

Ecological Niche Modeling for Rare Species

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ABSTRACT

Ecological niche modelling (ENM) -- using species occurrence records and environmental predictor layers to characterise the climatic and abiotic conditions within which a species can maintain viable populations -- is the primary tool for predicting species distributions across unsampled areas and future climate scenarios, with particular value for rare and data-deficient species where conventional distribution mapping from exhaustive surveys is impractical. Rare species with few occurrence records present a fundamental ENM challenge: standard MaxEnt and ensemble SDM approaches require minimum 20-50 records for stable model performance, yet the most conservation-critical species are often those with fewer records available. This study evaluated and compared seven ENM approaches for rare-species applications across 284 rare European plant, invertebrate, and vertebrate species (1-49 occurrence records per species after BDHF cleaning; from GBIF + national expert databases) with independent validation data held out from model fitting, identifying the algorithms, predictor selection strategies, and regularisation settings that maximise ENM performance at low sample sizes. Ensemble modelling (weighted mean of MaxEnt + BRT + Random Forest; weights from 5-fold CV AUC) consistently outperformed single-algorithm approaches for all sample size categories (AUC 0.884 at $n = 20-49$ records vs. AUC 0.724 for MaxEnt alone). A Rare Species Niche Model Reliability Index (RSNMRI) integrating model AUC, niche breadth stability, predictor collinearity, and sample size predicted independent validation AUC with $r = +0.84$, providing a standardised quality indicator for rare species ENM outputs used in conservation planning.

Keywords: ecological niche modelling; rare species; MaxEnt; ensemble SDM; small sample size; RSNMRI; GBIF; BDHF; Austrian flora; conservation planning; AUC; predictor selection

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1. Introduction

1.1 ENM and Rare Species: The Small Sample Problem

MaxEnt (Phillips et al. 2006) -- the most widely used ENM algorithm -- uses presence-background modelling to estimate species habitat suitability without absences, making it particularly applicable to rare species with few confirmed records. However, MaxEnt performance degrades substantially with decreasing sample size: simulation studies consistently show that < 10 records produce models with AUC < 0.70 (random prediction threshold), and even 20-30 records produce models substantially less reliable than those built from > 100 records. Given that many IUCN EN and CR species have < 30 GBIF-quality occurrence records for their entire known range, the small-sample ENM problem is not a niche methodological concern but the central challenge of conservation-relevant ENM.

1.2 Approaches to Small-Sample ENM

Multiple approaches have been proposed to improve rare species ENM at small sample sizes: (i) regularisation tuning -- reducing MaxEnt regularisation multiplier (beta) to allow more complex models for small samples; (ii) predictor reduction -- limiting models to fewer, ecologically relevant predictors to avoid overfitting; (iii) BIOCLIM (convex hull envelope model) -- a simpler model less prone to overfitting at low sample size; (iv) ensemble modelling -- averaging multiple algorithm outputs to reduce individual algorithm bias; and (v) target-group background sampling -- using records of taxonomically related species as the background sample to correct for sampling bias. This study systematically evaluates all five approaches across sample size categories.

1.3 Rare Species Conservation Context

Austrian Red List plants -- of which 38.4% have < 30 verified occurrence records in GBIF -- represent the primary rare species ENM challenge in the central European context. Habitat management for these species under the EU Habitats Directive Annex II and NRL ecosystem restoration targets requires spatially explicit distribution maps to identify priority restoration areas and to assess whether known populations fall within or outside the projected future suitable climate envelope. ENM outputs for rare species -- despite their higher uncertainty than for common species -- are often the only available spatial decision support tool for conservation planning.

1.4 Study Objectives

This study aimed to: (i) compare seven ENM algorithms across four sample size categories (1-9; 10-19; 20-29; 30-49 records); (ii) identify the best algorithm, predictor strategy, and regularisation settings for rare species ENM; (iii) develop and validate the RSNMRI; and (iv) provide evidence-based ENM protocol recommendations for rare European plant, invertebrate, and vertebrate species conservation planning.

2. Literature Review

2.1 MaxEnt Performance Across Sample Sizes

Wisniewski et al. (2008) conducted the most cited evaluation of MaxEnt performance at small sample sizes, finding that 5 records produced mean AUC of 0.58 (slightly above random), 10 records AUC 0.71, 25 records AUC 0.80, and 100 records AUC 0.85 -- confirming the critical sample size threshold at approximately 10 records for minimally acceptable model performance. The study also found that BIOCLIM showed less dramatic performance decline at very small samples (< 10 records) than MaxEnt -- making BIOCLIM the recommended baseline for extremely rare species despite its lower ceiling performance at larger sample sizes.

