ECOGRAPHY

Research article

Species-observer link and kernel density estimation of background points allow for sampling bias correction in bird species distribution models

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Ecography
2025: e08202
doi: 10.1002/ecog.08202

Subject Editor: Dan Warren
Editor-in-Chief: Miguel Araújo
Accepted 22 September 2025

Species distribution models (SDMs), broadly referring to both species distribution and ecological niche modelling frameworks, are widely used to predict habitat suitability. However, their performance can be biased by uneven sampling effort in occurrence data. Building on two existing approaches, we propose a novel method for sampling bias correction, consisting of the estimation of observer kernel densities for individual species and their subsequent weighting according to the relative contribution of individual observers to the total number of focus species presences. This approach, the 'presence-weighted observer-oriented approach' (PW-OOA), aimed to provide a better estimation of sampling effort, thus further improving SDM prediction performance. Using bird occurrence data from the Czech Republic, we modelled the distributions of 109 species using four approaches to bias correction: spatial thinning of species presences (STSP), target group occurrences background (TGOB), TGOB+ (tuned up by adjusting kernel smoothing bandwidths) and the new PW-OOA method. We compared the results with simple random background sampling. Models were evaluated using independent reference (presence–absence) data. The PW-OOA method outperformed the other approaches, with the greatest improvement detected for species with higher prevalence. However, as internal validation can be misleading with biased occurrences, we recommend TGOB+ as the most robust approach without independent data; with such data, PW-OOA is superior. While no single optimal combination of bandwidth and observers' weights was identified across species, the PW-OOA method provides a flexible framework to account for observer-specific sampling biases. This study demonstrates the crucial importance of considering the behavior of individual observers and sampling intensity smoothing when correcting for sampling bias in SDMs based on unstructured opportunistic occurrence data.

Keywords: background point selection, kernel density estimation, observer behavior, sampling bias correction, species distribution modelling, target group background

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Introduction

Correlative species distribution modelling (SDM) uses environmental data, species occurrence records, and statistical models to determine the key environmental factors that influence species distribution patterns, providing insights into their ecological niche and habitat preferences (Araújo and Guisan 2006, Zimmermann et al. 2010). SDM relies on species occurrence data, which often come from species occurrence databases such as Pl@ntNet, iNaturalist, eBird, or observation.org. By secondary sharing, the data can be aggregated into local (national) databases such as the Czech Species Occurrence Database (NCA CR 2022) or global databases such as GBIF (Global Biodiversity Information Facility). Thanks to these initiatives, the total number of species occurrences that can be subsequently used in SDMs has considerably increased (Bowler et al. 2022); however, many of these data are unstructured and biased in many ways.

Spatial, environmental, and temporal biases that can emerge during the entire acquisition and sharing processes constitute a major problem of species occurrence data (Beck et al. 2014, Boria et al. 2014, Moudrý et al. 2017, Gábor et al. 2020, Rocha-Ortega et al. 2021). Both voluntary and expert observers collect the species occurrence data with varying levels of randomness (opportunistic to standardized surveys), which makes the sampling bias a difficult factor to address (Isaac et al. 2014, Isaac and Pocock 2015). To correct for sampling bias, it is necessary to determine the sampling intensity (sometimes also known as sampling effort or observer effort). If not directly recorded, it can be estimated using various methods (Hill 2012, Hefley et al. 2013, Kramer-Schadt et al. 2013, Pardo et al. 2013, Komori et al. 2020, Boyd et al. 2021, Tessarolo et al. 2021, Zizka et al. 2021, Moudrý et al. 2024), such as those based on the distance to features representing human accessibility (Mandeville et al. 2022) or the spatio-temporal density of occurrences. The accurate identification of the patterns of bias in the occurrence data is, however, often difficult (Yackulic et al. 2013, Beck et al. 2014) because of the complex interactions among observers' behavior, geography, and species characteristics (Meineke and Daru 2021, Baker et al. 2022, Moudrý et al. 2024). As a consequence, SDMs that fail to account for sampling bias are likely to conflate habitat suitability with sampling effort, predicting a mixture of both (Araújo and Guisan 2006, Phillips et al. 2009, Barber et al. 2022, Fernandez et al. 2022). Objectively quantifying the bias correction efficiency requires the use of an independent, bias-free validation dataset (Vollering et al. 2019, Rocchini et al. 2023, Moudrý et al. 2024).

In addition, species occurrence records are typically represented only by presences, as absences are much more difficult to obtain because they are rarely recorded by observers. Therefore, models typically include the use of pseudo-absences selected randomly from the background (Wisz and Guisan 2009). An established strategy for addressing observation bias is the target-group background (TGB) method, which utilizes occurrences of multiple related species from the same target group (TG; e.g. birds) to inform SDMs about sampling effort intensity (Dudik et al. 2006, Elith and Leathwick 2007, Baker et al. 2024). This approach replaces uniform background data with a random background sample drawn from the TGB sampling distribution. Unlike spatial or environmental thinning, which may be unsuitable for species with low presence numbers (see the review by Moudrý et al. 2024), the TGB method does not reduce the number of focus species presences (Boria et al. 2014, Varela et al. 2014, Aiello-Lammens et al. 2015, Gábor et al. 2020). Elith and Leathwick (2007) and Syfert et al. (2013) showed on independent test data that TGB outperforms random background sampling. Botella et al. (2020) later built on this approach by taking into account the intensity of occurrences of all species from the TG to estimate the sampling effort in their TG occurrences background (TGOB) method. TGOB is well-suited for the currently collected data, where most occurrences are assigned geographical coordinates at the time of recording, unlike the spatially aggregated 'site', common in the past and addressed by TGB.

