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RESEARCH ARTICLE

ON THE USE OF NEIGHBORING HABITATS AS PREDICTORS OF SPECIES DISTRIBUTIONS

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Abstract. Choosing the appropriate scale for measuring environmental predictors is needed for accurately modelling species distributions. This need is becoming increasingly important with the use of high-resolution species distribution models (SDMs), emphasizing the challenge of aligning predictors with the spatial and ecological scales at which species interact with their environments. Focal predictors, which summarize landscape information within a spatially moving window, are powerful to account for neighboring information and scale dependency but have remained overlooked in SDMs. Using an automated selection procedure to identify the best predictors and measurement scales from a high-dimensional pool of candidates, including 13 nested circular focal

sizes from 25 m to 5 km radius for each landscape feature, this study evaluated the use of focal predictors through a set of national-scale, high-resolution SDMs for more than 7000 species across 17 major taxonomic groups. It further examined whether focal selection depended on species' mobility or body size. Among all species, focal predictors were selected at least once in ≥ 94% of the SDMs, highlighting their important role. For mobile species, larger focal windows were selected for the land use and land cover category, whereas sessile species were associated with larger focal windows for topographic predictors. For small species, predictors with smaller focal windows were more often selected. Given the importance of focal predictors across all studied taxa, adjusting the optimal scale for each predictor and species is of utmost importance to improve model performance and account for species' scale dependency.

Keywords. Animals, ecological niche modelling, focal predictor, multi-scale process, plants, spatial scale.

Introduction

Ecosystems and the species therein are under pressure such as climate change (Doney et al. 2012, Grimm et al. 2013, Pereira et al. 2024), habitat fragmentation (Haddad et al. 2015, Liu et al. 2018), and land-use change (Hasan et al. 2020, Gomes et al. 2021, Pereira et al. 2024), which have and will have drastic consequences on humans (Cardinale et al. 2012, IPBES 2019, Schmeller et al. 2020, IPCC 2023, Keck et al. 2025). Understanding how species interact with and are shaped by their environment is of utmost importance to determine the environmental drivers of species distribution, and further to accurately predict the impact of those pressures on species for efficient conservation planning (Guisan et al. 2013, Scherrer et al. 2019). In this regard, species distribution models (SDM) – also called ecological niche models (ENM) or habitat suitability models (HSM) – are powerful tools to achieve this goal (Guisan et al. 2013, 2017, Araújo et al. 2019, Zurell et al. 2020).

SDMs allow making a link between species' observations and their environment (Guisan et al. 2017, Araújo et al. 2019, Guisan and Zimmermann 2000). They specifically assume that a local occurrence of a species is shaped and explained by a suite of local environmental predictors. SDM is a field in constant discussion on theoretical and technical issues, such as modelling techniques, model evaluation and predictor selection (Franklin 1995, Araújo and Guisan 2006, Guisan et al. 2006, Austin and Van Niel 2011b, Smith et al. 2019, Collart and Guisan 2023).

A crucial step in the SDM process is selecting ecologically meaningful predictors (Austin and Van Niel 2011b, Guisan et al. 2017, Petitpierre et al. 2017, Fourcade et al. 2018). However, the selection of environmental predictors is often limited by the availability of relevant dataset across the study area and by gaps in knowledge on species' ecology (Mod et al. 2016, Scherrer and Guisan 2019). For instance, models are frequently built using widely available bioclimatic predictors, such as those from WorldClim (Fick and Hijmans 2017) or CHELSA (Karger et al. 2017). However, the lack of incorporation of habitat predictors driving species' habitat suitability at more local scales (e.g. land use and cover, hydrography, transportation network) can potentially impact the power and reliability of SDM predictions (Austin and Van Niel 2011b, Mod et al. 2016, Buri et al. 2017, Tessarolo et al. 2021, Collart et al. 2023).

Regarding variable selection, an important consideration is the measurement scale of environmental predictors (i.e. the size of the area that measurement summarizes). SDM predictors are often extracted from spatial grids where each pixel reflects the environmental conditions within its bounds. This approach overlooks the organism's interaction with its environment across multiple scales (Wiens 1989, McGill 2010), thereby oversimplifying the ecological niche complexity (Jaberg and Guisan 2001, Guisan and Thuiller 2005, Fournier et al. 2017, Scherrer et al. 2019), and failing to address scale dependencies (Razgour et al. 2011, Fournier et al. 2017, Sirami et al. 2017, Chase et al. 2018, Damschen 2018, Riva and Fahrig 2023). While numerous studies emphasized the necessity of covering the full scope of environmental dimensions driving species' ecology to develop accurate SDMs (Mod et al. 2016, Scherrer and Guisan 2019, Collart et al. 2024), the importance of considering neighbouring habitat characteristics in the vicinity of species observations has been rarely investigated in SDM studies, despite their role in influencing species presence/absence, abundance and richness (Silander and Pacala 1985, Mazerolle and Villard 1999, Pellet et al. 2004, Fahrig et al. 2011, Shirley et al. 2013, Halstead et al. 2019, Kotowska et al. 2022, Li et al. 2023, Tonetti et al. 2023, Riva et al. 2024).