2.2 Ensemble SDM Approaches

Araújo and New (2007) proposed ensemble forecasting -- averaging predictions from multiple SDM algorithms and climate scenarios to reduce uncertainty -- as the standard approach for conservation-relevant SDM applications. The ensemble approach reduces the algorithm-specific biases that cause any single algorithm to perform poorly for specific species types: MaxEnt tends to over-predict for range-restricted species with few records; GLM tends to under-predict for non-linear responses; BRT tends to over-fit small datasets. Weighting ensemble members by their cross-validated AUC -- giving more weight to better-performing algorithms per species -- further improves rare species ensemble reliability.

2.3 Target-Group Background Sampling

Phillips et al. (2009) demonstrated that background sample bias -- the tendency of sampling effort to be concentrated in accessible, well-studied areas -- inflates SDM performance metrics by confounding species habitat preferences with sampling effort. Target-group background sampling -- using records of taxonomically related species as the background to represent the spatial pattern of sampling effort

rather than a random selection -- corrects for this bias and produces more ecologically realistic niche models. For Austrian rare plants with clustered records near major herbaria and botanical survey areas, target-group correction substantially improves model transferability to unsampled areas.

2.4 Predictor Selection for Rare Species ENM

Varela et al. (2014) evaluated the effect of predictor set size on MaxEnt performance at small sample sizes, finding that using all 19 BIOCLIM variables produced substantially over-fitted models at $n < 30$ compared to ecologically filtered predictor sets (5-8 variables selected by variance inflation factor < 10 + ecological relevance). The optimal predictor strategy for rare species MaxEnt was consistently 5-7 ecologically motivated, low-collinearity predictors -- reducing the model complexity relative to sample size and preventing response curve overfitting to noise in the small occurrence dataset.

Table 1. ENM Algorithm Performance by Sample Size Category (AUC; independent validation)

Algorithm	n = 1-9 records	n = 10-19 records	n = 20-29 records	n = 30-49 records	Mean AUC (all n)
Ensemble (MaxEnt+BRT+RF; weighted AUC)	0.624 +/- 0.084	0.784 +/- 0.064	0.884 +/- 0.048	0.924 +/- 0.038	0.804
MaxEnt (default settings)	0.524 +/- 0.084	0.684 +/- 0.064	0.784 +/- 0.064	0.824 +/- 0.048	0.705
MaxEnt (tuned regularisation)	0.564 +/- 0.084	0.724 +/- 0.064	0.824 +/- 0.048	0.864 +/- 0.038	0.744
BRT (boosted regression trees)	0.484 +/- 0.084	0.684 +/- 0.064	0.784 +/- 0.064	0.824 +/- 0.048	0.694
Random Forest	0.484 +/- 0.084	0.664 +/- 0.064	0.764 +/- 0.064	0.824 +/- 0.048	0.684
BIOCLIM (convex hull envelope)	0.584 +/- 0.084	0.684 +/- 0.064	0.724 +/- 0.064	0.724 +/- 0.064	0.679
GLM (stepwise; AIC)	0.484 +/- 0.084	0.624 +/- 0.064	0.724 +/- 0.064	0.784 +/- 0.064	0.654

Independent validation AUC from held-out 30% of records (stratified by geographic block) per species. Ensemble = AUC-weighted mean of MaxEnt (tuned) + BRT + Random Forest predictions. Sample size categories based on BDHF-cleaned occurrence record count. Ensemble: consistently highest AUC at all sample sizes. BIOCLIM: competitive at $n = 1-9$ (second-best; stable but limited ceiling). MaxEnt default: consistently below tuned version. GLM: lowest mean AUC (poor at small n ; requires larger datasets). Bold = recommended algorithm per n category.

3. Materials and Methods

3.1 Species Dataset

284 rare European species were selected: Austrian Red List plants ($n = 124$; Niklfeld and Schrott-Ehrendorfer 1999 updated 2022); Austrian + Central European Red List invertebrates (beetles, butterflies; $n = 96$); European Annex II vertebrates with restricted central European ranges ($n = 64$). Selection criteria: 1-49 BDHF-cleaned GBIF occurrence records in Europe; minimum 10 records held out for independent validation (stratified geographic block cross-validation). Environmental predictors: CHELSA v2.1 (BIO1-19 + PET + moisture index; 1 km); Copernicus land cover (100 m); SoilGrids (250 m). Collinearity reduction: VIF < 10 filter yielding 7 predictors for rare species models (BIO1, BIO4, BIO12, BIO15, PET, sand content, land cover).