There are several assumptions under which TG(OB) can be used within the SDM framework. Fithian et al. (2014) for the first time introduced the *proportional bias assumption*, violated if different species are sampled by different groups of observers with varying spatial biases. Several other assumptions are listed and commented on by Yackulic et al. (2013), Ruete (2015), Vollering et al. (2019), and Botella et al. (2020, 2021). The condition of the homogeneity in reporting patterns among observers appears to be the most problematic to achieve; however, the existing methods, such as TGOB, can address this issue only partially.

Many studies have highlighted significant spatial and temporal disproportions in taxon recording and observer contributions within opportunistic species databases, often attributed to variations in observer quality and effort, as well as specific behavioral patterns (Sauer et al. 1994, Isaac and Pocock 2015, Boakes et al. 2016, Cecco et al. 2021, Hooykaas et al. 2022, Pocock et al. 2023). Recently, in their work developing an ensemble SDM on terrestrial mammals, Milanesi et al. (2020) introduced the term *observer-oriented approach* (OOA), in which TGOB filtering was based on records of observers who reported the focus species and additional predictors, such as the total number of observations and observers per pixel. August et al. (2020) used a suite of metrics derived from a butterfly TG to describe the temporal and spatial behavior of observers. Through PCA analysis, they identified four continuous axes that described most of the variation in the participants' behavior.

Ideally, these observer-related biases at the time of data collection should be eliminated. This is, however, difficult to achieve. For example, Botella et al. (2021) simulated the density of sampling effort by applying four different bandwidth values of kernel densities in plant species (which is, actually, the basis of the TGOB+ method) recorded by a database acquired using the mobile app Pl@ntNet with automatic species identification from photography. The combination of automatic species determination with selected immobile TG (plants) enabled them to mitigate the inconsistent identification skills of the observers. In other cases, it is necessary to consider the roles and characteristics of the individual observers. To overcome the issue of observer skills, Kelling et al. (2015) suggested an alternative approach including species accumulation curves. For example, the eBird project uses individual observers' checklists to ensure that all observed species are recorded, and to infer absences. This leads to a faster accumulation of records by observers with higher skill, which can be used to account for an important source of bias and control it (Steen et al. 2019, 2021). Both Bradter et al. (2018) and Henckel et al. (2020) retrospectively asked observers about the reporting consistency and filtered only occurrences from observers who always recorded the given species, which also allowed them to infer absences for SDM.

Our understanding of the influence of observer behavior on predictions of species distribution across a representative range of species with varying ecological characteristics is limited. In our study, we introduce a novel method, the presence-weighted observer-oriented approach (PW-OOA), designed to flexibly and species-specifically correct for observer-based sampling biases in SDMs. This method is based on estimating the kernel density (KD) for all observations recorded by a single observer and subsequent summation of KDs (resampled to rasters) weighted by the relative contribution of individual observers to the reporting of the focus species. This produces a bias raster for generating background points. The PW-OOA method assumes no environmentally based filtering or stratification. Background point simulation is inferred solely from TG occurrences in geographical space, with no additional covariates characterizing sampling effort employed.

To evaluate the performance of this method, we apply it to 1) a wide range of bird species with different ecological characteristics, 2) a study area influenced by multiple sources of bias, 3) test the results of SDM performance on an independent dataset, and 4) compare the performance with the most common approaches for background simuation+, i.e. random background (hereafter, *random*), TGOB, TGOB+ (inspired by Botella et al. 2021), and the thinning method (STSP, Aiello-Lammens et al. 2015). In addition, 5) effects of changing the KD bandwidth and/or pixel size-derived observers' weights on the performance of the TGOB+ and PW-OOA method will be investigated. A summary of our overall study design is presented in the Methods section (Fig. 1).

Methods

Study area

The study area encompasses the entire territory of the Czech Republic (central Europe). The region is characterized by a temperate continental climate with four distinct seasons. The altitude range extends from 115 to 1603 m a.s.l. At higher elevations, predominantly along the borders, coniferous

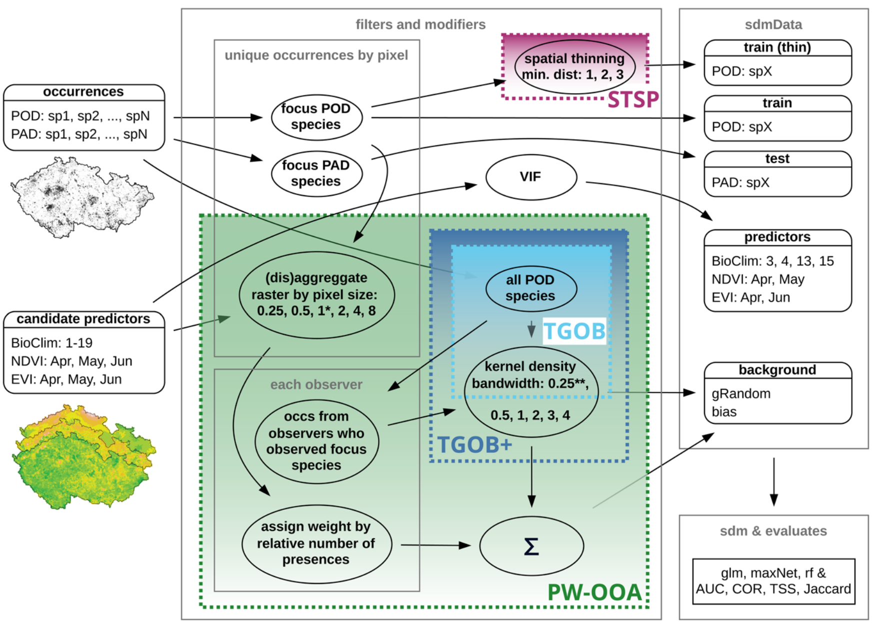

Figure 1. Study design summary: basic inputs/outputs (rectangular boxes) and methods (elliptical boxes) applied using the established SDM terminology used in Naimi and Araújo (2016). In addition to the 'basic' random background simulation method, color-coding is used to emphasize the differences among the four other sampling bias correction methods: spatial thinning of species presences (= STSP, purple), target group observer background (= TGOB, cyan), tuned TGOB+ (blue), and observer-oriented approach (= PW-OOA, green). Presence-only database (POD) and presence–absence database (PAD) with candidate predictors of bioclimate (BioClim), normalized difference vegetation index (NDVI), and enhanced vegetation index (EVI) on the left side are the basic inputs to the models. * indicates the default pixel size for raster (dis)aggregation and ** default kernel density bandwidth.