A solution to integrate this neighbor information into SDMs is to use so-called 'focal predictors', also called 'spatial moving windows', 'neighboring windows' or 'habitat area' (Pellet et al. 2004, Guisan and Thuiller 2005, Scherrer et al. 2019, Riva et al. 2024). These predictors are computed by applying a specific statistic that summarizes the information from neighboring pixels within a spatial moving window of predefined size and shape (Pellet et al. 2004, Guisan and Thuiller 2005, Bellamy et al. 2013, 2020, Bellamy and Altringham 2015, Scherrer et al. 2019). For instance, when applying a mean statistic, focal predictors will reflect the average conditions of neighboring habitats, which can increase, decrease, or match the value of the focal cell. Other statistics such as the minimum, maximum, standard deviation, or coefficient of variation for continuous data could also be computed to capture other ecological aspects such as environmental extremes or habitat heterogeneity. Therefore, the moving-window strategy allows accounting for multi-scale processes (Scherrer et al. 2019, Bellamy et al. 2020) while maintaining the finest possible resolution of the available data. This approach ensures that both local interactions, such as microclimatic conditions, and broader ecological processes, such as regional land-use patterns, are more accurately captured in the models (Lembrechts et al. 2019, Haesen et al. 2023, Lembrechts 2023, Kemppinen et al. 2024, Riva et al. 2024). Despite their high potential, focal predictors are often neglected in SDM studies. A query of the Web Of Science database for the period 1970–2025 identified only 317 out of 14 211 SDM-related papers (Supporting information) that mentioned terms such as 'neighboring habitat', 'neighboring landscape', 'focal predictor', 'focal covariate', 'multi-scale', 'spatial moving windows', 'neighboring windows' and, 'habitat area' in their abstract, keywords or title.

The question of determining the optimal measurement scale (i.e. the size of focal windows to consider) for a specific target species or group is a central challenge (Bellamy et al. 2013, Scherrer et al. 2019, Riva et al. 2023). The optimal measurement scale relies on the accessibility of habitats, on the spatial layout of interconnected habitats, and on the foraging range and behavior of the species (Eigenbrod et al. 2008, Zanini et al. 2009, Jackson and Fahrig 2012, Vicente et al. 2014, Villalobos-

Chaves et al. 2017, Krauel et al. 2018, Ancillotto et al. 2018, Scherrer et al. 2019, Harvey et al. 2023). While focal predictors have been employed for modelling a few mobile taxa, their relevance for predicting species distributions more broadly across multiple taxa is poorly known and, to our knowledge, has never been thoroughly studied in SDMs. For instance, the best measurement radius for marsh and forest cover used to predict the presence of Anopheles mosquitoes in French Guyana was found to be 400 m (Adde et al. 2016). For foraging bats in the south of the Lake District National Park in NW England, optimal measurement radii ranged between 100 and 500 m (Bellamy et al. 2013), but no optimal measurement scale was evidenced for bats in the Swiss Alps (Scherrer et al. 2019). Identifying the optimal neighbouring variables could also have important contributions for conservation management. For instance, Knüsel et al. (2024) highlighted that land-use around groundwater is affecting groundwater organisms well beyond the local protection zone, and greatest effects of urban and road surfaces was found between 100 m and 1 km for a threatened tree frog in a Swiss agricultural landscape (Pellet et al. 2004).

The objective of our study was to assess the use of focal predictors in SDMs by leveraging a recent study that developed a comprehensive set of national-scale, high-resolution SDMs for 7286 species of plants, fungi, and animals in Switzerland (Adde et al. 2025). This study applied an automated predictor selection procedure (Adde et al. 2023b) to identify the best predictors and optimal measurement scales from a highdimensional pool of 877 candidates (Külling et al. 2024). More specifically, we assessed whether:

1) The selected radius depends on the mobility of the organisms. In agreement with Guisan and Thuiller (2005), we hypothesized that predictors measured at larger radii will be more frequently selected for mobile organisms than for sessile ones (hypothesis 1; Fig. 1).
2) The body size of the organisms influences the selection of the radius. We hypothesized that larger-bodied organisms require larger radii, reflecting the positive relationship between body size or mass and habitat spatial scale (Holland et al. 2004, 2005, Fisher et al. 2011, Benjamin et al. 2014, Stuber et al. 2018, Hale et al. 2019) (hypothesis 2).
3) Patterns of radius selection in relation to organism mobility and body size are consistent across the categories of predictors, although their importance may vary. We hypothesized that the choice of radius used to generate focal predictors would be particularly important for land use and land cover (LULC) predictors, as already shown in several studies (Mazerolle and Villard 1999, Bellamy et al. 2013, Adde et al. 2016, Scherrer et al. 2019) (hypothesis 3).

Material and methods

MODELLING PROCESS

We took advantage of Swiss-wide SDMs at a 25 m resolution previously developed for 7286 species from 17 different taxonomic classes using the N-SDM modelling software (Adde et al. 2023a).

N-SDM uses a spatially-nested framework to integrate a 'global' model, which quantifies species responses to bioclimatic conditions across their entire range, with a 'regional' model that employs finer-scale habitat predictors (Guisan et al. 2025). In this study, global (European scale) and regional

(Swiss scale) models were combined using the 'covariate' N-SDM nesting strategy (strategy 4 in Table 1 of Guisan et al. 2025), where predictions from the global model serve as an additional predictor for the regional model. The default parameters of N-SDM were utilized for modelling the distributions of all available species (a copy of the ODMAP protocol is provided as Supporting information).

SPECIES DATA

Species occurrence records from 1980 to 2021 for Switzerland were provided by the Swiss Species Information Center InfoSpecies on 24 June 2022 (Andriollo et al. 2021) at a spatial resolution of 25 m, consistent with the resolution of the environmental predictors used in this study. For outside Switzerland, occurrences were downloaded for the same time period from the Global Biodiversity Information Facility (GBIF; www.gbif.org/) on 11 Jan. 2023 (https: //do i.org /10.1 5468/ dl.fk tyas). The final dataset comprised 7286 species from 17 different main taxonomic groups (Supporting information 3). For each species and scale (global and regional), 10 000 pseudo-absences were randomly generated across the target areas. These pseudo-absences were then weighted equally to the number of occurrences in the models to reach a prevalence of 0.5.