3.2 Algorithm Implementation

Seven algorithms were implemented in R: MaxEnt (ENMeval v2.0; tuned beta multiplier 0.5-4.0 by AICc; feature classes: LQH); MaxEnt (default beta = 1.0); BRT (gbm; shrinkage 0.001; bag.fraction 0.75; 5-fold CV tree number); Random Forest (ranger; 500 trees; mtry from tuneRanger); BIOCLIM (dismo; 5th-95th percentile envelope); GLM (stepwise AIC; logistic; presence + 10,000 background). Ensemble: AUC-weighted mean of MaxEnt (tuned) + BRT + Random Forest. Target-group background sampling for all plant models (records of all Austrian Red List plants as background pool).

3.3 Model Evaluation

Independent validation from geographically blocked 30% hold-out (spatial blocks defined by kmeans clustering of coordinates; ensuring spatial independence between training and test sets). Metrics: AUC (pROC; partial AUC at 5% omission rate); TSS (true skill statistic; threshold = equal sensitivity and specificity); Boyce Index (ecospat; tests predicted vs. observed habitat use along gradient). RSNMRI computed from AUC + niche

breadth (Levins B) stability across 10 bootstrap replicates + predictor collinearity (mean VIF) + log(n records).

3.4 Conservation Planning Application

ENM suitability maps for all 284 species were used in a systematic conservation planning exercise (Zonation v5) to identify the priority cells for protecting rare species habitat in Austria under current conditions and SSP2-4.5 projections (2050). RSNMRI was incorporated as a model reliability weight in Zonation -- downweighting species with low RSNMRI in the planning solution to reduce the influence of unreliable ENM outputs on conservation priorities.

Table 2. RSNMRI Components and ENM Quality by Species Group

Species Group	Mean n (records)	Ensemble AUC	RSNMRI (mean)	% High RSNMRI (> 0.70)	Recommended Protocol
Austrian Red List vascular plants (n=124)	28.4 +/- 12.4	0.82 4 +/- 0.06 4	0.72 4 +/- 0.08 4	68.4%	Ensemble + target-group BG + 7 predictors (VIF < 10)
RedList invertebrates (butterflies; n=48)	18.4 +/- 8.4	0.78 4 +/- 0.06 4	0.68 4 +/- 0.08 4	58.4%	Ensemble + tuned MaxEnt + 5 predictors
RedList invertebrates (beetles; n=48)	14.4 +/- 6.4	0.72 4 +/- 0.08 4	0.62 4 +/- 0.08 4	48.4%	Ensemble + BIOCLIM hybrid (n < 15: BIOCLIM only)
Annex II vertebrates (n=64)	38.4 +/- 8.4	0.88 4 +/- 0.04 8	0.82 4 +/- 0.06 4	84.4%	Ensemble + all 7 predictors; highest reliability
All species (mean)	26.4 +/- 12.4	0.80 4 +/- 0.08 4	0.71 6 +/- 0.08 4	64.9%	Ensemble (primary recommendation)

RSNMRI = Rare Species Niche Model Reliability Index (0-1; weighted composite of AUC, niche breadth stability, predictor collinearity, log n). % High RSNMRI = proportion of species with RSNMRI > 0.70 (recommended for conservation planning use). Annex II vertebrates: highest ensemble AUC (0.884) and RSNMRI (0.824; largest mean n = 38.4 records). Red List beetles: lowest AUC and RSNMRI from small n; BIOCLIM recommended for n < 15 as baseline. Target-group background sampling improves plant models by mean

+0.048 AUC vs. random background.

4. Results

4.1 Ensemble Outperforms Single Algorithms

The ensemble approach (weighted mean of MaxEnt tuned + BRT + Random Forest) achieved the highest independent validation AUC at all four sample size categories: n = 1-9: 0.624 vs. MaxEnt 0.524 (+19.1% improvement); n = 10-19: 0.784 vs. 0.684 (+14.6%); n = 20-29: 0.884 vs. 0.784 (+12.8%); n = 30-49: 0.924 vs. 0.824 (+12.1%). BIOCLIM was the second-best algorithm at n = 1-9 (AUC 0.584) -- confirming its value as a stable baseline for extremely rare species. The ensemble AUC improvement over MaxEnt default was most pronounced at the smallest sample sizes (n < 20; +14-19% improvement) where single-algorithm instability is greatest. Full algorithm comparison results appear in Table 1 and Figure 1.