forests dominated by spruce or mixed spruce–beech forests interspersed with meadows and pastures prevail. Lower elevations are primarily occupied by agricultural landscapes interspersed with urban areas. Besides tens of nature and landscape conservation areas of different categories, 41 'bird areas' have been designated to protect bird species. Together, the protected areas cover as much as 20% of the Czech Republic.

The combination of diverse habitat types (mountains versus lowlands, forests versus mosaic open landscape), varying accessibility from urban centers (suburban areas versus remote locations), and differences in the attractiveness to both citizen scientists and professional ornithologists (ornithologically significant regions are often more attractive than uniform forests and intensively cultivated agricultural land) make the territory of the Czech Republic ideal for studying sampling bias in species databases and potential strategies for its mitigation in SDM.

Species data

As independent presence–absence data are necessary to evaluate and mitigate sampling bias in presence-only data (Merow et al. 2013), we used two independent datasets for this study: 1) the Breeding Bird Survey – a presence–absence database (PAD) maintained by the Czech Society for Ornithology (2023), comprising data from systematic surveys based on a standardized methodology (Reif et al. 2022) and 2) the Czech Species Occurrence Database – a presence-only database (POD), which aggregates various types of ornithological data, ranging from specialized local surveys to occasional data from citizen scientists. This database encompasses all plant and animal taxa, with avian species being one of the most represented groups. While this database can be considered one of the most comprehensive national species databases globally (it contains millions of bird records over an area of 79 000 km^2, the majority with positional accuracy attributes), it contains various types of sampling bias resulting from uneven sampling effort. In both datasets, only occurrences recorded in the months of April to June in seasons 2019–2021 were selected. Both presence–absence and presence-only (PAD, POD) datasets were anonymized to protect certain sensitive species and to remove observer names.

PAD

Only experienced ornithologists contributed to this occurrence database fed by repeated standardized surveys, recording all species observed during two-hourly transects representing one randomly selected quadrat (pixel) (Reif et al. 2022) with a pixel size of approximately 3 km. For representativeness and to maintain a sufficient total number of pixels, we chose only pixels in which at least four surveys were performed. This yielded 154 pixels with presence–absence (PA) data across the study area, which served as reference (truth) data in our study and for calculating each species' prevalence (number of PAD presences divided by 154).

POD

The spatial pattern of POD occurrences and observer counts (Fig. 2) exhibits a bias that is difficult to explain solely on the basis of commonly reported sources of bias, such as population density, accessibility, or tourist attractiveness. We used 430 999 records from 5095 observers (Supporting information). Only occurrence data with a positional error of < 1 km were included to ensure the data positional accuracy is better than the pixel size of the predictors, as recommended by Moudrý and Šímová (2012).

Additional filtering

In total, 109 bird species with presence or absence in at least ten of the 154 PAD squares were included in the study to evaluate SDM predictions using several prediction performance metrics (e.g. AUC, TSS). In addition, to increase the spatial independence between the training and validation data (Araújo et al. 2005, Bahn and McGill 2013), only POD pixels not overlapping with PAD squares were used for POD-trained SDM.

All POD records of the same species and from the same observer located within a single 50 m pixel produced by downscaling (disaggregating) the raster of used predictors were considered duplicates. Following Pocock et al. (2023), we removed occurrences reported by the observers of unclear identity (e.g. 'anonymous', 'bird ringing station', single given or family names). Furthermore, observers with < 10 occurrences and < 3 species observed were removed. After the filtering, 329 328 records by 1408 observers remained in the POD dataset.

Spatial autocorrelation in environmental data

We calculated the Moran's I index (Gittleman and Kot 1990, Paradis and Schliep 2019) to test the spatial autocorrelation of the PAD data for each environmental predictor. The Moran's I index ranges from −1 to +1, indicating a strong negative to strong positive spatial autocorrelation. Values around zero indicate spatial randomness. The resulting Moran's I values ranged between 0.07 and 0.34 for each predictor (Supporting information), confirming the randomness of PAD sites and the low degree of positive spatial autocorrelation. These accurate and independent PA occurrence data were used as the reference dataset.

Predictors

We preselected 19 rasters from the Bioclim variables from the WorldClim dataset (Hijmans et al. 2005) and an additional six rasters representing two commonly used vegetation indices (NDVI, EVI) for three discrete months (April, May, and June) derived from MODIS satellite imagery (MOD13A3; Didan and Munoz 2019). Satellite composite images used in our study were taken between 2019 and 2022. All BioClim and MODIS rasters were finally aggregated to a 3 km resolution (with individual predictors aggregated as the median values of all included pixels) to match the grid of the PAD dataset. Subsequently, we downloaded these rasters from the Google Earth Engine (GEE) repository. To avoid multicollinearity among rasters, VIF analysis was performed using the R library package 'usdm' (Naimi et al. 2014) with functions *vifcor* and subsequently *vifstep* over all 25 rasters with thresholds set to 0.7 and 2.0, respectively. Only the eight least

