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The Best of Two Worlds: Using Stacked Generalisation for Integrating Expert Range Maps in Species Distribution Models

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ABSTRACT

Aim: Species distribution models (SDMs) are powerful tools for assessing suitable habitats across large areas and at fine spatial resolution. Yet, the usefulness of SDMs for mapping species' realised distributions is often limited since data biases or missing information on dispersal barriers or biotic interactions hinder them from accurately delineating species' range limits. One way to overcome this limitation is to integrate SDMs with expert range maps, which provide coarse-scale information on the extent of species' ranges and thereby range limits that are complementary to information offered by SDMs.

Innovation: Here, we propose a new approach for integrating expert range maps in SDMs based on an ensemble method called stacked generalisation. Specifically, our approach relies on training a meta-learner regression model using predictions from one or more SDM algorithms alongside the distance of training points to expert-defined ranges as predictor variables. We demonstrate our approach with an occurrence dataset for 49 bat species covering four biodiversity hotspots in the Eastern Mediterranean, Western Asia and Central Asia.

Main Conclusions: Our approach offers a flexible method to integrate expert range maps with any combination of SDM modelling algorithms, thus facilitating the use of algorithm ensembles. In addition, it provides a novel, data-driven way to account for uncertainty in expert-defined ranges not requiring prior knowledge about their accuracy, which is often lacking. Integrating expert range maps into SDMs for bats resulted in more realistic predictions of distribution patterns that showed narrower niche breadths and smaller range overlaps between species compared to traditional SDMs. Our approach holds promise to improve

assessments of species distributions, while our work highlights the overlooked potential of stacked generalisation as an ensemble method in species distribution modelling.

1 | Introduction

While global biodiversity is declining rapidly (Pimm et al. 2014), our knowledge about species′ distributions often remains limited (Diniz-Filho, De Marco, and Hawkins 2010). This lack of detailed information for many regions and taxa, referred to as the Wallacean shortfall (Hortal et al. 2015), translates not only into knowledge gaps in biogeography and ecology but also into real barriers to conservation planning to ensure that limited conservation funding is spent most effectively (Hochkirch et al. 2021). Species distribution models (SDMs) have become a central tool for addressing the Wallacean shortfall, allowing to characterise species′ niches by combining occurrence records with environmental predictors for predicting species′ distributions (Elith and Leathwick 2009; Guisan and Thuiller 2005). Yet, although SDMs can accurately assess the environmental suitability of habitats (i.e., map *potential distributions*), they typically lack information on other factors limiting species′ ranges, such as barriers to dispersal or biotic interactions (i.e., competitive exclusion). This, in turn, means that the usefulness of SDMs for mapping *realised distributions* of species can be limited, as their inability to identify range limits often results in an overprediction of species′ ranges, particularly when distributions are modelled across large geographic extents (Calabrese et al. 2014; Merow, Wilson, and Jetz 2017; Soberón 2007). While methods for capturing dispersal and biotic interactions within SDMs have been proposed (Ovaskainen et al. 2016; Zurell 2017), their applicability is often limited due to a lack of adequate datasets or missing knowledge about underlying ecological processes.

A widely applicable solution to improve SDMs′ capability for assessing realised distributions lies in their combination with external information on species′ range limits (Domisch, Wilson, and Jetz 2016; Fletcher Jr. et al. 2019; Merow, Wilson, and Jetz 2017). Most commonly, range information is available in the form of expert-based range maps, which offer estimates of species′ range extents derived from occurrence information as well as expert knowledge about geographical, biotic or environmental range limits. Although expert range maps cannot directly disentangle how biotic interactions and dispersal limit ranges, they allow to incorporate the effects of these processes indirectly by characterising realised range limits. The most important database of range maps (particularly for terrestrial animals) is offered by the International Union for the Conservation of Nature (IUCN), which provides expert-defined ranges for more than 150,000 species (IUCN 2022). Expert range maps are frequently criticised for being coarse in resolution (meaning that species will often be absent from many areas within the expert-defined range), incomplete in terms of species coverage or outdated (Higino et al. 2023; Ramesh et al. 2017). Despite these shortcomings, expert range maps can provide information on range limits that is complementary to data generated by SDMs (Merow, Wilson, and Jetz 2017). While range maps characterise a species′ extent of occurrence (i.e., its range limits), SDMs offer fine-scale representations of suitable habitats, making approaches combining both datasets promising for improving distribution assessments (Domisch, Wilson, and Jetz 2016; Ellis-Soto et al. 2021; Merow, Wilson, and Jetz 2017).

Several approaches have sought to combine these relative strengths of expert range maps and SDMs, such as using range maps directly as predictors in SDMs (Domisch, Wilson, and Jetz 2016) or adding spatial offset terms to models that are fit via point process models or related approaches (e.g., Maxent; Merow, Wilson, and Jetz 2017). The latter approach is particularly promising as it allows to account for uncertainty in expert range maps by incorporating user-defined decay curves that reflect a priori expectations about the accuracy of expert range boundaries. Applying this approach, however, can be challenging for two reasons. First, defining spatial offsets and decay curves can be difficult if prior information on the accuracy of range maps is missing, potentially leading to bias introduced by decisions on the strength and decay of the offset term. Second, while the use of algorithm ensembles has become a key approach in species distribution modelling (Araújo et al. 2019; Araújo and New 2007), several widely used and well-performing machine learning algorithms (e.g., random forests or support vector machines) do not feature offset terms.

Here, we suggest stacked generalisation (Wolpert 1992) as an alternative approach for integrating external range information enabling flexible combinations of multiple SDM algorithms. Designed as an ensemble method for combining multiple modelling algorithms, stacked generalisation uses the predictions of models built at one level as the input for a meta-learner built at a second level (Naimi and Balzer 2018). Although being widely applied in machine learning (Sesmero, Ledezma, and Sanchis 2015), and despite the general proliferation of algorithm ensembles in SDM studies (Buisson et al. 2010; Hao et al. 2019), stacked generalisations have rarely been used with SDMs (but see Bonannella et al. 2022; El Alaoui and Idri 2023). Here, we demonstrate the use of stacked generalisation as an approach for integrating expert range information with one or more SDM algorithms. Using available occurrence datasets for characterising expert map accuracy, our approach offers an alternative, data-driven method to integrate expert range maps in SDMs while accounting for their uncertainty.