To assess the influence of organism mobility on radius selection, we classified species as 'mobile' or 'sessile '. A species was considered 'mobile' if its individuals can move more than 25 m over a short period of time, with 25 m corresponding to the resolution of the species occurrence data and habitat suitability models used in this study. A species was considered 'sessile' if its individuals cannot move, for example plants, or move less than 25 m over a short period of time, for example small soil organisms (see the Supporting information for the detailed species classification). Based on this rule we identified 2461 mobile and 4825 sessile species (see the Supporting information for the detailed species list). To assess the influence of the species' body size, we created 4 size categories (< 10 cm; [10; 25 cm[; [25; 50 cm[and > = 50 cm). Before categorizing species by their height/length ('size' hereafter) based on global databases, we homogenized taxonomy with the 'taxize' R package (Chamberlain and Szöcs 2013) using GBIF (www. gbif.org/), ITIS (Integrated Taxonomic Information System; www.itis.gov), NCBI (National Center for Biotechnology Information; https: //ww w.ncb i.nlm .nih. gov/t axono my), and OTT (OpenTree Taxonomy; https ://gi thub. com/O penTr eeOfL ife/r efere nce-t axono my) databases to avoid issues on taxonomic name between country and global designation. The size classification was based on different definitions of the body size, depending on taxa and data availability. For amphibians, diplopods, odonates, reptiles and spiders, we used the median value of the body size (Oliveira et al. 2017; www.bodentierhochvier.de; Waller et al. 2019; www.InfoSpecies.ch; Pekár et al. 2021, respectively); for birds the median value of the wings' length (www.Vogelwarte.ch); for bivalves and gastropods the median value of the shell's diameter (www.molluscabase.org and www.InfoSpecies.ch); for bryophytes the mean size of gametophyte (van Zuijlen et al. 2023); for stoneworts and tracheophytes the median value of the vegetative part (www.InfoSpecies.ch and Kattge et al. 2020); for fish the maximal size of body length (Brosse et al. 2021 and www.InfoSpecies.ch); for mammals the average adult body length (Soria et al. 2021). As size information was missing for most fungi and insect species, we assigned them to the '< 10 cm' category (Supporting information 3). Based on this rule we identified 4800, 581, 598 and 1307 species assigned to the body size categories <10 cm, [10; 25 cm[, [25; 50 cm[, and ≥ 50 cm, respectively (see the Supporting information for the detailed species list).

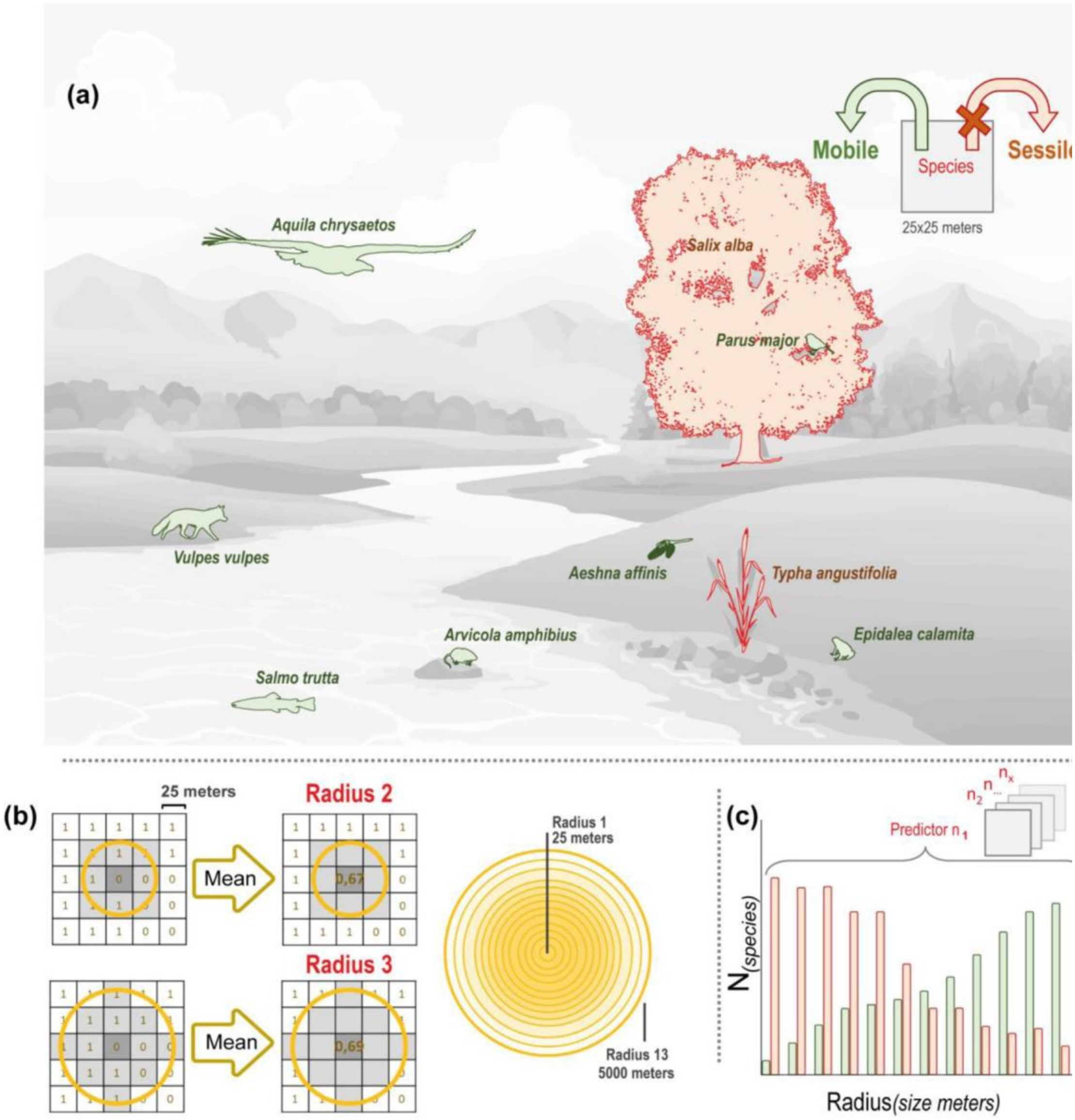

Figure 1. Conceptual representation of the use of focal predictors in species distribution models (SDMs) for mobile and sessile species. (a) Example of a community landscape illustrating sessile species (red shapes, e.g. white willow *Salix alba*) and mobile species (green shapes, e.g. great tit *Parus major*, royal eagle *Aquila chrysaetos*). (b) Illustration of the 13 measurement radii evaluated in this study, ranging from 25 m (source pixel size; no focal window applied) to 5000 m. For each pixel, a mean statistic was calculated across all pixels within the specified radius. (c) Identification of the optimal measurement radius yielding the best univariate SDM performance for each species and predictor. These optimal radii were then summarized according to species' mobility status and body size.