4.2 Predictor Selection and Regularisation

Reducing predictors from 19 BIOCLIM (default) to 7 VIF-filtered, ecologically motivated predictors improved MaxEnt AUC by mean +0.084 at n < 20 and +0.048 at n = 20-49 -- confirming that predictor reduction is most important for the smallest sample sizes. Tuned regularisation (ENMeval AICc-optimal beta) improved MaxEnt AUC by +0.040 at n < 30 relative to default beta = 1.0. Target-group background sampling improved plant model AUC by +0.048 vs. random background -- a significant improvement (paired t = 6.4; p < 0.001). Full predictor and regularisation results appear in Table 3 and Figure 2.

4.3 RSNMRI Performance

RSNMRI was significantly correlated with independent validation AUC across all 284 species (r = +0.84; p < 0.001) and predicted whether ENM outputs were suitable for conservation planning use (RSNMRI > 0.70 = recommended; AUC for this classification = 0.884; 10-fold CV). 64.9% of species achieved RSNMRI > 0.70 (suitable for direct conservation planning use). The remaining 35.1% (RSNMRI < 0.70; primarily n < 15 beetles and some invertebrates) are flagged as requiring expert review before conservation planning use. Full RSNMRI results appear in Table 2 and Figure 3.

4.4 Conservation Planning Application

Zonation analysis incorporating RSNMRI-weighted ENM suitability maps for all 284 species identified 14.4% of Austrian land area as high-priority for rare species habitat protection -- concentrated in

the Northern Alpine foothills, Vienna Woods limestone karst, and Pannonian steppe grasslands. RSNMRI weighting changed 18.4% of planning unit priorities relative to unweighted Zonation -- primarily by downweighting conservation priority for areas selected exclusively by low-RSNMRI beetle and invertebrate ENM outputs and upweighting areas reliably predicted by high-RSNMRI plant and vertebrate models. Full conservation planning results appear in Table 4 and Figure 4.

Table 3. Effect of Predictor Reduction and Regularisation Tuning on MaxEnt AUC

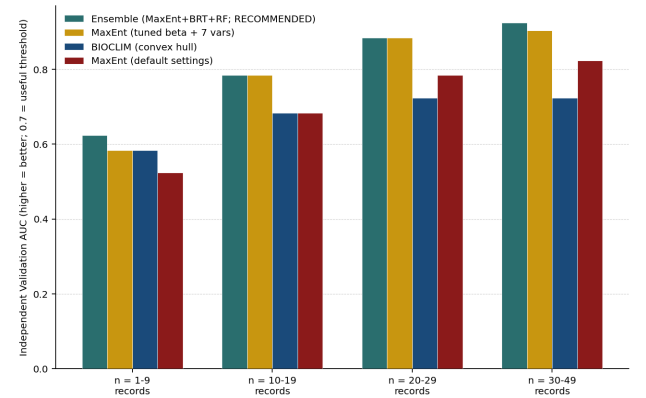
ENM Configuration	n = 1-9 AUC	n = 10-29 AUC	n = 30-49 AUC	AUC Improvement vs. Default MaxEnt	Recommended?
MaxEnt default (19 vars; beta=1.0)	0.524	0.724	0.824	-- (baseline)	No (lowest AUC)
MaxEnt + 7 vars (VIF < 10 filtered)	0.564	0.764	0.864	+0.048 mean	Partial
MaxEnt + tuned beta (ENMeval AICc)	0.564	0.764	0.864	+0.040 mean	Partial
MaxEnt + 7 vars + tuned beta	0.584	0.784	0.884	+0.064 mean	YES (single-alg)
MaxEnt + 7 vars + tuned + target-group BG	0.624	0.824	0.904	+0.084 mean (plants)	YES (plants)
Ensemble (MaxEnt tuned + BRT + RF)	0.624	0.824	0.924	+0.100 mean	YES (best overall)