In the following, we first introduce our approach and highlight issues important to consider in its application. Then, we assess our approach by applying it to a presence-only occurrence dataset for 49 bat species collected across a large geographic extent covering four biodiversity hotspots in the Eastern Mediterranean, Western Asia and Central Asia. Specifically, we compare the predictive performance as well as resulting distribution maps of (1) single-algorithm SDMs, (2) ensembles of SDM algorithms built with stacked generalisations and (3) stacked generalisations including expert range maps.

2 | Stacked Generalisation for Integrating Expert Range Information in SDMs

Stacked generalisation is an ensemble method for combining multiple models, often built with different algorithms, using their individual predictions as training data in a meta-learner (Naimi and Balzer 2018; Wolpert 1992). Here, we apply this approach to integrate one or more SDM algorithms with expert range maps. By using the expert map as an additional model containing complementary information to SDMs, that is, a coarse-scale estimate of range limits, our approach leverages the advantages of stacked generalisations, which have been shown to perform particularly well when combining heterogeneous input models (Sesmero, Ledezma, and Sanchis 2015).

Multiple potential approaches exist to combine SDMs with expert range maps via stacked generalisation. One approach is creating a predictor variable for the meta-learner by assigning a fixed value ratio to training points lying inside versus outside the expert-defined ranges, thereby allowing control of how much weight is given to the expert map (Merow, Wilson, and Jetz 2017). However, this approach assumes that the probability of occurrence is the same at any distance outside the expert range, although a continuously decreasing probability with increasing distance from the expert range should be expected (Merow, Wilson, and Jetz 2017). Therefore, we instead use the spatial distance of the training points to the expert range boundaries as a predictor in the meta-learner (Figure 1). This predictor, hereafter referred to as *distance term*, describes the (relative) probability of observing the modelled species within a given distance of the expert-defined range, thereby characterising the uncertainty of the expert map. This approach is conceptually similar to including spatial offsets with decay curves in point process models (Merow, Wilson, and Jetz 2017), and results in predicted habitat suitability values smoothly decreasing outside the expert range. However, in contrast to user-defined offsets, the distance term of the meta-learner is derived from the occurrence records used to train SDMs. While using the same datasets for fitting SDMs and assessing the uncertainty of the expert range maps might introduce bias if the collection of occurrence records is influenced by knowledge about expert ranges (Merow, Wilson, and Jetz 2017), such a data-driven approach will be particularly useful when accurate and representatively sampled occurrence records are available or if prior knowledge about the accuracy of expert range maps is lacking.

While the approach by Merow, Wilson, and Jetz (2017) allows control of the shape of the decay curve by choosing several curve parameters, in stacked generalisations, the analyst can influence the shape of the fitted distance term through the choice of the meta-learner algorithm or the functional form of the distance term. As a baseline approach we here use logistic regression as a meta-learner, which is widely used in stacked generalisations and results in distance terms following a logistic function similar to the smooth decay curves proposed by Merow, Wilson, and Jetz (2017). Conceptually, adding the distance term to a logistic regression meta-learner can be seen as adding a constant 'offset' to all areas inside the expert-defined range (i.e., areas with distance = 0). This offset is described by the intercept of the logistic regression and expresses the (relative) probability of observing the species inside the expert range given suitability predictions of 0 from all SDM algorithms. Predictions by the meta-learner will decrease with increasing distance from the expert range according to the distance term (Figure 1).

By relating individual species' occurrences to expert ranges, our approach accommodates species-to-species variability in the uncertainty of expert ranges. However, due to a lack of presence records or highly accurate expert range maps, in some cases, only few or no presence records might lie outside expert ranges, which will cause (quasi-)complete separation in the meta-learner. We propose two potential solutions to this issue. First, if species-specific distance terms should be used, bias-reduced logistic regression can be applied for fitting meta-learners (Firth 1993). This commonly recommended strategy for dealing with (quasi-)complete separation in logistic regressions ensures finite parameter estimates and results in responses (i.e., distance terms in our case) that are less steep compared to standard maximum-likelihood estimation (Heinze and Schemper 2002). Second, when occurrence data from multiple related taxa are available, species-specific distance terms of meta-learners might be replaced with 'target-group' distance terms, which can be calculated by fitting a meta-learner based on training points from multiple or all available species. In this case, the distance term characterises the uncertainty (probability of occurrences lying outside expert ranges) across all included taxa and does not vary between species, similar to applying the same decay curve across species when integrating range maps as spatial offsets in point process models (Merow, Wilson, and Jetz 2017). We provide R code demonstrating the implementation of our stacked generalisation approach for building expert-informed ensembles (see data availability statement).

3 | Method Application

3.1 | Study Area and Bat Occurrence Data

Our study area covers 6.5 million km² and intersects four global biodiversity hotspots (following Myers et al. 2000): the eastern part of the Mediterranean hotspot, the Caucasus hotspot, the Irano-Anatolian hotspot as well as partially covering the Mountains of Centrals Asia hotspot (Figure 2). Our study area represents the contact zone between the Western and Eastern Palearctic species pools, where fine-scale information on the distribution of bats is lacking. Expert range maps for most bat species in the region are available but estimates of species' range limits are uncertain or outdated for many species. Thus, our study area provides an interesting case for illustrating how our approach can generate fine-scale distribution data for under-researched regions of global conservation importance while accounting for varying uncertainty in available expert range information.