PREDICTOR DATA

To model the species distribution of individual species, we utilized a set of 877 candidate predictors organized into eight main categories: bioclimatic (n = 19), edaphic (n = 78), hydrologic (n = 27), land use and cover (LULC; n = 494), population density (n = 13), topographic (n = 156), transportation (n = 25), and vegetation (n = 65) extracted from the 25-m resolution SWECO25 database (Külling et al. 2024). For global-level models, only bioclimatic predictors (n = 19) were considered, with a spatial resolution of 25-m resolution within Switzerland (https ://do i.org /10.5 281/z enodo .1063 5681), and 30-arc-second outside Switzerland (Karger et al. 2017). Regional models incorporated all predictor categories. Focal predictors, computed for edaphic, LULC, topographic, transportation and vegetation categories by applying a pixellevel function calculating the average value in a circular moving window of 13 radii ranging from 25 m (i.e. local value, no neighborhood considered) to 5 km, were directly extracted from the SWECO25 database (Fig. 1b; Külling et al. 2024). The input data were all continuous except for LULC, which were all categorical. The final focal values represented either the raw average within the focal window (e.g. mean slope), or the percentage cover of each LULC class within the window. The radii were selected to represent fine-scale (25–500 m), medium-scale (1000–2000 m), and landscape-scale (3000– 5000 m) processes, with increment of radii following a quasilogarithmic pattern to avoid redundant information at larger scales while ensuring sufficient resolution at smaller scales (Supporting information).

PREDICTOR SELECTION

As an initial step, predictors identified as potentially irrelevant for modelling a species (or group of species) were excluded based on an 'expert table' created in collaboration with species specialists in the national InfoSpecies expertise centers (www.infoSpecies.ch; Supporting information). In our case study, all predictors were used for mobile and sessile species except edaphic predictors for mobile species.

Common practices for predictor selection in SDM studies typically involve expert-based sets of predictors, subsequently reduced/filtered using VIF or correlation analyses, or dimensionality reduction approaches such as principal component analyses (Brauner and Shacham 1998, Dormann et al. 2013, Mod et al. 2016, Guisan et al. 2017, Petitpierre et al. 2017, Júnior and Nóbrega 2018). While expert knowledge is valuable for ensuring ecological interpretability, this approach quickly becomes intractable when modelling large numbers of species across high-dimensional predictor spaces, and may introduce biases toward commonly used variables (Adde et al. 2023b). Here, we used an automated embedded selection procedure developed by (Adde et al. 2023b) at both global and regional levels using its default parameter. This procedure was designed to handle candidate sets ranging from tens to thousands of predictors, which is well suited to perform radius selection for predictors and thus account for species-specific spatial scale dependency. Their main advantage over filtering-only methods is that they interact directly with the target algorithms and evaluate predictors in a multivariate context. Although moderately important predictors might be excluded during automatic selections, the framework was designed to model numerous species in a high-dimensional context, where species-specific fine-tuning is not computationally feasible. When working with a large number of species, a balance between efficiency and performance was therefore required and was shown to be efficient in more than 80% of the tested models in Adde et al. (2023b).

In brief, the covsel algorithm first (step A) reduces the dimensionality of the dataset by filtering out less informative predictors from collinear pairs (default threshold: Pearson correlation coefficient |r| > 0.70) based on p-values resulting from univariate generalized linear models (GLM; Nelder and Wedderburn 1972) with binomial probability distribution and logit link. To allow identifying the best measurement radius for each predictor, step A was sequentially applied at three levels: 1) at the predictor level (i.e. selecting the best radius among the 13 available for a same predictor as suggested by Bellamy et al. (2013), 2) the category level (i.e. within thematic predictor categories) to maximize the diversity of predictor, and 3) using all remaining predictors from the two previous levels. In step B, to identify which predictors carry the strongest signal, the remaining predictors are then used to train models with algorithm-specific regularization techniques: elastic-net GLMs (Zou and Hastie 2005), generalized additive models with null-space penalization (GAM; Marra and Wood 2011), and guided regularized random forest (RF; Deng and Runger 2013). For each algorithm, a ranked list of predictors is produced based on internal criteria (regularized coefficient magnitude for GLM, χ^2 statistic for GAM, impurity based importance for RF). Predictors are then ranked based on their importance scores in these models. These ranked lists are then combined, giving priority to predictors consistently selected across algorithms and the top k predictors are retained, with k set by default to round(log2(number of occurrences)). To ensure models remain parsimonious, k was capped at a maximum of 12 as model performances tend to decrease with numbers of predictors around this threshold (Brun et al. 2020). We chose a logarithmic function to determine the optimal number of predictors, allowing the number to increase with sample size while avoiding unrealistic values for very large datasets. The common rule of thumb of 'one predictor per ten occurrences' (Harrell et al. 1996) is appropriate for small sample size but becomes unsuitable for species with many records. To achieve a smoother and more balanced scaling, we applied a base-2 logarithm rather than base-10. For example, a base-2 yields 7 and 14 selected predictors for species with 100 and 14 000 occurrences, respectively; whereas a base-10 would result in only 2 and 4 selected predictors; and the common rule of 'one predictor per ten occurrences' rule-of-thumb would select 10 and 140. In addition, given the large number of species in this study, we focussed our study on selection frequency within the models and we did not test the relative error reduction achieved by each predictor. Such analyses require calculating intermediate model fits after the sequential inclusion of each variable. These analyses were however not feasible within the current framework and scope of this study. While focusing on selection frequency may be less precise than sequential error reduction, it is considerably less computationally intensive and more reasonable to apply in a multi-species, high-dimensional, multi-algorithm framework such as the one presented here.