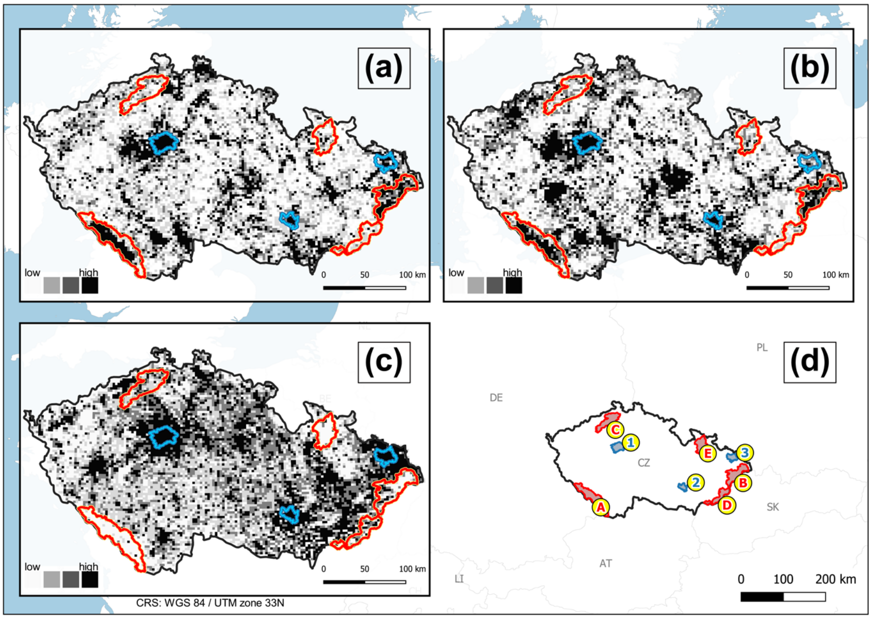

Figure 2. Number of bird occurrences (a) and unique observers (b) from presence-only database (POD) compared to human population density (c) (Czech Statistical Office 2021) in the Czech Republic represented by a black–white quartile gradient on a 3 × 3 km grid. All three presented phenomena showed low to medium levels of correlation (0.14–0.59) with local spatial discrepancies. Three largest cities (blue polygons, 1–3) and five largest protected landscape areas (red polygons, A–E) are highlighted (d). Sparsely populated protected areas (A and B) exhibited high intensity in the number of observers and observations. The opposite phenomenon can be observed in protected areas C and D. However, the high population density of the three largest cities is not reflected in the high number of records and observers for the third largest city (3). The POD data show many similar contradictory trends upon closer inspection. Thus, it is difficult to identify a single or just a few major sources of bias.

correlated rasters (Supporting information) were used in the final models.

Background points simulation

Presence-background modelling complements species presences by generating background points representing the environment. However, the default assumption that species occurrences are unbiased samples from the species' distribution is not met for most presence-only occurrence data. If species occurrences suffer from sampling bias, the same bias should ideally be reflected in background points (Elith and Leathwick 2007, Barber et al. 2022). A straightforward implementation, particularly within software like Maxent, is to input all occurrences within the target group as the background data (Phillips et al. 2009, Merow et al. 2013). However, with approximately 300 000 background points in our POD, at least some kind of reduction would be necessary for computational reasons. It should be also noted that POD used in our study covers 80% of 3 km pixels out of 9844 pixels making up the entire area of the Czech Republic. An alternative is to sum up the number of observations per pixel over the intended grid size and normalize all pixel values to a range from 0 to 1 (with the pixel containing the highest number of TG ocurrences set to 1 to obtain a default bias raster (Fig. 1) that can be utilized to simulate new background points. This method of generating background points from the default raster is close to the idea of directly using all points from the TG or TGOB, respectively (Phillips et al. 2009, Fourcade et al. 2014, Botella et al. 2020). A more advanced approach lies in determining KD and applying it to manipulate background points to places with the highest sampling effort (Barber et al. 2022).

Kernel density and kernel bandwidth change

Kernel density (KD) estimation is a non-parametric method for estimating the probability density function of a random variable, providing a smooth, continuous approximation of the underlying data distribution. We used the 'spatstat' R package (www.r-project.org, Baddeley and Turner 2005) to calculate the Gaussian KD from two-dimensional point (occurrences) patterns. The calculation was performed 1) for the full dataset irrespective of the observers (KD_{TGOB+}) and 2) for each individual observer ($KD_{PW\text{-}OOA}$). $KD_{PW\text{-}OOA}$ was subsequently normalized so that the density over the entire area of the Czech Republic for each individual observer was equal to 1 (normalized $KD_{PW\text{-}OOA}$, $nKD_{PW\text{-}OOA}$). KD bandwidth (KDB, also known as sigma, smoothing, size, or radius) is one of the fundamental parameters affecting the calculation of KD. Many automatic KDB selectors are available; however, the estimates they yield may differ. It is apparent that, in the SDM-related literature, there is no general empirical agreement regarding the ideal KDB (Discussion). For the example shown in Fig. 3A, different automatic algorithms for determining the KDB (i.e. scott, diggle, and CvL from the *spatstat*) estimated very different KDB values (0.12, 0.39, and 0.65, respectively). Hence, we assigned a set of KDBs (0.2, 0.3, and 0.4) in that figure manually for illustration.

The application of very low values of KDB (in our study area, 0.25 was sufficient) resulted in the generation of a bias raster corresponding to the 'default bias raster' (Background points simulation) purely using the number of observations per pixel, thus representing the TGOB method. Applications of a wider KDB range (0.25, 0.5, 1, 2, 3, and 4 times the default pixel size) are referred to as the TGOB+ method here (see Fig. 1 'kernel density bandwidth'), inspired by Botella et al. (2021), who tested four different values of the bandwidth parameter in their study.

Presence-weighted PW-OOA method

The PW-OAA approach allows for the simulation of the distribution of background points based on two parameters: the KDB and the observer weight (OW, example shown in Fig. 3B). Observer weight is the relative contribution of the individual observer to the total number of focus species presences – in other words, the percentage of observations for the focus species reported by the particular observer over the entire area of the Czech Republic, calculated based on a particular level of data (dis)aggregation to a specific pixel size (i.e. grid size). Note that, for example, three observations by the same observer within one pixel count as a single observation.