To delineate our study area, we fully included all countries in which the sampling of our bat occurrence records was primarily conducted (Afghanistan, Albania, Armenia, Azerbaijan,
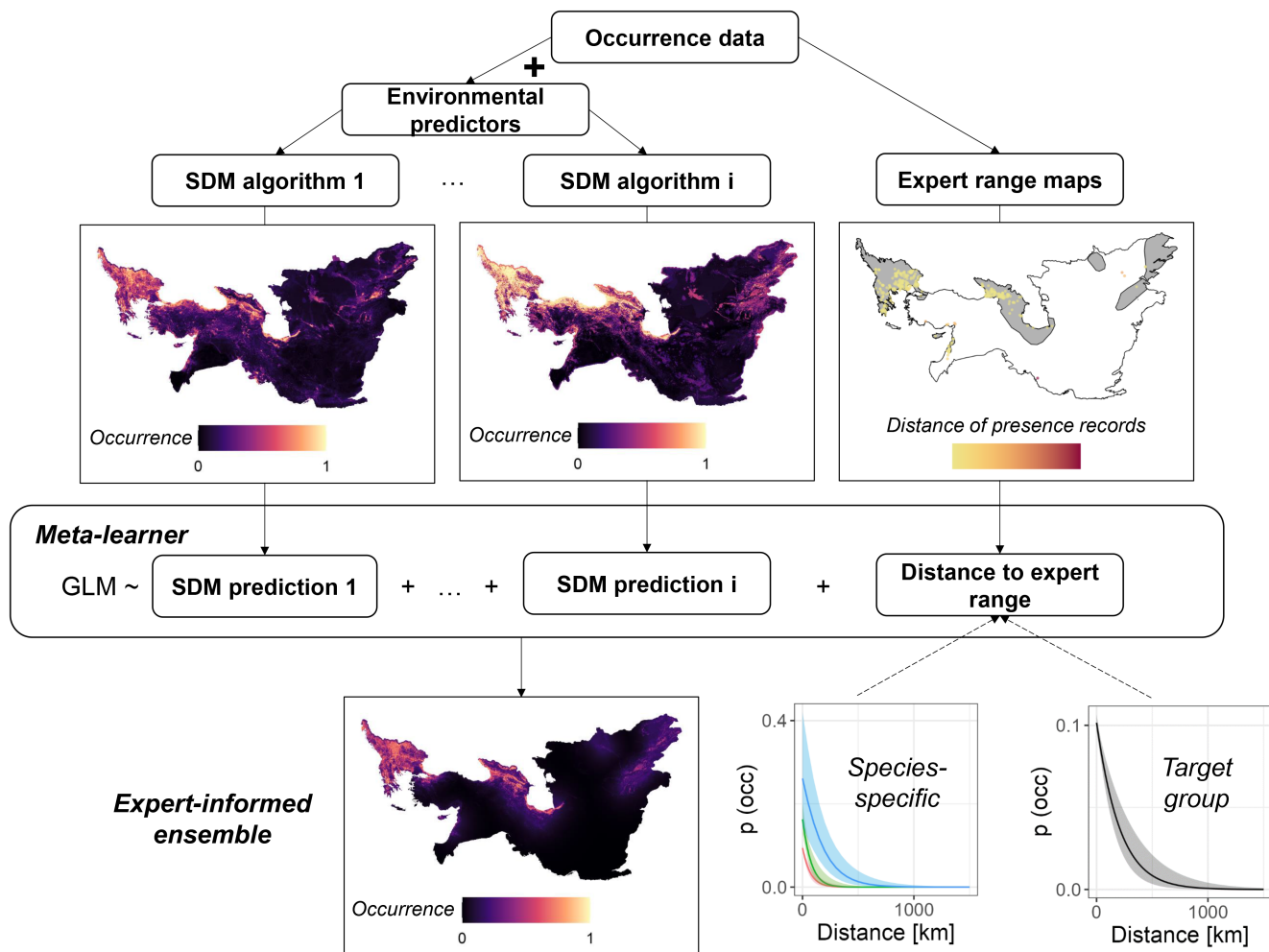
FIGURE 1 | Schematic overview of stacked generalisation for combining SDM algorithms with expert range maps. Predictions of multiple SDM algorithms are used together with the distance of occurrence data to the expert range as predictor variables in a logistic regression meta-learner, which then is used to predict the species' distribution. Maps show examples of one bat species in our dataset (*Nyctalus noctula*). Map panel for expert range shows IUCN range in grey with presence records coloured according to their distance to the IUCN range. Shown maps are in Albers equal area projection. IUCN, International Union for the Conservation of Nature; SDM, species distribution model.

Bulgaria, Georgia, Greece, Iran, Israel, Montenegro, Syria and Turkey). The borders of our study area were defined based on ecoregion boundaries (Olson et al. 2001).

We collected and harmonised bat occurrence datasets from various sources, including national databases, field records and literature data (see Appendix S1 for an overview of all data sources). In total, we gathered 37,714 occurrence records from 61 taxa. To ensure the quality of records used for model training, we removed all instances in which a species-level identification was impossible or problematic (e.g., uncertain identification within complexes of morphologically highly similar species). In addition, we removed records collected before 1970 to avoid a temporal mismatch between occurrence records and predictor variables (Milanesi, Della Rocca, and Robinson 2020).

Where appropriate, we reclassified records to account for recent genetic analyses that have led to a subdivision of species complexes into multiple cryptic species. This reclassification was done based on available information on the distribution of

cryptic species (see Appendix S2 for details on taxonomic revisions within species complexes as well as an overview of species). To remove spatial duplicates and reduce sampling bias, we thinned occurrence records (Boria et al. 2014). As thinning records may reduce model performance for rare species (Steen et al. 2021), we classified species according to the percentile values of sample prevalence (i.e., number of raster cells with presence records) into three classes (low, intermediate and high prevalence). We then thinned records with minimum distances of 1, 5 and 10 km for species with low, intermediate and high prevalence, respectively.