Finally, note that following the 'covariate' nesting strategy (Guisan et al. 2025), we re-applied predictor selection at the regional level with the global model output included as a forced predictor. If any regional predictor was identified as collinear with the global predictor, it was automatically discarded. This ensures that redundancy and potential bias are reduced in the nested modelling framework (Adde et al. 2023a).

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MODEL FITTING AND EVALUATION

Five algorithms were used to model species distributions: GLM, GAM, MaxNet (Phillips et al. 2017), RF, and light gradient boosted machine (GBM; Ke et al. 2017). The default values from N-SDM were used for hyperparameter tuning. Models were evaluated using a 100 split-sample cross-validation strategy, using 70% of the data to calibrate the models and the remaining 30% for validation. When applicable, the training and testing species occurrence points defined at the global level were mirrored in the corresponding split samples at the regional level. This procedure prevents any overlap of information between training and testing data across modelling levels. In addition, it was shown that in such rugged mountainous landscapes (such as our study area), spatial correlation between training and test sets (in a repeated split-sample cross-validation) is very limited, potentially decreasing the risk of inflated predictive performance (Pottier et al. 2013, Chevalier et al. 2021).

For each model, the best hyperparameters were defined using the average 'Score' of three evaluation metrics including the Somer's D (= 2×AUC − 1; (Somers 1962), the maximum values of the true skill statistic (maxTSS; Guisan et al. 2017), and the continuous boyce index (CBI; Hirzel et al. 2006).

PREDICTOR IMPORTANCE

Relative predictor importance scores, ranging from 0 to 1, were automatically generated by N-SDM via the nsdm.varimp function. This function extracts algorithm specific raw measures directly from each fitted model and then rescales them by the within model maximum. For GBM, we used the total split gain. For GLM, we used the absolute value of the Wald z statistic. For GAM, we used the χ^2 statistic of each smooth term. For RF, we used a mean decrease in Gini impurity. For MaxNet, we summed the absolute values of all feature coefficients associated with each predictor (Adde et al. 2023a).

FOCAL RADIUS SELECTION ANALYSES

To summarize the radius selection by predictor category, because several predictors from the same category with different radii could be selected for a species, we took the median value of the selected radii for each species per category of predictor. To test the three hypotheses of the study, i.e. 1) the selected radius depends on the mobility of the organisms; 2) the size of the organism influences the selection of the radius; 3) the radius selection patterns based on organism mobility and size are consistent across predictor categories, but their importance varies), all selected radii were visualized using violin plots and compared using a summary table that included the mean, median, and standard deviation (SD) of the radii. Comparisons were made across each predictor category, for both mobile and sessile species, across the four size categories, and for each taxon covered in the study. Kruskall–Wallis tests followed by post hoc pairwise Wilcoxon tests were performed to assess statistical significance of the differences between the groups (i.e. mobility, body size and taxa). As numerous pairwise comparisons were made, p-values were adjusted with a Bonferroni correction.

Results

MODEL PERFORMANCES

Models had on average a Somer's D of 0.97 ± 0.02, a MaxTSS of 0.91 ± 0.05, and a CBI of 0.78 ± 0.18 (see the Supporting information for individual model performances). Differences in terms of average model performances were observed between taxa, with Somer's D, MaxTSS and CBI, ranging from 0.94 ± 0.02 to 0.99 ± 0.01, 0.81 ± 0.09 to 0.95 ± 0.03, and 0.34 ± 0.28 to 0.89 ± 0.17, respectively. Stoneworts had on average the lowest model performances, while models of amphibians were on average the highest (Supporting information).

OVERALL FOCAL PREDICTOR SELECTION

For each modelled species, focal predictors were selected at least once in ≥ 93.8% of the studied species for each of the five categories of predictors (Supporting information). The lowest median and mean radius selection were for the transport (100 m and 401 m, respectively), topographic (100 m and 835 m, respectively) and vegetation (200 and 1209 m, respectively) categories. In contrast, the highest values were found for the edaphic (850 m and 1319 m, respectively) and LULC (2550 m and 2562 m, respectively) categories. Except for the transport category, which had a relatively low standard deviation (SD) of 772 m, the other four categories showed higher variability, with SDs ranging between 1376 and 1734 m.

MOBILE VERSUS SESSILE SPECIES

Differences in selected radii size between mobile and sessile species were found across predictor categories. In the LULC category, slightly larger radii were selected for mobile species than for sessile species, with medians of 2750 and 2550 m, respectively (p-value < 0.01; Fig. 2, Supporting information). For topographic predictors, both groups shared a low median radius of 100 m, but sessile species had a higher mean radius (958 ± 1461 m) compared to mobile species (612 ± 1,173 m; p-value < 0.001). In the vegetation category, mobile species had a slightly larger median radius (200 m) than sessile species (150 m), though this difference was not statistically significant. Finally, for transport-related predictors, both groups shared the same median radius of 100 m.