For the newly proposed PW-OOA method, the normalized kernel densities of individual observers ($nKD_{PW\text{-}OOA}$) were multiplied by OWs (defined by 0.25, 0.5, 1, 2, 4, or 8 times the default pixel size; see Fig. 1 '(dis)aggregate raster' pixel sizes), yielding presence-weighted KDs, which were then summed up across all observers ($\Sigma\ nKD_{PW\text{-}OOA}$) for each pixel size. From this, it was possible to derive candidate bias rasters to simulate background points to serve as input for SDMs. Within the scope of this paper, we generated 36 sets (6 KDBs × 6 OWs combinations) of bias rasters per species for the PW-OOA approach.

SDM

We used random forest (RF), generalized linear models (GLM), and Maxnet (Phillips et al. 2017) to represent modelling methods for presence-background SDMs with low, moderate, and high performance (Valavi et al. 2021a). These were implemented using the R package 'sdm' (ver. 1.2-56, Naimi and Araújo 2016, www.r-project.org). All SDMs were set identically to internal 3-fold cross-validation, 20 replications, and sampling 10 000 background points with replacement in order to allow their spatial manipulation (in the space limited by the 9844 pixels of the study area). All other parameters were kept in default.

Ideally, the final model selection or validation should be performed using independent data (Araújo et al. 2005). Models based solely on biased occurrence records cannot be reliably fitted to a wide range of species without independent data (Stolar and Nielsen 2015, Baker et al. 2024). SDM

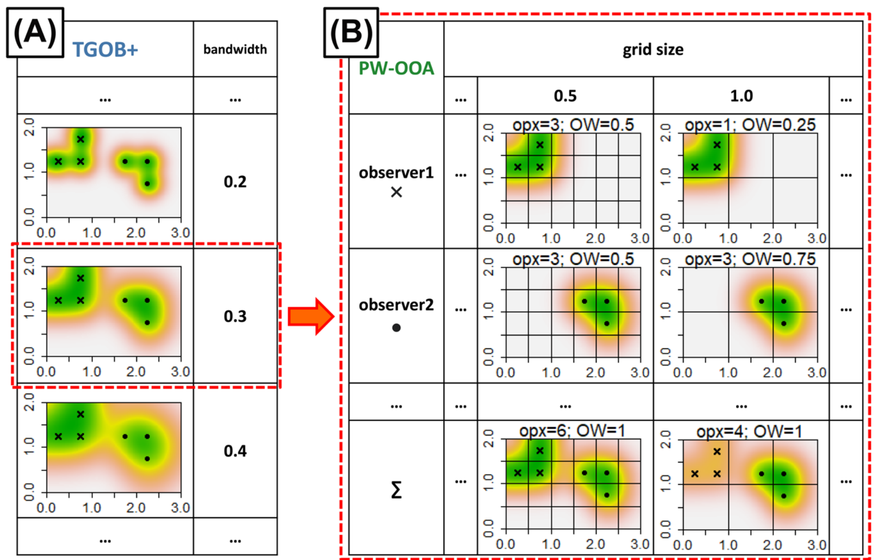

Figure 3. Comparison of principles of the TGOB+ and PW-OOA methods. (A) plots the effect of changing the kernel density bandwidth (KDB) on the distribution of kernel density (KD) when not distinguishing among individual observers for the six occurrence points (TGOB+ method) recorded by two observers (distinguished by a cross or a dot for observers 1 and 2, respectively). (B) demonstrates the PW-OOA approach on an example with a KDB of 0.3. For both, the used grid sizes (0.5, left column and 1.0, right column) and the total number of occupied pixels (i.e. pixels with presences, opx) were determined, and the normalized KD of each observer was then weighted (multiplied by OW). At a grid size of 0.5, the occurrences of both observers cover three different pixels each time and are thus assigned identical weights (OW = 0.5). Therefore, the resulting KD (∑) is identical to that in (A) (dashed red rectangle). At a grid size of 1.0, all three occurrences of the first observer (crosses) fell within a single pixel, whereas the second observer (dots) occupied three different pixels. Thus, the first observer was assigned a lower weight (OW = 0.25) than the second observer (OW = 0.75). This was reflected in the final sum (∑) of the lower KD values around the points of the first observer. Observer weight (OW), target group occurrences background (TGOB), TGOB+ (tuned up TGOB by adjusting kernel smoothing bandwidths) and presence-weighted observer-oriented approach (PW-OOA).

approaches that account for sampling biases combining PO and PA data have recently been published (Fithian et al. 2014, Koshkina et al. 2017, Fletcher et al. 2019, Peel et al. 2019, Mäkinen et al. 2023). Under these circumstances, we decided to replace internal (withheld) data with independent unbiased PAD to be able to evaluate the true potential of the tested sampling bias correction methods.

To obtain the most representative prediction performance of the tested sampling bias correction methods, we decided to evaluate models by the set of three commonly used threshold-independent metrics (area under the receiving operating characteristic curve, AUC; Pearson correlation, COR; true skill statistic, TSS) integrated in the 'sdm' package, supplemented with a threshold-dependent one (Jaccard's similarity index, specificity = sensitivity, Leroy et al. 2018). All metrics were calculated on both the POD (internal random 3-fold cross-validation based on biased presence occurrences) and PAD (which was used for the independent evaluation to select best performing model and subsequently used in all reported results) datasets.

Results

A comparison of all four sampling bias correction methods across Maxnet and GLM and across multiple evaluation metrics reveals similar trends (Supporting Information). For clarity, we further present only the results using AUC and SDMs produced with Maxnet, as this algorithm consistently outperformed GLM and RF across all performance metrics in our study. Species 'sp49' was excluded from the results due to frequent failure (up to 90% of replications) to converge with the Maxnet modelling method, particularly under the random and STSP approaches. Random forest failed to deliver a gradual improvement in average prediction performance for the progressions: random to STSP, and TGOB+ to PW-OOA. This outcome contrasted with the trends observed for Maxnet and GLM.