As expert information on species range limits, we compiled IUCN range maps for all species, using only those parts of ranges classified as 'extant'. This led to four species being excluded from modelling since no range map was available. Finally, we selected species with a minimum of 30 remaining records since modelling rare species with very few records typically requires targeted approaches and can be highly uncertain (Breiner et al. 2015). This step resulted in 9650 presence records from 49 species.
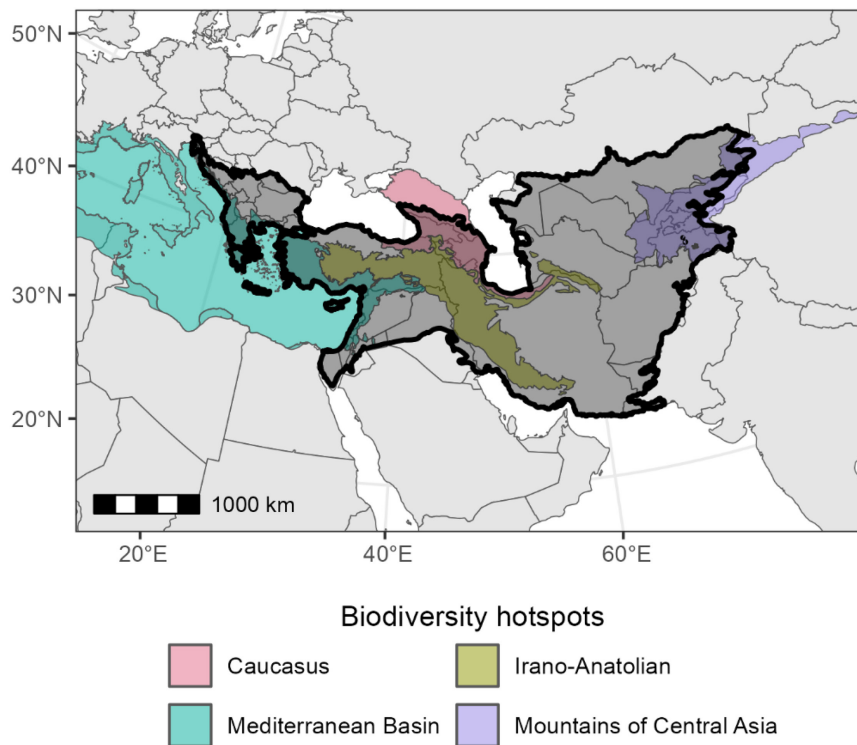
FIGURE 2 | Extent of the study area shown as black polygon and intersecting global biodiversity hotspots shown as coloured polygons. Map is in Albers equal area projection.

3.2 | Species Distribution Modelling

We used presence-background SDMs (Elith and Leathwick 2009) to characterise the distributions of bats in our study area. For modelling, we compiled a set of 40 candidate predictor variables, indicating four key dimensions of habitat suitability for bats: climate, land cover and vegetation productivity, topography and geology and human pressure and modification (Table 1). While target resolution of our SDMs was $1 \, km^2$, we derived all predictor variables at three spatial scales (1, 5 and $10 \, km^2$), resulting in 120 candidate variables. Including coarser scales derived through moving window averaging allows better characterising habitat conditions at the scale of bat home ranges (e.g., available forest cover within the surrounding area of a bat roost).

We sampled background points using two approaches: first, a target group bias grid, created from kernel density estimation based on all presence records in our dataset. Using the density of bat occurrence records as sampling weights for background points allows characterising sampling effort and helps to mitigate the influence of sampling bias in presence-background SDMs (Barber et al. 2022; Inman et al. 2021; Syfert, Smith, and Coomes 2013). Second, we used simple random sampling across the entire study area. For each species, we sampled background points equal to 10 times the number of available presence records.

We used three SDM algorithms: Maxent (R-package *dismo*; Hijmans, Phillips, and Elith 2020), random forests (R-package *randomForest*; Breiman et al. 2022) and boosted generalised additive models (GAMs, R-package *mboost*; Hothorn et al. 2022). Following recommendations by Valavi, Elith, et al. (2021), we used downsampled random forests, in which subsamples of the

background points are used within each individual tree in order to correct class imbalances. In the first modelling step, we performed variable selection by fitting univariate models (with default parameters) for all 120 candidate variables and evaluating their predictive performance using the area under the receiver operating characteristic curve (AUC) and Pearson correlation between the predicted and observed presence (COR) in a five-fold cross-validation (Valavi, Guillera-Arroita, et al. 2021). For selecting the best-performing model, we combined AUC and COR into a single performance score by rescaling their values across all tested models to a 0–1 scale and calculating the mean of rescaled AUC and COR values. Based on this combined performance score, for each species, we selected the set of variables offering the best predictive performance while having correlation coefficients $|r| < 0.7$ (Dormann et al. 2013). Using the selected variables in a second fivefold cross-validation, we tuned algorithm parameters for all species (selecting regularisation multipliers for Maxent, *mtry* and *maxnodes* parameters in random forest and the number of boosting iterations in boosted GAMs; see Appendix S4 for details).

3.3 | Stacked Generalisations

We implemented stacked generalisations in two ways. First, we created pure algorithm ensembles (hereafter *SDM ensembles*) solely relying on the predictions of the three SDM algorithms as predictors in the meta-learner. Second, we created *expert-informed ensembles* additionally including information from IUCN range maps. Additionally, we compared two approaches for adding distance terms to the meta-learner. First, we used species-specific distance terms, using the distance of species-level training points to the species' IUCN range as a predictor in the meta-learner.

TABLE 1 | Overview of environmental predictor variables used in species distribution models.

Category	Predictor	Available time steps	Data source
Climate	19 bioclimatic variables	1981–2010 (average)	CHELSA climate data (Karger et al. 2017)
Land cover and vegetation productivity	Six land-cover proportions (agriculture, forest, shrubs, herbaceous vegetation, bare and sparse vegetation and water)	1992–2020 (annual)	ESA CCI land cover
	Nine Landsat-based spectral-temporal metrics (cumulative, minimum and seasonality metrics for Tasselled Cap greenness, brightness and wetness indices)	1990, 1995, 2000, 2005, 2010, 2015	Landsat satellite imagery (Oeser et al. 2020)
Topography and geology	Terrain ruggedness index	—	(Amatulli et al. 2018)
	Presence of karstifiable rocks	—	World Karst Aquifer Map (Chen et al. 2017)
Human pressure and modification	Human modification index	1990, 2000, 2010, 2015, 2017	(Theobald et al. 2020)
	Accessibility (travel time to cities)	2015	(Weiss et al. 2018)
	Nighttime lights	1992–2018	(Zhao et al. 2022)
	Forest landscape integrity index	2019	(Grantham et al. 2020)

Second, we calculated a target-group distance term, which we derived by fitting a logistic regression to the distances of all bat occurrence records in our dataset (i.e., all 49 species). To deal with (quasi-)complete separation in species-specific distance terms, we used bias-reduced logistic regression implemented in the R-package *brglm2* (Kosmidis et al. 2023) for fitting meta-learners.