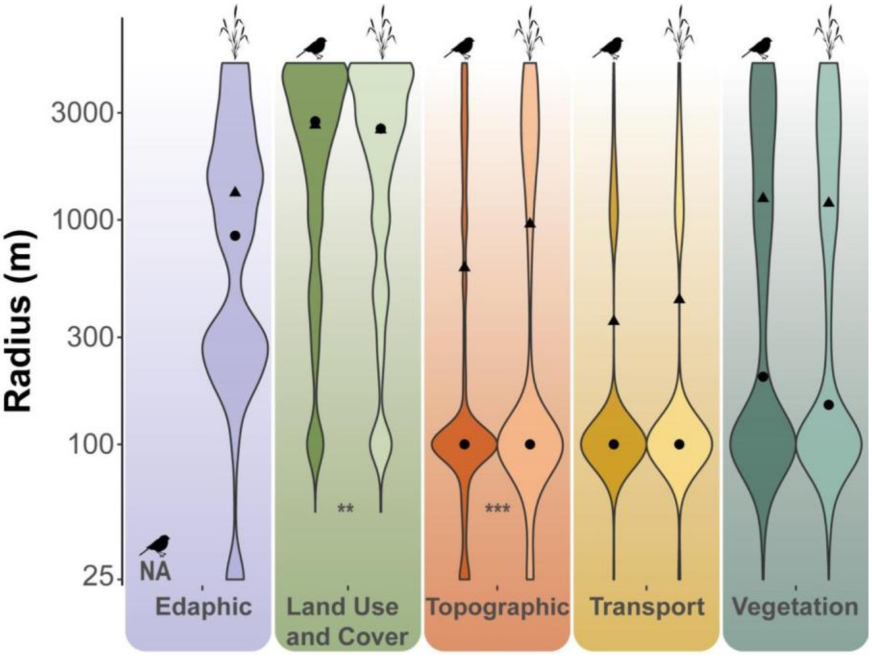

Figure 2. Distribution of selected radii for mobile (darker colors, represented by a bird icon) and sessile (lighter colors, represented by a plant icon) species across predictor categories. Violin plots display the range and density of selected radii with black dots indicating median values and black triangles indicating mean values. Note that the edaphic category was not assessed for mobile species due to the constraints in the expert-based predictor filtering table. Statistical significance of pairwise differences were assessed using Wilcoxon test, with ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; none: Non-significant. (Supporting information).

DOES SPECIES BODY SIZE MATTER?

Significant differences in selected radii were observed across body size categories for all predictor categories except topography. Very small species (< 10 cm) had significantly smaller selected radii compared to larger species for most predictor categories (Fig. 3, Supporting information). In the edaphic category, the median value was 300 m for very small species and was between 900 m to 1250 m for the other body size categories (p-values < 0.01). In the LULC category, median radius significantly increased with body size from 2500 m to 3000 m (p-values < 0.05). For transport and vegetation predictors, significant differences were observed between very small species and larger species (p-values < 0.01), while no significant differences were observed among the three remaining body size categories ([10–25 cm], [25–50 cm], and ≥ 50 cm), with median selected radii of 100 m and 1000 m, respectively. For topographic predictors, median radii were consistent across all four body size categories, with a value of 100 m.

DOES THE TAXA MATTER?

Among the taxa considered, angiosperms, gymnosperms, and gastropods exhibited the largest selected radii, with median values of 1100 m, 1500 m and 1500 m, respectively (Supporting information). In contrast, the other taxa had smaller median radii of 300 m. LULC predictors were associated with the highest median radii across taxa. The smallest values were observed for bivalves and stoneworts (450 m), while the largest were for amphibians, gastropods, and malacostracans, each

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reaching 4000 m. For topographic predictors, the median radius was consistently 100 m across most taxa, with the exception for birds (231 m), bivalves (2550 m), and malacostracans (900 m). In the transport category, large radii were rarely selected. Median radii ranged from 25 to 100 m for most taxa. Mammals had the highest mean radius in this category (1023 m), but also the largest variability, with a SD of 1483 m. The vegetation category showed the greatest heterogeneity across the 17 taxa. Median radii ranged from 100 m for bryophytes, stoneworts, diplopods, fungi, insects, and reptiles to 3275 m for amphibians. Fungi had significantly smaller radii than most other taxa, with a mean radius of 494 m (p-values < 0.01).

Discussion

Predicting species distribution is key for successful management and adaptation to current and future environmental conditions from large (Isaac et al. 2020) to fine (Kemppinen et al. 2024) spatial scales. Yet, the way different predictors influence ecological processes at each spatial scale is still a matter of intense investigation (Scott et al. 2002, McGill 2010, Vicente et al. 2014, Jackson and Fahrig 2015, Rapacciuolo and Blois 2019, Guisan et al. 2025). One way to assess this is to use focal predictors in SDMs, characterizing the neighboring information and allowing to identify the optimal spatial scale at which a certain environmental characteristic affects species distributions (Pellet et al. 2004, Bellamy et al. 2013, Vicente et al. 2014, Scherrer et al. 2019, Deneu et al. 2021, Riva et al. 2023, Knüsel et al. 2024). However, no study had so far conducted a thorough assessment of the use of focal predictors in species distribution models (SDMs) across numerous environmental predictors and taxa.

We tested whether quantifying environmental characteristics in the neighborhood of species observations was important using a large set of national-scale, high-resolution, SDMs fitted for more than 7000 species (Adde et al. 2025). Although these focal predictors are likely to play an important role in ecological understanding, especially in landscape studies (Riva et al. 2024), they have been most often neglected in SDM studies and mostly used in studies focusing on animals (Bellamy et al. 2013, Adde et al. 2016, Scherrer et al. 2019, Theux et al. 2022). Here, by considering 13 measurement radii in the set of candidate environmental predictors used for modelling each individual species, we showed for the first time that these types of predictors were frequently selected, and potentially with high importance, in SDMs computed for a large number of species and taxonomic groups, including both mobile (e.g. large vertebrates) and sessile organisms (e.g. plants). Among all species, focal predictors were selected at least once in > = 94 % of the SDMs for each of the five studied categories of environmental predictors (i.e. edaphic, land use and cover, topographic, transport and vegetation). These high percentages reflect the necessity of further testing for the importance of focal predictors when modelling species distributions if we want to generate more accurate models.