The results of the comparison of all used bias correction methods in terms of the SDMs prediction performance (AUC) across all species are presented in Table 1. A gradual improvement in AUC (the bold numbers on the diagonal) towards the PW-OOA method can be observed. This is consistent with the mutual comparisons of the number of species in which the model in the row significantly outperformed the one in the column. Figure 4 shows the comparison of the average AUC and COR for 108 species, indicating both the (in)consistency of results and overall performance trends among all five methods. The three selection/evaluation scenarios represent practical situations that arise depending on the availability of independent evaluation data.

Figure 5 shows the prediction performance improvement of the PW-OOA and TGOB+ methods over the random background method, measured as AUC (diff), which is partially driven by species prevalence. These results support the previous conclusions in more detail. The PW-OOA method demonstrated significant improvements over the existing correction methods, as evidenced by a comparative increase in AUC values across most species, indicating more accurate habitat suitability predictions. In four species, the PW-OOA method improved performance by more than 20 percentage points (p.p.). In total, the AUC performance was enhanced by more than 10 p.p. in 18 species compared to the random method, while 13 bird species exhibited a slight (of up to 3.6 p.p.) decrease in AUC. In the TGOB+ method, we observed an AUC improvement of more than 10 p.p. in 14 species, while a drop of up to 6.4 p.p. occurred in 20 species. Figure 5 also illustrates that the success of sampling bias correction using each of the approaches increased with species prevalence.

Table 1. Comparison of all five methods (random, STSP, TGOB, TGOB+, PW-OOA) using Maxnet in terms of prediction performance (AUC) for the 108 species of interest. The values represent the number of species for which the model in the row significantly outperformed the model in the column (unpaired two-samples Wilcoxon test, p-value < 0.05). The bold numbers on the diagonal show the mean AUC of the respective method across all species. Spatial thinning of species presences (STSP), target group occurrences background (TGOB), TGOB+ (tuned up TGOB by adjusting kernel smoothing bandwidths) and presence-weighted observer-oriented approach (PW-OOA).

	random	STSP	TGOB	TGOB+	PW-OOA
PW-OOA	95	90	79	59	**0.719**
TGOB+	84	76	54	**0.703**	25
TGOB	69	57	**0.686**	0	15
STSP	49	**0.673**	37	18	13
random	**0.661**	31	36	17	8

Regarding the selection of optimal parameters for the presence of the thinning distance and KDB (Supporting information), identifying a consistently ideal value for KDB or observers' weight is challenging. Individual selected values of the parameters showed their best performance for 5 to 56 species, showing that it is impossible to determine a single universal best-performing set of parameters suiting all species.

To assess the reliability of internal validation metrics, we compared them against the performance on the independent PAD dataset (Fig. 4). A critical pattern emerged: an inverse relationship was observed between performance on internal and external validation for the most effective bias correction approaches (PW-OOA and TGOB+). Specifically, approaches that performed best on the independent data often showed lower performance metrics during internal 3-fold cross-validation on the presence-only data. Conversely, the random approach, which performed poorly on independent data, showed inflated performance metrics during internal validation, tending to overestimate its true predictive ability. This finding has direct practical implications for modellers. Based on our results, we recommend TGOB+ as the most robust approach when an independent dataset is unavailable, even though its performance on internal metrics may appear suboptimal. When an independent dataset is available for evaluation, however, PW-OOA is clearly the superior method.

Further, to document the performance improvement achieved by tuning the two presented approaches (TGOB+

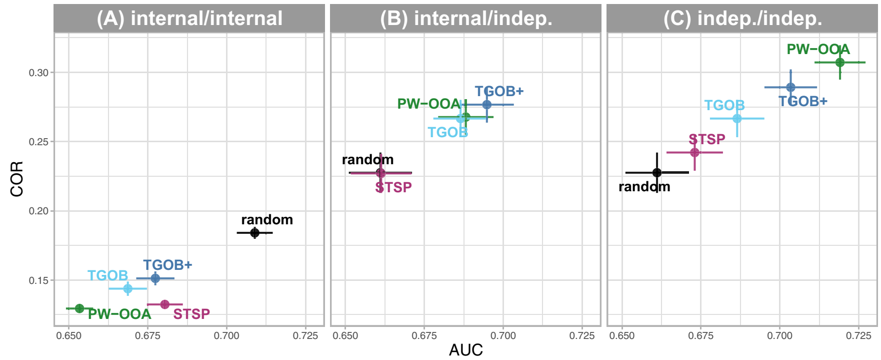

Figure 4. The mean AUC (x-axis) and COR (y-axis) of the five presence and/or background simulation methods calculated from 108 bird species. The bars (around each model) represent standard errors that reflect the variation among all species. The three panels show results from different selection/evaluation scenarios: (A) internal/internal, where both model selection and the corresponding AUC displayed on the x-axis were based on the internal random cross-validation (POD); (B) internal/indep., where models were selected using internal random cross-validation (POD) while the AUC displayed on the x-axis was calculated using the independent PAD; and (C) indep./indep., where both model selection and the corresponding AUC displayed on the x-axis were based on the independent PAD. Spatial thinning of species presences (STSP), target group occurrences background (TGOB), TGOB+ (tuned up TGOB by adjusting kernel smoothing bandwidths), and presence-weighted observer-oriented approach (PW-OOA).

and PW-OOA), we compared their performances to the traditional TGOB and default PW-OOA approach (Supporting Information). These two baseline variants were defined by a default bias raster and default parameter settings (nKD_{TGOB} of 0.25 and $nKD_{PW\text{-}OOA}$ of 0.25 and pixel size for OW of 1).