A critical consideration when using stacked generalisations is the risk of overfitting the meta-learner. A widely adopted strategy for this purpose, referred to as *Super Learner* (Naimi and Balzer 2018; van der Laan, Polley, and Hubbard 2007), uses out-of-sample predictions (i.e., from cross-validation) for training the meta-learner. Using out-of-sample predictions for training the meta-learner provides a more honest measure of the performance of input algorithms, enabling the meta-learner to learn how to optimally combine input algorithms for achieving good out-of-sample performance. To assess the effect of the *Super Learner* strategy on predictive performance, we compared meta-learners trained on out-of-sample versus in-sample predictions.

We compared the predictive performance of all three tested modelling approaches using fivefold cross-validation: (1) single-algorithm SDMs (i.e., Maxent, random forest and boosted GAMs), (2) SDM ensembles and (3) expert-informed ensembles. In addition to AUC and COR values, we calculated the area under the precision–recall curve (PRAUC) as a further performance metric, which specifically targets the prediction of presences and is particularly useful when evaluating models for rare species (Sofaer, Hoeting, and Jarnevich 2019).

To create distribution maps for all species, we predicted all models for the most recent time step (target year for prediction:

2020). To compare mapped distribution patterns between SDM ensembles and expert-informed ensembles, we calculated two metrics: first, species-wise niche breadth using Levins' B2 metric, describing the uniformity of predicted suitability in geographic space (Warren et al. 2021), and second, range overlaps calculated using Schoener's D metric, describing the similarity of predicted suitability between species pairs (Warren, Glor, and Turelli 2008). Integrating information on species' range limits should correct for the overprediction of species' realised ranges by SDMs due to missing information on the effect of dispersal limitations and biotic interactions (Merow, Wilson, and Jetz 2017). We thus hypothesise that expert-informed ensembles should result in narrower estimates of niche breadth and smaller range overlaps between modelled species.

4 | Results

The accuracy of IUCN range maps varied considerably across bat species. On average, 73% of presence records fell inside expert-defined ranges (interquartile range: 22%), with records lying at an average distance of 50 km beyond expert-defined range boundaries (interquartile range: 30 km). These differences in the accuracy of expert range maps translated into considerable variation in species-specific distance terms and thus clear differences in how predicted suitability values declined outside expert ranges when using expert-informed ensembles. In the case of accurate expert ranges, suitability sharply declined outside expert ranges, leading to the exclusion of (often large) areas identified as environmentally suitable by SDMs but lying outside species' ranges (e.g., *Myotis myotis* in Figure 3). Conversely, when occurrence records
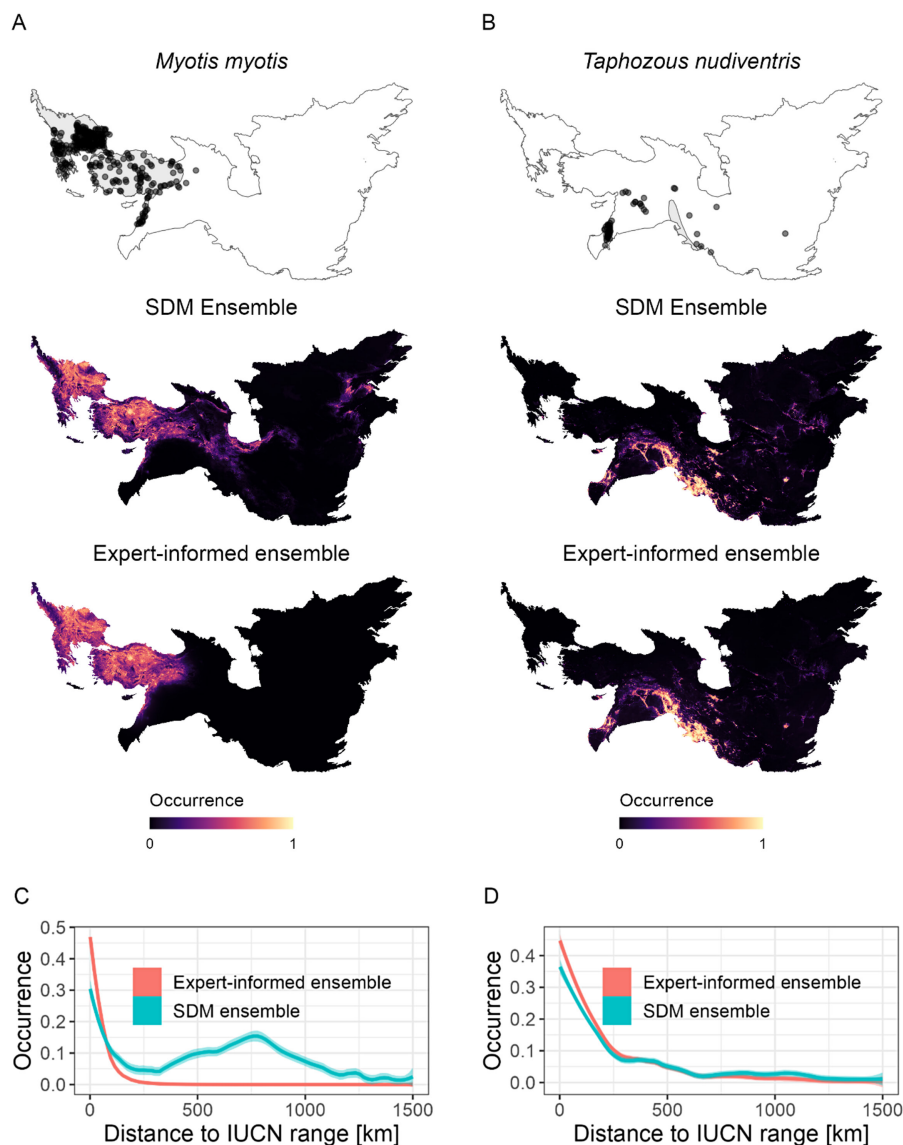
FIGURE 3 | Comparison of distribution maps (A and B) and decline in predicted occurrence probabilities outside expert ranges (C and D) for two example species with high (*Myotis myotis*) and low expert map accuracy (*Taphozous nudiventris*). Distribution maps based on IUCN ranges (including available presence records), SDM ensembles and expert-informed ensembles are shown. Expert-informed ensembles correspond to models built with species-specific distance terms. Plots of decline in predicted occurrence probabilities outside expert ranges (C and D) are based on loess smooth to the data. Maps are in Albers' equal area projection. IUCN, International Union for the Conservation of Nature; SDM, species distribution model.

indicated that expert range maps were inaccurate, SDMs clearly dominated the predictions of expert-informed ensembles, making it possible to identify areas outside IUCN ranges as likely occupied by species (e.g., *Taphozous nudiventris* in Figure 3). When using target-group instead of species-specific distance terms, suitability values declined at similar rates outside expert ranges across species (Appendix S4).

