices. This conclusion aligns with previous studies that deliberately employed very large background extents to incorporate inaccessible areas and major dispersal barriers for European or Palaearctic species (Scherrer *et al.*, 2021; Guisan *et al.*, 2025), although these studies did not systematically compare multiple PA strategies nor apply residual autocorrelation-guided

variable selection. Unlike approaches that require detailed connectivity data to account for dispersal constraints (e.g., hydrographic-network methods; Parreira & Nabout, 2023), our framework achieves substantial improvements in barrier realism through the choice of pseudo-absence generation strategy alone, making it readily applicable to terrestrial species at macroregional scales, while remaining consistent with previous efforts to incorporate biological information into pseudo-absence selection (Chapman *et al.*, 2019). This design forces the model to distinguish between climatically suitable but inaccessible areas (for example southern Svalbard) and regions that are both unsuitable and inaccessible (for example the Thar or Libyan Desert).

Supplementary Table P.1 illustrates how variable selection influenced model behaviour. Methods incorporating autocorrelation filtering retained two particularly important variables, whereas in several models without this filtering (Figs. P.1, P.3, P.23) the BIO9 variable was removed from the final model. This indicates that variable SAC-pruning does not necessarily eliminate biologically meaningful predictors.

Overall, our results indicate that the choice of pseudo-absence generation strategy is a key determinant of both model performance and biological plausibility. Residual autocorrelation-guided selection consistently improved model quality: all four top-performing models employed this step, and the best of them (Global+AC) achieved the most balanced combination of discriminatory performance, spatial generalisability, and Biogeographic Realism.

All four models demonstrated strong predictive performance on the independent test set, with bootstrap-confirmed AUC values of 0.970–0.988 and TSS values of 0.880–0.940 at the optimal threshold (Table P.9). For the two models trained on Palaearctic or regional extents (Global+AC, Palaearctic+AC), cross-validation means closely matched independent test estimates and fell within the 95 % bootstrap confidence intervals, confirming stable generalisation. For the two globally-trained models (EuGlobal with Range+AC, EuGlobal SRE with Range+AC), CV means fell below the bootstrap CI lower bounds, driven by fold 1 spanning the entire Southern Hemisphere – a structurally inevitable consequence of the global training extent applied to a European species, rather than evidence of instability.

Global+AC achieved the highest Biogeographic Realism score (Tables P.1, P.9) while maintaining the lowest residual spatial autocorrelation among realistic models (Moran's I on test residuals = 0.183), and the smallest training–test divergence across all key metrics. Under standard threshold optimisation, the model achieved test AUC = 0.987 and TSS = 0.940. Under the most conservative recalibration scenario (additive shift of –0.10, enforcing FNR = 0 for zero missed positives), TSS declined to approximately 0.86 with FPR  $\approx$  0.12–0.16 – a deliberate trade-off that prioritises hotspot detection over specificity in spatially heterogeneous landscapes (Tables P.10 and P.11). Although  $\Delta$ TSS approached the threshold of possible overfitting after recalibration, Global+AC outperformed its non-autocorrelated counterpart in balancing model fit and spatial generalisability across both evaluation frameworks.

### Effect of range-based pseudo-absence restriction

The metrics selected for analysis may be overestimated when pseudo-absence sampling excludes the species' geographic range (Leroy *et al.*, 2017). Our results partially support this statement. Max TSS (Train) in the range-exclusion models exceeds that of the range-inclusion models by 0.064 ( $p = 0.0066$ ). A statistically significant difference is also observed for AUC (Train), although the magnitude of the difference is small (0.017;  $p = 0.0468$ ). For the test data, Max TSS (Test) is higher in the range-exclusion models by 0.093 ( $p = 0.0006$ ) (Table P.3).

Differences in AUC (Test) and spatial autocorrelation metrics between the approaches are generally small. The main exception is Cross-Moran's I, which differs by 0.2667 ( $p = 0.0185$ ). Higher Cross-Moran's I values in the range-exclusion models indicate stronger transfer of spatial structure between training and test datasets.