Discussion

Our findings demonstrate that correcting for individual observer behavior using PW-OOA significantly improves SDM predictive accuracy compared to conventional bias correction methods. The PW-OOA method outperformed all other approaches, improving AUC scores by up to 29 percentage points. On average, PW-OOA improved the AUC by six percentage points compared with random background points. The ranking of individual bias correction methods in improving the overall performance of SDMs over all 108 species was as follows: STSP < TGOB < TGOB+ < PW-OAA. An exception to this is the random forest modelling method. Valavi et al. (2021a, 2021b) highlight that default random forest is inherently one of the worst-performing models when dealing with class imbalance and sample overlap. Our PW-OOA method frequently results in such data conditions. Consequently, PW-OOA's performance is especially impacted by the limitations of a default random forest configuration.

We found that the effects of different sampling bias correction methods (STSP, TGOB, TGOB+, PW-OOA) on the resulting prediction of habitat suitability were inconsistent among species. This is an important finding as, in common SDM practice, it is not uncommon to just adopt models from the literature acquired from a small set of species that may be not representative and use them for modelling a different species. This notion is supported by Lee-Yaw et al. (2021), who found possible publication bias among studies that evaluated the discrimination ability of SDMs for single versus multiple species datasets, with studies reporting only a few species tending to show higher success rates. In our study, we used 108 bird species that represent the full spectrum of ecological requirements. Our results regarding the TG(O)B method clearly support earlier findings (Warton et al. 2013, Stolar and Nielsen 2015, Ranc et al. 2016), reporting that species-specific responses to TG background simulation can in some cases even worsen the model performance. Indeed, a recognized limitation of TG(O)B is its potential to confound species richness gradients with sampling intensity (Warton et al. 2013).

Baker et al. (2024) reported that no single method for sampling bias correction performed best across all species and that the evaluation using internal test data was generally a poor indicator of the true effect of sampling bias correction. Furthermore, our finding that internal validation metrics were misleading for the best-performing models has significant practical implications. It demonstrates that relying solely on internal random cross-validation with biased, presence-only data can lead modellers to select suboptimal bias correction strategies. This underscores the critical importance of using independent, spatially segregated, or presence–absence validation datasets whenever possible to reliably assess model performance, a conclusion supported by another recent study (Dubos et al. 2022). In line with the recent work of Ten Caten and Dallas (2023), our results demonstrated that when using the most commonly used approach of sampling bias correction, i.e. STSP, a significant improvement in sampling bias correction was observed only in less than half of the modelled species (45%), despite using the best-performing thinning distance for each species. Note that this selection of best-performing parameters was only possible as we had reference (true) data, which is not always the case in SDM studies.

Previous studies have revealed the inconsistent involvement of individual observers in reporting the presence of

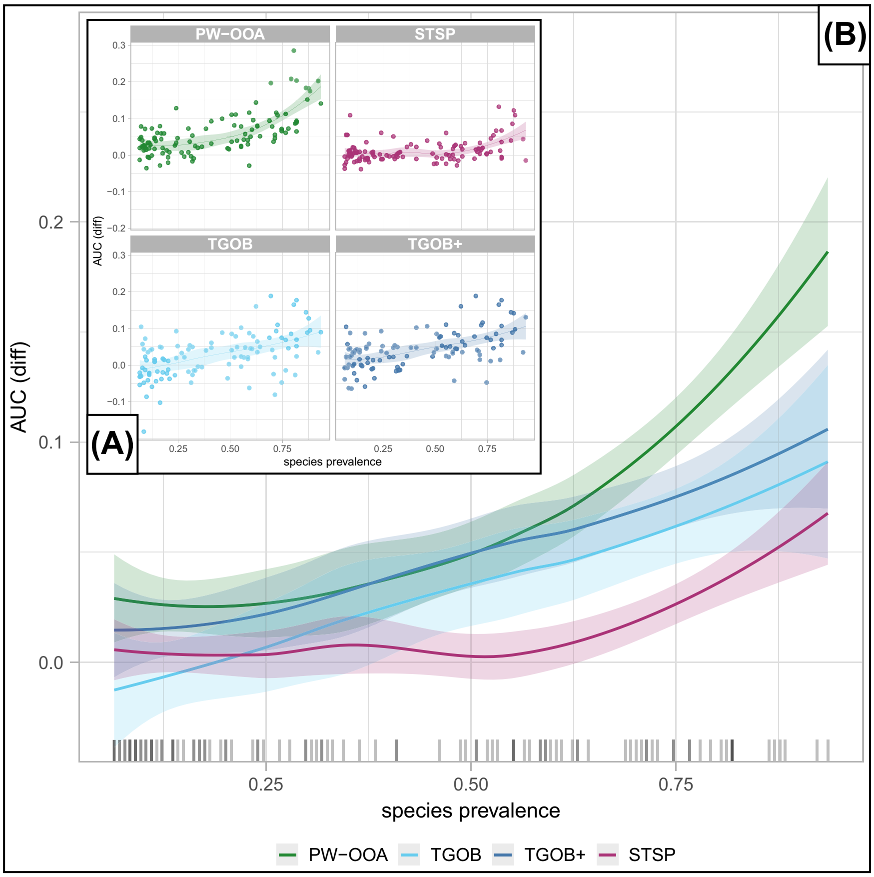

Figure 5. Comparison of species distribution model (SDM) prediction performance of 108 bird species differing in species prevalence (the ratio of the number of pixel with species presence to the total number of 154 presence–absence dataset (PAD) pixels) measured as AUC improvement over the random method (AUC (diff) = difference between the STSP, TGOB, TGOB+, or PW-OOA versus the random method). Locally estimated scatterplot smoothing (LOESS) regression lines, a non-parametric method that fits a smooth curve using locally weighted polynomial regression, are shown with 95% confidence bands. (A) represents each bias correction method overview with each species' AUCs distributions, while (B) compares all the LOESS regression lines in one overlay, with individual species marked (25% transparent to visualize overlap) along the x-axis. Spatial thinning of species presences (STSP), target group occurrences background (TGOB), TGOB+ (tuned up TGOB by adjusting kernel smoothing bandwidths), and presence-weighted observer-oriented approach (PW-OOA).