SDM ensembles built via stacked generalisation showed a slightly higher mean predictive performance than single-algorithm SDMs. However, training on out-of-sample predictions was necessary to achieve optimal predictive performance in all stacked generalisations (i.e., using the *Super Learner* approach; see Appendix S5). Expert-informed ensembles built with species-specific distance terms achieved the highest mean predictive performance according to AUC, COR and PRAUC

values (Figure 4). However, absolute values of the performance metrics and their relative differences between approaches depended on the background sampling strategy. Models built with random background points showed higher AUC, COR and PRAUC values and clearer differences between the approaches. Among models built with target-group background points, improvements of expert-informed ensembles with species-specific distance terms over single-algorithm SDMs were statistically significant at a 5% level only for COR values, while improvements were significant for all three performance metrics in models built with random background points (see Appendix S6).

Performance improvements of expert-informed ensembles compared to SDM ensembles generally decreased with the mean distance of presence records to expert ranges (i.e., increasing performance gains with higher expert map accuracy; Figure 5). In
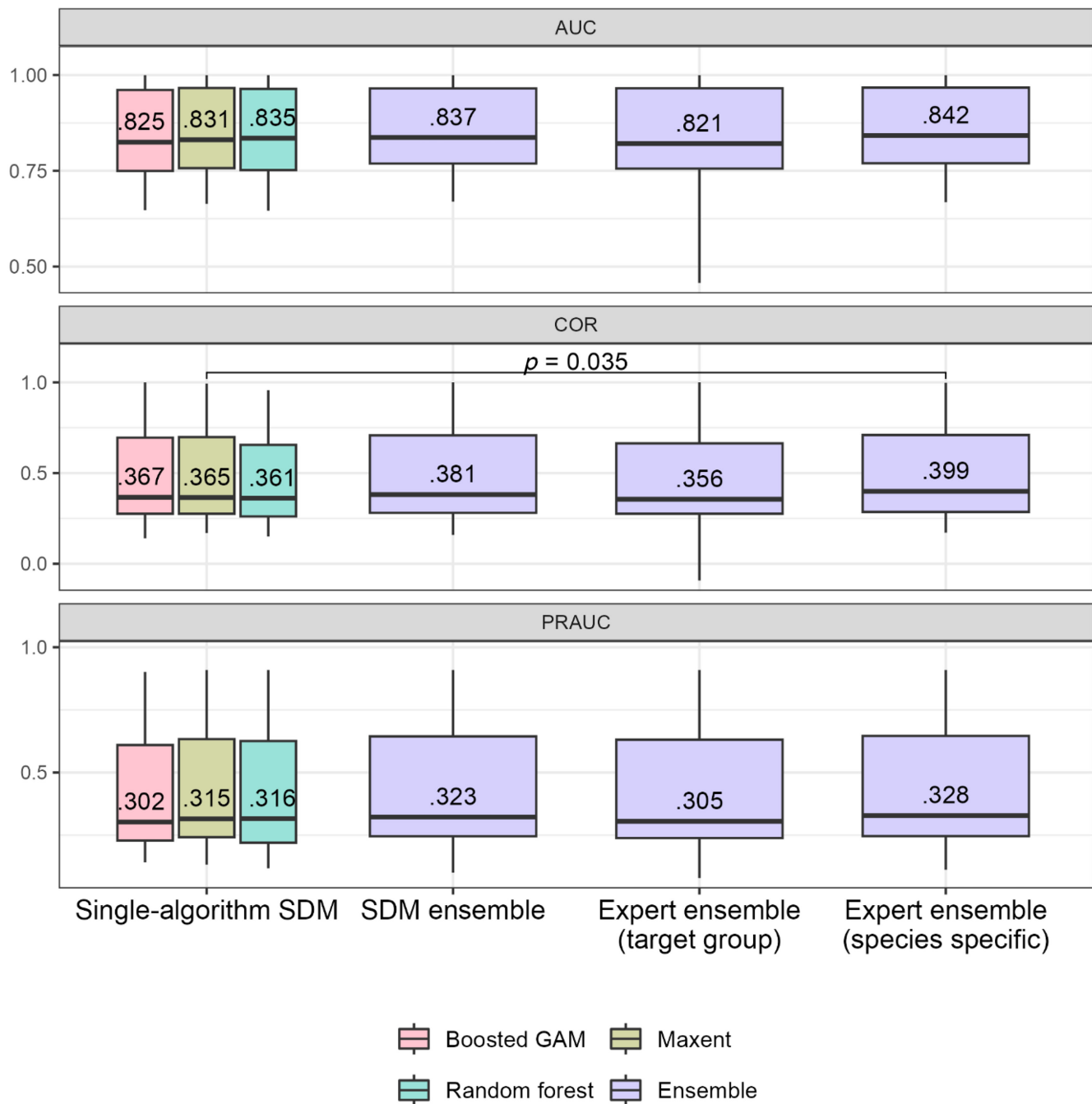
FIGURE 4 | Predictive performance of modelling approaches for 49 bat species in Eastern Mediterranean, Western Asia and Central Asia according to three performance metrics (AUC, COR and precision–recall AUC), evaluating models built with target-group background points. *p*-values <0.05 of pairwise comparisons with Wilcoxon tests are shown on top of boxplots. Performance of models built with random background points is shown in Appendix S6.

addition, performance improvements tended to be higher for species with fewer available occurrence records as well as for species with smaller range extents (see Appendix S6), but these relationships were considerably weaker than for expert map accuracy.