Lack of pseudo-absence sampling within the species' geographic range reduced overfitting in several models (lower  $\Delta$ AUC and  $\Delta$ TSS), but its effect on spatial autocorrelation is inconsistent and model-dependent.

### **SRE filtering and spatial autocorrelation**

The comparative analysis (Tables P.5–P.8) shows that SRE filtering does not provide a consistent reduction of spatial autocorrelation across the EuGlobal, Global, and Palaearctic pseudo-absence strategies. Although small decreases in Moran's I were occasionally observed for training residuals, these effects were marginal and were counterbalanced by slight increases in SAC on test subsets and in cross-Moran's I values. Importantly, none of these differences reached statistical significance, indicating that the observed fluctuations represent noise rather than a directional effect.

Improvements in Biogeographic Realism, when observed, were inconsistent and often accompanied by underprediction at range margins. These findings suggest that SRE should not be relied upon as a primary tool for controlling spatial autocorrelation in broad-extent SDMs, and that random sampling from a carefully defined geographic background combined with autocorrelation-guided variable selection offers a more robust alternative. The environmental-contrast principle underlying SRE appears insufficient to disrupt broad-scale spatial structure in the presence data 1970–2000 and may even reinforce weak artefacts by sampling pseudo-absences from environmentally extreme but spatially clustered regions.

### **Alternative strategies for random sampling of pseudo-absences**

The Western Palaearctic method (Fig. P.29–30, Table P.6) minimised residual autocorrelation, consistent with Barbet-Massin *et al.* (2012). However, it produced ecologically implausible predictions and substantially lower discriminatory performance (test AUC 0.67–0.87) compared with methods incorporating climatically hostile background (test AUC  $\geq 0.984$ ). Limiting pseudo-absence sampling to a restricted spatial domain can therefore generate unrealistic predictions.

Similarly, the Radii method with spatial buffers produced unsatisfactory results (Fig. P.31), confirming the findings of Da Re *et al.* (2023).

The Buffer method, which samples pseudo-absences within a 500 km buffer around the known range but excludes areas within 30 km of presence points, produced mixed outcomes. In its baseline configuration (without SRE filtering), it reduced overprediction in the Libyan Desert but simultaneously underpredicted suitability in southwestern and northeastern range margins (Fig. P.32). Applying SRE filtering (quantile 0.1) to the Buffer method improved predictions but underestimated them in the northern part of the range (Fig. P.34–35) and in the Karakum Desert (Fig. P.35). Autocorrelation-guided variable selection in the Buffer method (Fig. P.33, P.35) generally degraded predictive performance, indicating the sensitivity of this approach to variable pruning.

Overall, these results highlight that methods with spatially restricted pseudo-absence domains (Western Palaearctic, Radii, Buffer) are prone to either producing implausible suitability in barrier regions or failing to capture peripheral range areas, and they do not benefit consistently from autocorrelation-guided selection.

But the final interpretation may depend on the temporal coverage of the occurrence records, the applied filtering procedures and the specific dataset version.

### Comparative performance of the four best models

Four models consistently outperformed others: EuGlobal with Range+AC, EuGlobal+SRE with Range+AC, Global+AC, and Palaeartic+AC. All share two features: (1) random pseudo-absence sampling from broad extents including climatically unsuitable regions, and (2) autocorrelation-guided variable selection. However, each exhibits distinct spatial trade-offs.

EuGlobal with Range+AC maximised spatial independence (lowest cross-Moran's I) but showed minor underprediction in southwestern range margins. EuGlobal+SRE with Range+AC produced the most realistic predictions for northern islands (Svalbard, Greenland), yet retained some residual spatial structure. Palaeartic+AC eliminated Arctic artefacts but reduced coverage in the eastern range and southern Libyan Desert. Global+AC provided the most balanced performance across all criteria: full range coverage, minimal artefacts in barrier regions, and the lowest test autocorrelation among realistic models. Its temporal transferability was confirmed on 30,639 independent records.

The choice depends on research priorities:

Maximum spatial independence → EuGlobal with Range+AC

Northern marginal areas → EuGlobal+SRE with Range+AC

Western Palaeartic core regions → Palaeartic+AC

Default for most applications → Global+AC

For studies where a single best model cannot be identified, an ensemble average of all four is recommended.