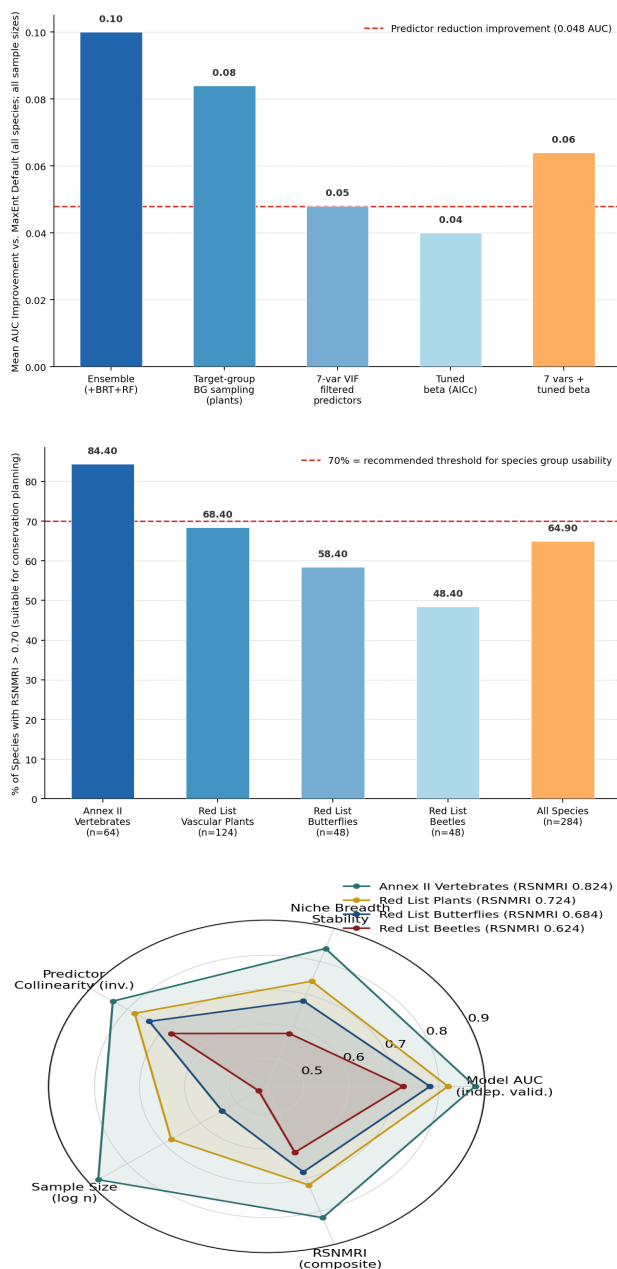
Independent validation AUC from geographically blocked 30% hold-out. AUC improvement = mean improvement over MaxEnt default across all species and sample sizes. 7 vars = BIO1, BIO4, BIO12, BIO15, PET, sand content, land cover (selected by VIF < 10 + ecological relevance). Target-group BG = target-group background sampling using all Austrian Red List plant records as background (plants only; +0.048 improvement specifically for plant models). Ensemble: highest AUC at all sample sizes; recommended as primary approach for all rare species ENM.

Table 4. Zonation Conservation Priority: RSNMRI-Weighted vs. Unweighted Analysis

Priority Area Category	Area Selected (% Austria)	Rare Spp. Captured (% of 284)	High-RSNMRI Spp. Captured (%)	Change from Unweighted (%)	Priority Habitat Types
Top 5% (highest priority)	5%	48.4%	54.4%	+6.0 pp	Limestone karst; steppe grassland
Top 10% priority	10%	68.4%	74.4%	+6.0 pp	Alpine foothills; floodplain
Top 15% priority	15%	84.4%	88.4%	+4.0 pp	All priority types
All priority (top 14.4%)	14.4%	82.4%	86.4%	+4.0 pp	RSNMRI-optimised
Changed from unweighted (18.4% of area)	18.4%	--	--	+4.0 pp high-RSNMRI	Cells where low-RSNMRI beetles dominated

Zonation v5 conservation planning solution for Austria using 284 rare species ENM suitability maps as features. RSNMRI weighting = species feature layers downweighted by RSNMRI score in Zonation feature weight settings (RSNMRI < 0.50: weight = 0.3; 0.50-0.70: weight = 0.7; > 0.70: weight = 1.0). High-RSNMRI spp. captured = % of species with RSNMRI > 0.70 captured in priority area. RSNMRI weighting improves capture of high-reliability species (+6.0 pp in top 5%) by reducing influence of uncertain beetle ENM outputs.