Considering mapped distribution patterns, expert-informed ensembles resulted in lower niche breadths (i.e., less uniform distribution of predicted suitability in geographic space) for 83% of species compared to SDM ensembles. On average, species-wise niche breadths obtained from expert-informed ensembles were 21% lower compared to niche breadths derived from SDM ensembles (Figure 6A; $p = 0.038$). Range

overlaps between species pairs (i.e., similarity of predicted suitability) derived from expert-informed ensembles were lower than overlaps predicted by SDM ensembles in 90% of the cases. On average, overlaps were 30% lower in expert-informed ensembles compared to those obtained from SDM ensembles (Figure 6B; $p < 0.0001$).

5 | Discussion

Addressing the Wallacean shortfall is critical to biogeographical research and conservation planning, yet accurately mapping

species' realised distributions through species distribution modelling presents a significant challenge. Here, we developed a new approach for integrating expert information on range limits in species distribution models by making use of stacked generalisation, an ensemble method widely applied in machine learning but still underexplored in the context of SDMs. Testing our approach with a dataset covering 49 bat species demonstrated its flexibility and promise for improving species distribution mapping helping to combine the key strength of SDMs (characterising environmentally suitable habitats) with that of expert range maps (characterising range limits) without requiring prior knowledge about expert range maps or having to rely on specific modelling algorithms. In a broader context, we add to the growing toolbox of integrated SDM approaches, providing an important step towards more accurate assessments of species' distributions.

The application of our approach showed that it effectively enables the exclusion of areas lying outside species' realised range limits while preserving fine-scale predictions of
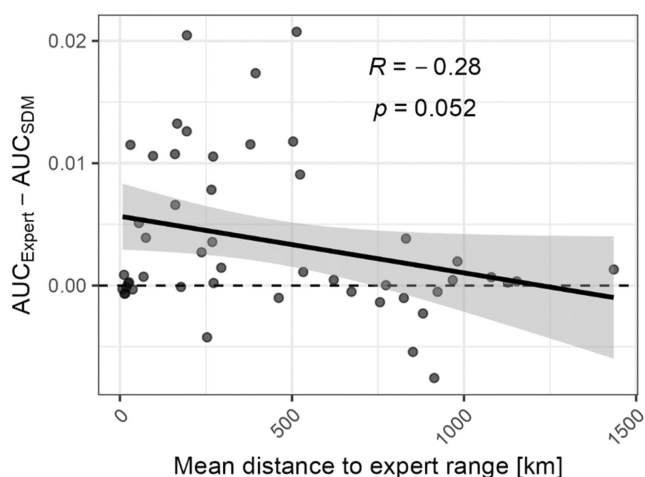
FIGURE 5 | Improvement in predictive performance of expert-informed ensembles compared to SDM ensembles in relationship to expert map accuracy (mean distance of presence records to expert range, including points inside the range with distance = 0). Data for expert-informed ensembles with species-specific distance terms and target-group background points are shown, with linear trend plotted on top. SDM, species distribution model.

habitat suitability, which offers a key strength of SDM approaches (Mainali et al. 2020). At the same time, when enough presence records are recorded outside expert-defined ranges, expert range maps exert minimal influence on mapped distributions, demonstrating the flexibility of our approach towards varying levels of expert map accuracy. As an alternative to using expert range maps, range extents could also be incorporated into SDMs by using occurrence data directly (Burgman and Fox 2003; Palacio et al. 2021). However, occurrence-based range extents often show low overlap with expert-defined ranges (Aronsson et al. 2024) or require absence of information that is commonly not available (Palacio et al. 2021). More generally, like other integrated SDM approaches, our approach takes advantage of expert-defined ranges as independently derived data on species ranges (Merow, Wilson, and Jetz 2017).

Using expert-informed ensembles did not lead to statistically significant performance gains compared to pure SDM ensembles in our performance assessment, yet the predicted distribution patterns changed significantly by incorporating expert range maps (i.e., in terms of predicted niche breadth and overlap). However, we caution that differences in performance might be underestimated as we did not have an independent validation dataset on species distributions available, limiting us to cross-validations on datasets containing background points instead of true absence information. Our approach primarily addresses the issue of overprediction by SDMs in environmentally suitable regions not inhabited by a species, which should mainly be reflected in an improved prediction of absences (model specificity) but cannot be properly characterised when evaluating models using background points (Sofaer, Hoeting, and Jarnevich 2019). This is likely why our cross-validation suggests only a small performance gain, even though range predictions for many species changed strongly by removing suitable habitats outside their ranges. In addition, our results confirm that the choice of background sampling strategy has a strong impact on performance assessments of presence-only SDM approaches (Jarnevich et al. 2017; VanDerWal et al. 2009). Regarding the integration of expert range maps with SDMs, we found that potential gains in predictive performance depend on the accuracy of expert range maps. Moreover, varying distance terms across species (i.e., using species-specific instead of target-group distance terms) improved predictive performance in our assessment.
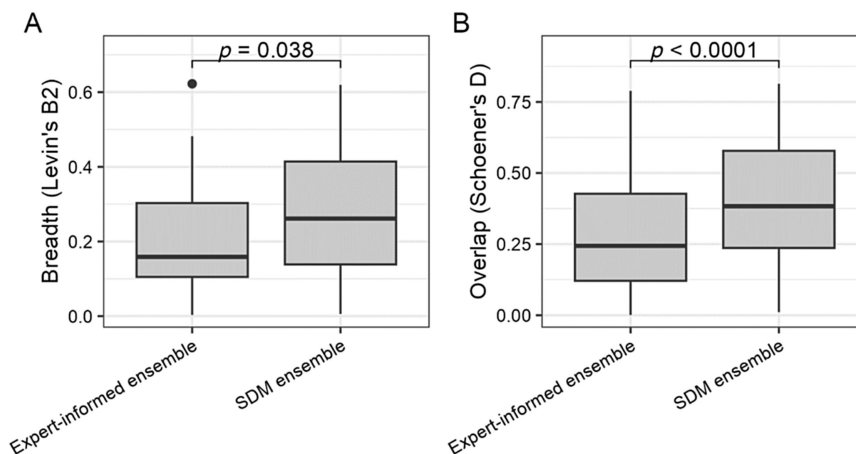
FIGURE 6 | Distribution of (A) niche breadths and (B) range overlaps of bat species according to SDM ensembles versus expert-informed ensembles. *p*-values of pairwise comparisons (Wilcoxon test) are shown on top of the boxplots. SDM, species distribution model.