Thus, several models achieved very high AUC values while producing geographically less plausible predictions. Our results suggest that statistical performance alone is insufficient to guarantee ecologically meaningful SDMs. This finding highlights the need to complement statistical evaluation with Biogeographic Realism criteria.

### Residual diagnostics

The residual distribution of the best model deviates somewhat from normality (Fig. P.36). Although strict normality is not required for *bart.step* residuals, approximate normality facilitates reliable diagnostics and interpretation. Non-normal residuals do not invalidate the model, but may indicate the presence of unmeasured predictors, contagious biological processes such as dispersal limitation (Chipman *et al.*, 2010), or hidden intraspecific structure similar to that described for *Phyllotis darwini* (Gutiérrez-Tapia & Palma, 2016), where individual lineages show different responses to climate gradients.

Residual spatial autocorrelation remained moderate across most models, reflecting large-scale spatial structure typical of continental SDMs. It indicates that the model retains some spatial structure from the training data, a typical trade-off in broad-scale SDMs where spatial autocorrelation cannot be fully removed without compromising prediction realism. Such levels are typical for SDMs in macroabiotic layers, although they are rarely reported explicitly in the literature. These values should therefore be interpreted as an inherent limitation of continent-scale modelling rather than as a model-specific failure (Dormann *et al.*, 2007).

Autocorrelation-guided selection of predictors generally increased macroecological plausibility, demonstrating the potential of this approach.

The 'year' variable was often retained after correlation filtering (Supplementary Table P.1), indicating potential temporal structure in the data. "Year" may reflect temporal trends in data collection intensity or actual changes in abundance/distribution. Although temporal autocorrelation could be reduced by iterative point removal (by analogy with the V

algorithm), our focus here was exclusively on spatial effects. Its potential influence on species reporting intensity and spatial bias warrants deeper investigation in future analyses, especially when combining historical and recent records.

## IMPLICATIONS FOR PSEUDO-ABSENCE SAMPLING

Lobo *et al.* (2010) and Barve *et al.* (2011) argue against including extreme absences (“there are no elephants in Antarctica”). But this constraint should apply to the result, not necessarily to the sampling strategy (“the model should yield no predictions of elephants in Antarctica”). PA selection should reflect the biogeographic matrix in which the species does not exist. Sampling pseudo-absences from a global extent forces the model to learn the environmental signature of absence across the full realised environmental space (Jackson & Overpeck, 2000) outside the realised niche of the species.

Our findings support the view that SDMs should be treated as ecological hypotheses rather than purely statistical models (Austin, 2002; Warren *et al.*, 2022).

Our results are consistent with a growing body of SDM studies showing that the definition of background or pseudo-absence data strongly influences model behaviour. The present study contributes to this discussion by demonstrating that different pseudo-absence strategies can lead to substantial differences in the large-scale Biogeographic Realism of predictions, even when the same modelling algorithm and predictors are used.

### Recommended workflow

For *bart.step* models based on 1970–2000 bioclimatic layers and the approaches tested here, the Global+AC strategy produced the most consistently plausible predictions under the evaluation framework used in this study. It was also the only method that correctly predicted high suitability in northern Morocco and the Atlas Mountains, where independent occurrence records confirm the species’ presence.

We therefore suggest that random sampling of pseudo-absences from the Euro-Afro-Asian mismatch matrix can mitigate spatial inaccuracies and sampling bias typical of large biodiversity databases 1970–2000. This approach better represents the full spectrum of environmental conditions between the equator and the Arctic than more or less spatially limited strategies.

Nevertheless, further evaluation is required, especially for species with ranges substantially larger or smaller than that examined here. In such studies, it is necessary to ensure data identity, full methodological transparency and reproducible scripts, since statistical workflows contain multiple decision points that may influence final outcomes.

For further methodological reflections on additional improvements to this modelling framework, see Appendix W.

Taken together, the workflow used in this study combines three complementary levels of model evaluation: (1) statistical performance metrics, (2) spatial cross-validation, and (3) biogeographic plausibility of predicted distributions.

Such multi-level validation may help identify models that are statistically accurate but geographically unrealistic, a problem that remains common in large-scale SDMs.