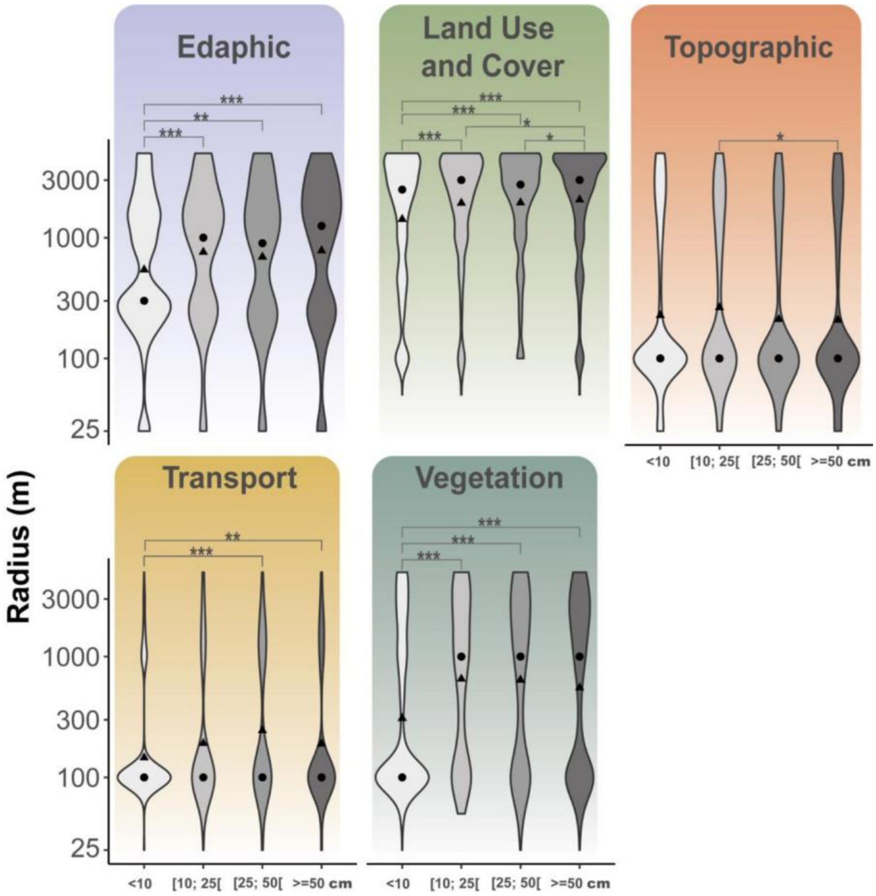

Figure 3. Distribution of selected radii across species body size classes (< 10 cm, [10–25 cm], [25–50 cm], and ≥ 50 cm) and predictor categories. Violin plots display the range and density of selected radii, with black dots indicating median values and black triangles indicating mean values. Statistical significance of pairwise differences were assessed using Wilcoxon test, with ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; none: Non-significant. (Supporting information).

More specifically, we tested if radius selection was influenced by organism mobility (hypothesis 1) and size (hypothesis 2), with consistent patterns across predictor categories, but varying levels of importance within each (hypothesis 3).

Firstly, our results showed that when comparing mobile with sessile species, we found no significant differences in selected radii for most of the categories of environmental predictors. Surprisingly, for topographic predictors, the mean selected radius was significantly greater for sessile than for mobile species (958 m versus 612 m, respectively), showing a wider influence of the surrounding landscape for sessile than for mobile species in this category. This result challenges our first hypothesis that the radius of the selected focal predictors should be greater for mobile than for sessile organisms (Guisan and Thuiller 2005). However, it corroborated previous studies showing that fine-measurement-scale topography is not sufficient to improve our understanding of species distribution patterns (as shown for land plants in Pradervand et al. 2014, Man et al. 2022, Chytrý et al. 2024), and that large-measurement-scale topography information is also important as a result of local effects of wider landscape configurations or the 'spatial mass effect' as discussed in Chytrý et al. (2024) and Leibold (2004). The landscape configuration can for instance explain soil erosion or wind effects on convex situations and water or sediment accumulation on concave ones as indirectly captured by 'focal' topographical predictors (e.g. topographic position; Van Niel et al. 2004, Austin and Van Niel 2011a). The spatial mass effect refers to the survival of sink populations in marginally suitable areas, facilitated by the dispersal of individuals from nearby optimal habitats (Shmida and Whittaker 1981). Indeed, species thriving in a favorable macroenvironment (such as a southfacing slope for species adapted to warm conditions) produce numerous propagules, enabling the establishment and persistence of populations in less suitable microhabitats (Shmida and Whittaker 1981, Leibold et al. 2004, Chytrý et al. 2024). For instance, a species adapted to cold conditions would be unlikely to colonize cold micro-habitat (such as small pits) in a south-facing slope, due to dispersal limitations. Even when colonization is successful, populations are likely to remain limited, making them vulnerable to extinction due to demographic or environmental stochasticity (Chytrý et al. 2024). In contrast, the median focal radius of the LULC was significantly more important for mobile than sessile species (2750 and 2550 m, respectively), aligning with the hypotheses of Guisan and Thuiller (2005) of greater radii expected for mobile species. This phenomena can be more easily explained with the spatial mass effect affecting sessile species, or could also be an effect of the importance of resources in the surrounding (i.e. associated with the concept of species home range; Jaberg and Guisan 2001, Braunisch and Suchant 2010) and the habitat patch size and habitat fragmentation, which are also known to impact species distributions (Heegaard et al. 2007, Stein et al. 2014, Fahrig 2017, Fahrig et al. 2022, Riva et al. 2024). Nevertheless, the high focal radius observed for sessile species at this stage remains unexpected and would require further analyses along the explanations suggested above.