Our approach offers an alternative to applying user-defined spatial offsets in point-process models as proposed by Merow, Wilson, and Jetz (2017). Choosing between stacked generalisation and spatial offsets as ways to integrate expert range maps boils down to selecting different styles of modelling approaches: relying either on prior knowledge when using spatial offsets or on available occurrence datasets when using stacked generalisations for characterising expert map accuracy. The appropriateness of using stacked generalisations thus hinges on whether available occurrence records can accurately capture expert map accuracy. The accuracy of the distance terms, and hence the usefulness of our approach will likely be considerably reduced when modelling rare species with very few available records, or if records are biased towards expert ranges (e.g., expert range maps affect sampling intensity or species identification; Merow, Wilson, and Jetz 2017). However, in many cases, occurrence records provide a more comprehensive and up-to-date picture of species distributions compared to expert range maps. Moreover, occurrence records will often be the best available (or only) type of data for evaluating expert range maps, as other a priori information on their accuracy is difficult to obtain. As exemplified by our dataset, expert map accuracies typically vary strongly across species. Stacked generalisation provides a simple yet effective data-driven approach allowing one to account for this variation when assessing many species at once. If occurrence datasets for individual species are deemed too incomplete or biased for characterising expert map accuracy, target-group distance terms can be used as an alternative. Both these options are conceptually similar to manually defining spatial offsets in point process models based on available evidence on expert map accuracies (Merow, Wilson, and Jetz 2017), yet eliminate the need for subjective decisions potentially biasing results. In sum, our approach provides a widely applicable data-driven alternative for integrating expert range information in SDMs, proving particularly useful when accurate and comprehensive occurrence datasets are available.

An additional key advantage of our approach lies in its flexibility to combine expert range maps with any combination of modelling algorithms, thereby facilitating the use of algorithm ensembles. In contrast to the use of spatial offsets in point process models, stacked generalisations can be easily combined with machine learning algorithms that do not include offset terms. This enables the use of algorithms such as random forest, often found to be one of the best-performing algorithms in comparisons of SDM approaches (Valavi, Guillera-Arroita, et al. 2021). With SDM ensembles performing better than any individual modelling algorithm in our dataset, our results also point towards the potential of stacked generalisations as a method for combining modelling algorithms more generally. Illustrating the advantages of the *Super Learner* approach (Naimi and Balzer 2018; van der Laan, Polley, and Hubbard 2007), we achieved improved performance when using out-of-sample predictions for training the meta-learner. Studies on the performance of SDM ensembles have highlighted that they do not necessarily improve predictive performance over single algorithms, particularly when using default parameter settings (Hao et al. 2020). To optimise the predictive performance of SDM ensembles built using stacked generalisation, we recommend combining a diverse set of algorithms (e.g., combining parametric and tree-based models; Naimi and Balzer 2018; Phillips et al. 2023) and carefully tuning the parameters of all input

models (Valavi, Guillera-Arroita, et al. 2021). It has been shown that in large samples, the *Super Learner* approach performs at least as well as the best-performing individual algorithm (van der Laan, Polley, and Hubbard 2007; van der Laan and Dudoit 2003). Yet, despite its potential, stacked generalisation has remained neglected in the context of species distribution modelling (El Alaoui and Idri 2023), with studies typically relying on unweighted or weighted model averaging for combining algorithms and stacked generalisation not being considered in systematic assessments of SDM ensemble methods (Hao et al. 2019, 2020). We recommend stacked generalisation as a versatile approach for combining SDM algorithms, which should be included in future comparisons of SDM ensemble methods.

In most cases, the integration of expert range maps resulted in considerably less uniform occurrence predictions and decreased range overlap between species, likely reflecting more realistic predictions of bat distributions in our study area. Both SDMs and expert range maps tend to overpredict the occurrence of species since they are missing information on factors limiting species' ranges (dispersal and competition in the case of SDMs, and habitat suitability in the case of expert ranges). Integrating both data sources can therefore improve estimates of individual species' distributions as well as species richness (Ellis-Soto et al. 2021). By separating environmental constraints from other limiting factors, the combination of SDMs and expert ranges can help to better understand the influence of nonenvironmental factors affecting range limits (i.e., biotic interactions and dispersal). For example, contrasting potential range overlaps derived from SDMs with realised range overlaps derived from expert-informed models can provide a window into the potential role of interspecific competition in shaping species' ranges (Novella-Fernandez et al. 2021). For some species, such as migratory or invasive species, integrating expert range maps might only be practical if sufficient auxiliary information is available (e.g., seasonal ranges or introduced vs. native ranges). Overall, our approach has broad applicability in ecological research and conservation planning, making it possible to update species' conservation status, better identify conservation priorities through more accurate species richness mapping and provide new ecological insights into factors determining species' range limits.

Our approach adds to the growing toolbox of integrated species distribution modelling approaches by providing a flexible and easily applicable approach for integrating SDMs with readily available information on species' range limits. As SDMs have become one of the most widely used tools in ecological and biogeographical research, an increasing recognition of their shortcomings has developed (Franklin 2010; Lee-Yaw, McCune, and Pironon 2022). Recently, integrated modelling approaches have been proposed that try to enhance SDMs by combining them with additional sources of information (Fletcher Jr. et al. 2019; Miller et al. 2019). Integrated SDM approaches already offer key innovations for improving the mapping of species' realised distributions (Jung 2023; Miller et al. 2019). The broader adoption of these methods combined with a rapid growth in the availability of biodiversity data will be critical for filling knowledge gaps about the distribution of species and overcoming the Wallacean shortfall.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data used for building species distribution models (SDMs) are available via a Dryad data repository, along with R code demonstrating the implementation of our stacked generalisation approach for integrating SDMs with expert range maps: https://doi.org/10.5061/dryad.6q573n65m, https://datadryad.org/stash/share/4UG2MDuUgX0H0SnAr9ikEz0Sk4LBLRRSuZcyj1swIQ0.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.