### Implications for landscape ecology and conservation planning

The wood mouse, one of the most widespread small mammals in European cultural landscapes, serves as an excellent umbrella species for fine-grained habitat mosaics – including hedgerows, small woodlands, riparian corridors, field margins, and extensively

managed grasslands – that characterise much of Atlantic and Central Europe. The permeability of the agricultural matrix for this and many other small terrestrial vertebrates depends almost entirely on the density and connectivity of linear and small-patch habitat elements rather than on broad-scale climate alone.

Our study shows that conventional SDM workflows that sample pseudo-absences only from climatically analogous regions (Western Palaearctic or buffer zones around the range) can systematically overestimate habitat suitability in absolute dispersal hurdles (Sahara, Anatolian and Iranian deserts, Arctic tundra and northern islands) and, more importantly, can produce unrealistic suitability surfaces inside the highly fragmented European agricultural landscape. Poor or inconsistent modelling practices can lead to inappropriate inference and misguided conservation actions (García-Díaz *et al.*, 2019). In contrast, the proposed Global+AC method – random pseudo-absences from a large, climatically unfavourable but biogeographically significant background space, combined with autocorrelation-driven variable selection – clearly identifies the potential macrodistribution of a species and produces suitability maps that accurately outline the contours of permeable matrix.

The biologically realistic predictions generated by our workflow offer direct applications for several key areas of applied landscape ecology:

### **Designing and prioritising ecological networks and green infrastructure under the EU Biodiversity Strategy for 2030**

The resulting suitability surfaces can be used as resistance layers in least-cost path and circuit-theory connectivity models (e.g., Linkage Mapper (McRae & Kavanagh, 2011), Circuitscape (McRae *et al.*, 2009)). Areas currently showing moderate-to-high suitability but lacking structural connectivity (e.g. large arable blocks in eastern Germany, Hungary or Ukraine) emerge as clear priority zones for hedgerow restoration or riparian buffer creation.

### **Targeting agri-environment schemes and High Nature Value farmland support**

Payment schemes under the Common Agricultural Policy (CAP Eco-schemes, AECM) (Pe'er *et al.*, 2022) are increasingly required to deliver measurable biodiversity outcomes. Our suitability surfaces can serve as a baseline layer for connectivity models such as Circuitscape or Linkage Mapper; actual connectivity gains would require validation against fine-scale land-use and habitat data.

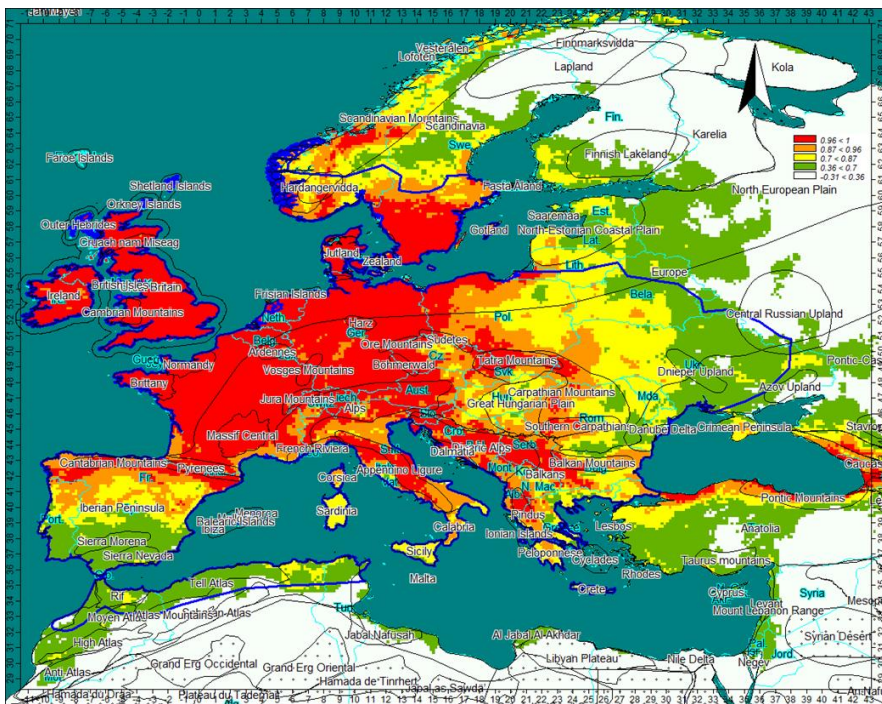
### **Rewilding and post-industrial restoration**