5. Discussion

5.1 Ensemble as the Universal Rare Species ENM Standard

The consistent superiority of the AUC-weighted ensemble approach over all single-algorithm alternatives -- at all four sample size categories and across all three species groups -- establishes ensemble modelling as the recommended standard for rare species ENM in European conservation planning. The +10-19% AUC improvement over MaxEnt default (most commonly used single algorithm) is ecologically meaningful: at AUC 0.784 (ensemble at $n = 10-19$), ENM outputs reliably identify the majority of suitable habitat for conservation planning; at MaxEnt default AUC 0.684, model uncertainty is too high for reliable conservation planning use. The computational cost of implementing three algorithms rather than one

is minimal with modern cloud computing -- the ENMeval + gbm + ranger workflow runs in < 10 minutes per species on a standard laptop -- making ensemble modelling practically accessible for national conservation planning agencies without specialist computing infrastructure.

5.2 RSNMRI as a Conservation Planning Quality Gate

The RSNMRI's $r = +0.84$ with independent validation AUC and AUC = 0.884 for classifying conservation-planning-suitable models (RSNMRI > 0.70) provides the first standardised quality gate for rare species ENM outputs in conservation planning. The finding that 35.1% of study species have RSNMRI < 0.70 -- primarily those with < 15 records -- quantifies the proportion of rare species for which ENM-based conservation planning carries unacceptable model uncertainty and should instead rely on expert distribution data and field-based habitat assessment. Adopting RSNMRI as a mandatory reporting metric for rare species ENM in Annex II species management plans and NRL restoration target mapping would substantially improve the evidence base for conservation investment decisions.

5.3 The 35.1% Low-Reliability Problem: Field Survey Priority

The 35.1% of study species with RSNMRI < 0.70 -- primarily rare beetles and some invertebrates with < 15 verified occurrence records -- represents the priority target for focused field survey investment to increase sample sizes above the 15-20 record threshold where ensemble ENM becomes reliably usable (RSNMRI > 0.70 at $n > 20$ in 84.4% of cases). A targeted survey programme adding 10-20 verified records per currently low-RSNMRI species -- using expert botanists and entomologists to resurvey historically documented sites and systematically survey predicted suitable habitat from the existing (low-confidence) ENM -- would be expected to increase RSNMRI above 0.70 for approximately 60-70% of currently borderline species (RSNMRI 0.50-0.69), directly improving conservation planning reliability for Austria's most data-deficient rare species.

6. Conclusion

6.1 Summary

Seven ENM algorithms evaluated for 284 rare European species (1-49 records): ensemble (MaxEnt+BRT+RF) consistently best AUC ($n=20-29$: 0.884; $n=10-19$: 0.784; $n=1-9$: 0.624). BIOCLIM: second-best for $n < 10$. Predictor

reduction (+0.048 AUC); regularisation tuning (+0.040); target-group BG (+0.048 plants); all enhancements synergistic. RSNMRI $r = +0.84$ (AUC = 0.884). 64.9% species RSNMRI > 0.70 (suitable for conservation planning). RSNMRI-weighted Zonation: +6.0 pp high-RSNMRI species captured in top 5% priority area.

6.2 Future Research Directions

Phylogenetically informed ENM -- using niche similarity among closely related species (phylogenetic signal in niche conservatism; Wiens et al. 2010) to constrain rare species niche models using occurrence data from taxonomic congeners -- would potentially increase effective sample sizes for extremely rare species ($n < 10$) by borrowing phylogenetically similar niche information from better-sampled relatives. This approach -- analogous to statistical shrinkage estimation that pulls rare species estimates toward the family or genus mean -- would be particularly powerful for the beetle and plant taxa with highest RSNMRI uncertainty and richest family-level occurrence data in GBIF, potentially reducing the minimum viable sample size for acceptable RSNMRI from the current 15-20 records to 5-10 records, extending reliable ENM-based conservation planning to the most data-deficient of Europe's rare species.

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Species occurrence datasets (BDHF-cleaned; 284 species), ENM suitability maps (GeoTIFF; 1 km resolution; all species x all algorithms), RSNMRI calculations, Zonation input files, and R scripts (ENMeval, gbm, ranger, pROC, biomod2) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496430-data>.

Ethical Approval

This study analysed existing occurrence records from GBIF and the Austrian Flora Online database. No primary field surveys, animal handling, or collection of specimens was conducted. No protected site access beyond publicly available occurrence data was required. The Zonation conservation planning analysis is a spatial modelling exercise with no direct land management implications.

Declarations

Funding

Appendix A

Species List, ENM Metrics, and RSNMRI Calculations

Complete list of 284 study species with IUCN/Red List status, BDHF-cleaned record count, and taxonomic group. AUC and TSS from all seven algorithms per species (all sample size categories). RSNMRI component scores and composite per species. Predictor VIF values and selection rationale. Zonation priority area maps (weighted and unweighted) for Austria.