Secondly, previous studies suggested that the optimal spatial scale of influence of environmental predictors (Vicente et al. 2014) could be related to the size of the organisms (Pincebourde and Woods 2012, Luan et al. 2020), with larger species occupying larger physical spaces being best related to predictors at coarser resolution (Morse 1974, Jaberg and Guisan 2001, Pincebourde and Woods 2012, Collart et al. 2024). We accordingly expected that larger radii would be selected for larger species. We indeed observed that the smallest species (< 10 cm) were significantly more associated with smaller radii than larger species (> 10 cm) for all of our categories of environmental predictors, except topography. No significant differences were shown for the remaining three body size categories in the radius size selection for edaphic, topographic, transport, and vegetation predictor categories. Only in the LULC category was the median focal radius found to be increasing with species body size. These results are consistent with previous studies showing a positive trend between body size (or mass) and habitat measurement scale (Holland et al. 2004, 2005, Fisher et al. 2011, Benjamin et al. 2014, Stuber et al. 2018, Hale et al. 2019). According to Fisher et al. (2011) and Holling (1992), some habitat patches are too small to support organisms of a certain size, while others are too far apart for their movement capabilities. Within each habitat patch, species must either be small enough to survive on resources within their range of movement, or large enough to efficiently use multiple patches. As a result, the likelihood of a species of a given size being found in a specific habitat is closely tied to the surface area of the latter (Holling 1992, Fisher et al. 2011), which is likely to be reflected by focal predictors.

Thirdly, in our study, no clear patterns occurred across the 17 major taxa groups evaluated. This pattern could be explained by the low number of species in certain taxon. For instance, there were no significant differences in the radius selected for the bivalve's group (number of species = 7) with others, yet this taxon had the highest radius median in the topographic category. Even if the LULC category was the one with the highest number of significant differences between taxa, it remained a low overall percentage of significant radius size selection (16.2%; 22/136 comparisons were significant). At this stage, based on our results, we cannot recommend selecting radius size at the overall taxon level; species-level selection remains necessary.

In addition, focal predictors can be generated using different statistics to summarize the neighboring habitat, which can have different ecological interpretations. Here we use the mean statistic which characterizes the influence of different measurement scales on species occurrences. In a mountain context, this mean statistic can help determine whether the focal pixel lies within a larger north-facing slope. A species adapted to cold conditions is unlikely to reach a small cold micro-habitat on a south-facing slope because of dispersal limitations (Chytrý et al. 2024). For binary data, such as land use and cover classes, an average value reflects class coverage in the neighborhood, which was shown to influence species occurrence (Fahrig 2013, Watling et al. 2020, Riva et al. 2023). However, other metrics could be performed to reflect other ecological meanings (Riva et al. 2024). For example the diversity of habitat categories in the neighborhood, or statistics such as the standard deviation and coefficient of variation can be performed to characterize habitat heterogeneity which was shown to influence the distribution of invasive plant species (O'Reilly-Nugent et al. 2016) or tree species (Shen et al. 2013). The minimum or maximum values could also be measured to provide insights into environment extremes relevant to species' ecological limits. Therefore, the selection of the statistic employed to generate focal predictors should be carefully considered depending on the study's objectives, study organisms or study area characteristics and guided by ecological knowledge (Popovic et al. 2024, Riva et al. 2024).

Finally, despite the observed differences in selected radii by mobility, size class and taxon, we do not recommend using the outputs presented in this paper as-is to select an optimal radius for a species belonging to one of these broad classes. Species may belong to the same size category and be mobile, yet differ greatly in their diet and habitat size preferences. For example, bats in Switzerland, although similar in size and considered mobile species, exhibit different diets and environmental needs (Jaberg and Guisan 2001, Scherrer et al. 2019). While all are insectivorous, they require distinct environmental predictors and radii to adequately capture habitat heterogeneity (Bellamy et al. 2013). Therefore, assigning a single focal radius per predictor category to entire groups is not appropriate due to this substantial variability (Scherrer et al. 2019). Instead, we recommend to perform radius selection for each species and each predictor individually, as proposed byn Bellamy et al. (2013) and Scherrer et al. (2019) in order to improve model performance and account for species-specific spatial scale dependency.

Conclusion

With an increasing interest in modelling species distribution at fine spatial scale (Lembrechts et al. 2019, Patiño et al. 2023, Kemppinen et al. 2024), the question of which spatial scale an environmental predictor operates becomes increasingly important. Focal predictors offer a powerful means to account for species-specific spatial scale dependency. These predictors address this challenge by incorporating information on neighboring habitats, habitat amount and habitat heterogeneity, factors that all influence species presence/ absence, abundance and richness (Guisan and Thuiller 2005, Fahrig et al. 2011, Shirley et al. 2013, Fournier et al. 2017, Chase et al. 2018, Riva and Fahrig 2023, Li et al. 2023, Tonetti et al. 2023, Riva et al. 2024). In our study, focal predictors were frequently selected across species, showing their overall importance to predict species distributions. Yet no consistent patterns emerged between taxonomic groups strongly suggesting selecting the most appropriate measurement scale for each predictor and for each species to improve the accuracy of species distribution models.

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Author contributions

Flavien Collart and Pierre-Louis Rey share first authorship. Antoine Guisan and Antoine Adde share last authorship. Flavien Collart: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Resources (equal); Software (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). PierreLouis Rey: Conceptualization (equal); Data curation (equal); Methodology (supporting); Resources (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). Florian Altermatt: Funding acquisition (equal); Writing – original draft (supporting); Writing – review and editing (supporting). Nathan Külling: Resources (equal); Writing – original draft (supporting); Writing – review and editing (supporting). Antoine Guisan: Conceptualization (lead); Funding acquisition (equal); Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). Antoine Adde: Conceptualization (equal); Data curation (equal); Resources (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal);

Data availability statement

Data are available in the Supporting information.

Supporting information

The Supporting information associated with this article is available with the online version.

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