In abandoned military training areas, open-cast mining sites and former collective farms of Central and Eastern Europe, decision-makers need to know whether passive rewilding will be sufficient or active planting of woody corridors is required. The lower predicted suitability outside hedgerow and riparian networks indicates that these landscapes are less likely to sustain viable populations or facilitate dispersal, suggesting that many areas may remain functionally isolated without deliberate corridor creation. Meanwhile, the sharp suitability gradients produced by our models mark where such interventions are broadly warranted; refining this macro-scale framework with finer-scale predictors — following the hierarchy outlined in §Niche interpretation and spatial scale (Pearson & Dawson, 2003) — would enable more precise siting of corridors and riparian vegetation for a given species and landscape. The same framework can also be applied to other species, or even to suites of species, by overlaying the resulting predicted suitability rasters to identify shared priority zones for conservation and restoration.

### Assessing fragmentation risk under future land-use intensification or abandonment

Coupling our SDM projections with land-use scenarios (e.g., EU-RUINS, CLUE-S) would allow quantitative assessment of how future hedge-row removal or restoration could affect functional connectivity. Landscapes with a low predicted probability of species dispersal, coupled with the low permeability of the Eurasian matrix, may represent barriers between populations. In our case, according to Fig. 9, low and moderate predictive probabilities (0.36–0.87) cover the southwestern and eastern parts of the species' range, including the northeastern regions of Poland, Romania, Greece, non-western Ukraine, and also the Great Hungarian Lowland, the Dnieper Upland, the southern half of the Iberian Peninsula, including the Sierra Nevada and Sierra Morena mountains, and the coastal part along the Atlas Mountains, located in northwest Africa.

**Fig. 9: A more detailed map of the potential distribution of *A. sylvaticus* (Global+AC method).**



Central Bohemia, Moldova, the islands of Sicily and Sardinia, southern Sweden and Norway have medium prediction probabilities (0.7–0.87). While our findings may support landscape-scale assessments relevant to EU biodiversity frameworks (including CAP-related planning), such applications should be treated with caution. Our models reflect macroclimatic suitability only and do not incorporate fine-scale land-use configurations, habitat fragmentation, or local management practices.

It is interesting from a zoogeographical point of view that in the north, southeast, and east of the range, the mountains exhibit a characteristic opposite to the barrier – they have a high probability of suitability. The adjacent flat areas have a suitability lower than these mountainous areas. In the northwest of Europe and the southwest of the range, this indicator

becomes indistinguishable from adjacent flat areas, gradually deteriorating to the south. This spatial pattern of suitability, where mountains act as corridors rather than barriers in certain regions, could further inform the prioritisation of conservation efforts.

## CONCLUSIONS

This study identifies the pseudo-absence generation strategy as the most critical factor determining the Biogeographic Realism of species macrodistribution models. For *A. sylvaticus*, only strategies that explicitly incorporated absolute dispersal barriers and a hemispheric hostile matrix – by randomly sampling pseudo-absences across Euro-Afro-Asian extent while excluding the known range polygon – succeeded in eliminating macroecologically implausible suitability, while also providing realistic coverage of the southwestern range edge (Morocco, Pyrenees). Subsequent predictor selection aimed at minimising residual SAC further removed subtle artefacts and sharpened the contrast between permeable and impermeable parts of the macroecological landscape.

The recommended workflow is computationally efficient, fully reproducible, and relies solely on widely available bioclimatic data 1970–2000, enhancing its utility for continental-scale studies. It produces distribution models that not only achieve sufficient discriminatory performance (AUC > 0.97, TSS > 0.86, but see §Threshold shifting for calibration and validation details) but, crucially, are biologically plausible at the landscape scale that matters for practical conservation. We therefore propose the following operational protocol for terrestrial vertebrates inhabiting fragmented, human-dominated landscapes:

1. Sample background randomly from the entire structurally defined (and largely inaccessible) portion of the Euro-Afro-Asian extent, rigorously excluding the expert-delineated realised range polygon.