species in occurrence databases (MacPhail and Colla 2020). Correcting for this (for example, on the basis of some observer-related attribute present in the data, such as linking to checklist, time spent in the area, or observer's trajectory in the area) was shown to result in a substantial improvement in the accuracy of SDM predictions (Johnston et al. 2021). Such attributes are, however, often not available (as is the case in our data). In such a case, the method of accounting for sampling bias by assigning observer weights (derived from the observer-reported presences) proved to be the most effective method for correcting the sampling bias of all methods employed in our study. The fact that the PW-OOA method is straightforward, not requiring any additional predictors about possible sources of bias (e.g. population density and road network; see Dubos et al. 2022) or species ecological characteristics (traits) constitutes its indisputable benefit. It increases the versatility of PW-OOA use, which allows better utilization of the continually growing amount of occurrence data from citizen science projects.

KDB selection is considered a fundamental model selection problem in mathematical statistics (Mammen et al. 2011). KDB change possesses a biological rationale as it might indicate the maximum dispersal range (distance from existing occurrence), in which the intensity of occurrences increases (Renner et al. 2015). Typically, authors manually choose a single KDB, such as 10 km in Ranc et al. (2016), 20 km in Lee-Yaw et al. (2018), 50 km in Vollering et al. (2019), 200 km in Elith et al. (2011), or test multiple widths ranging from 3 to 500 km, such as Botella et al. (2021) or Inman et al. (2021). In some cases, the KDB is not given, set automatically, defaults, or is difficult to infer (Jarnevich et al. 2017, August et al. 2020, Botella et al. 2020, Chauvier et al. 2021, Barber et al. 2022, Da Re et al. 2023).

Artificially generated sampling bias combined with a virtual species (Botella et al. 2021) or virtual ecologist approach (Zurell et al. 2010, Miller 2014) can be too simplistic and fail to reflect the complexities of bias patterns observed in real life (Moudrý 2015, Barber et al. 2022). At the same time, it is unrealistic to expect that our newly proposed PW-OOA method would be able to fully correct for sampling bias in all species (especially considering that none of currently known methods is able to do so). Still, PW-OOA outperformed the other tested methods and confirmed that this approach is promising and calls for further research, which should also focus on selecting the ideal kernel bandwidth to enhance our understanding of bias intensity related to the environment. Such research could also focus on the development of automated tools for optimizing KDBs and observer weights.

We also consider it worth exploring the scalability of PW-OOA to other taxon groups, regions, and species occurrence databases that may hold different bias structures for observer behavior. Birds are, besides plants, the most commonly collected TG and, therefore, the most abundant taxon in the species occurrence databases. How PW-OOA would perform on datasets with significantly (by an order of magnitude) fewer occurrences than the 300 000 utilized in our study remains an open question. Assuming that the bias remains constant for each observer, it would be reasonable to examine the filtering of all observer records, regardless of their TG association, in order to obtain the whole intensity of the sampling effort.

Our study design has several spatial constraints that should be acknowledged. First, it remains an open question how niche truncation caused by the limited study area of the Czech Republic may affect the results. Furthermore, the fixed 3 km resolution of the PAD dataset can be considered a limiting factor in our study, as the spatial resolution at which environmental variables and species presence data are analyzed affects both the accuracy and predictive power of SDMs (Moudrý and Šímová 2012, Moudrý et al. 2023). However, having an independent dataset allowing us to evaluate the sampling bias correction was crucial in our case and enabled us to adhere to the recommendations of good practice presented by Araújo et al. (2019).

Future studies could focus on systematically optimizing KD parameters to further enhance bias correction performance. Several promising directions include the use of movement ecology data (e.g. typical species dispersal distances) to inform biologically meaningful kernel bandwidths, integration of expert-based ecological knowledge to guide kernel selection, or the application of automated, data-driven techniques such as cross-validation or information-theoretic approaches (e.g. AIC-based optimization) to find species-specific or context-specific optimal bandwidths. Combining biological realism with statistical rigor could lead to more adaptive bias correction frameworks, particularly in multi-species or multi-region SDM applications.

Moreover, the PW-OOA approach offers strong potential for broader application beyond birds. It could be eventually adapted to other taxonomic groups commonly monitored through citizen science, such as plants or insects, where observer-driven sampling biases are also prevalent. Given the explosive growth of occurrence data from mobile applications and opportunistic records across taxa, extending PW-OOA could significantly improve the robustness of biodiversity models globally.

Acknowledgements – We would like to thank correcta.cz for helpful comments and English proofreading.
Funding – This research was funded by an IGA (Internal Grant Agency) grant awarded by the Faculty of Environmental Sciences at the Czech University of Life Sciences (grant no. 2022B0040), by the Technological grant agency of the Czech Republic (grant no. SS02030018 DivLand), and by Horizon Europe project EarthBridge (ID: 101079310) funded by the European Union. Views and opinions expressed are, however, those of the author(s) only and do not necessarily reflect those of the European Union. Neither the European Union nor the granting authority can be held responsible for them. Computational resources for all R scripts were provided by: (1) the e-INFRA CZ project (ID: 90254), supported by the Ministry of Education, Youth and Sports of the Czech Republic; and (2) the ELIXIR-CZ project (ID: 90255), part of the international ELIXIR infrastructure.
Conflict of interest – The authors declare no conflict of interest.

Author contributions

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Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/ecog.08202.

Data availability statement

Data are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15497910 (Balej et al. 2025).

Supporting information

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

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