2. After initial model calibration, iteratively remove predictors that contribute most to residual SAC.

3. Although Global+AC provided the most balanced performance, the choice among the four top-performing models may depend on specific research goals: EuGlobal+SRE+Range performed better on northern islands (Svalbard) but underpredicted in southwestern margins; Palaearctic+AC minimised Arctic artefacts but showed reduced coverage in the eastern range. For applications prioritising complete range coverage, an ensemble average of the four models may be considered.

4. After determining the most plausible potential macrodistribution and its abiotic macrovariables, add the most important available scenopoetic variables at a finer scale consistent with the majority of the data to the model. Test the feasibility of the resulting micropotential distribution predictions at the spatial resolution specified in the table (Pearson & Dawson, 2003), if possible preserving the previously derived potential macrodistribution in the model. To account for existing data on biotic interactions, their predicted distributions will likely need to be overlaid as a separate layer, taking into account abiotic macrovariables that are favourable to both species.

By aligning pseudo-absence generation with fundamental landscape-ecology principles – matrix permeability, corridor networks and absolute biogeographic barriers – the resulting models become directly usable for designing ecological networks, targeting hedgerow and riparian restoration, prioritising agri-environment measures and evaluating connectivity outcomes of the EU Biodiversity Strategy. This approach narrows the persistent gap between statistically sophisticated species distribution modelling and the spatial realities of conservation planning in Europe's fragmented rural landscapes.

## SUMMARY

Our study demonstrates that the method of pseudo-absence generation substantially affects the macroecological plausibility, spatial autocorrelation, and predictive accuracy of species macrodistribution models. Although methods based on random sampling PAs from a small area, including the species' range, reduced residual SAC, they often produced implausible predictions. Selection via the Surface Range Envelope (SRE) method, which filters for ecological contrast, did not provide significant advantages. Contrary to recent recommendations (Da Re *et al.*, 2023; Broussin *et al.*, 2024), environmental contrast filtering (SRE) predominantly reduced macroecological realism, particularly when applied to small background patches, resulting in excessive fragmentation in Southern Europe and North Africa. In contrast, combining background filtering (e.g., Euro-Afro-Asian extent) coverage excluding the species' range as a location with a high probability of its presence) with residual autocorrelation-guided selection yielded more realistic and spatially consistent predictions for *A. sylvaticus*.

SAC and variable importance emerged as subsequent critical factors influencing model quality.

These findings emphasise the need to align pseudo-absence generation strategies with the specific modelling goals – whether optimising predictive accuracy, minimising overfitting, or improving Biogeographic Realism. Despite promising outcomes, further work is needed to test these methods across species, scales and environments, especially under future climate scenarios. Future studies may extend the Biogeographic Realism framework by incorporating additional dimensions of biological realism, as appropriate to the modelling context (Record *et al.*, 2018; Franklin, 2023; Da Re *et al.*, 2024).

While this study focussed on climatic drivers, future applications should complement the derived baseline model of large-scale predictors by incorporating more detailed, available variables that play a key role in landscape ecology. The custom R functions developed in this study offer a reproducible workflow for spatial thinning, stratified sampling, and residual analysis, and may be useful for future research in ecology and biogeography at more detailed scales. Barriers operate at different spatial scales, from local features (rivers, fields) to regional ones (deserts, mountain ranges).

The proposed Global+AC workflow has immediate practical implications for the design of ecological networks, agroecological targeting, rewilding, and connectivity assessment under future land-use change.

The R scripts, supplementary tables, and detailed algorithmic steps are available in the repository: [https://codeberg.org/reviewer12345/Supplementary\\_Information](https://codeberg.org/reviewer12345/Supplementary_Information), Appendix - <https://codeberg.org/reviewer12345/MURINAE>.

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## CONFLICT OF INTERESTS

The author declares no conflict of interest related to this article. There was no funding for this study.

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