

SDM sampling bias correction methods - an overview

In the best case scenario, species distribution models (SDM) are developed using data from well-designed surveys that include both presences (*klātbūtne*) and absences (*iztrūkums*), collected across an environmentally and spatially representative area. However, studies like this are usually not feasible as they require a large amount of resources. Opportunistic (*gadījuma rakstura*) datasets, such as museum collections, citizen science projects, and websites, already contain a wealth of information about where species occur. However, this kind of data usually lacks information about true absences or repeated sampling (*atkārtota paraugošana*). The need to utilize these observations has naturally led to the development of an array of SDM methods suitable for presence-only data (Elith et al., 2011). Of these, the most commonly used is maximum entropy (MaxEnt, Phillips, 2004), which stands out due to its high predictive accuracy (*prognozēšanas precizitāte*, Merow et al., 2013) and ability to handle complex interactions between responses and predictors (Elith et al., 2011). It is also easy to apply, particularly so since the launch of the MaxEnt software (Phillips et al., 2006).

Although MaxEnt provides a way to model species distributions without true absence data, all SDM methods still depend on underlying assumptions (*pieņēmumi*). A large part of researchers tend to falsely believe that using MaxEnt relieves you from these prerequisites (Yackulic et al., 2013). This is likely because it seems that the lack or removal of potentially false absences solves the problems related to them, such as imperfect detection (*nepilnīga konstatēšana*, Elith et al., 2011). Unfortunately, the mainstream acceptance of SDMs has outpaced methodological development and refinement of the methods (Boria et al., 2014).

In reality, the probability (*varbūtība*) of a location being included in a presence-only dataset is a combination of three probabilities: (1) the probability that the location was surveyed; (2) the probability that the location is occupied by the species; (3) the probability that in the case of the location being sampled and occupied, the species was detected (Yackulic et al., 2013). Ecologists are mainly interested in the occurrence probability (*sastopamības varbūtība*, 2) and look for ways to remove the influences of the other probabilities mentioned. Therefore, one of the prerequisites is that the area of interest has been sampled randomly (*nejauša paraugošana*, Phillips

et al., 2009). Using opportunistic observations often violates this assumption, as the observations from citizen science projects or websites are often biased towards cities, roads and/or other easily reachable locations or environments where the species can be observed more easily. The negative impact of bias (*novirze*) is much stronger for presence-only models. In presence-absence models, sample selection bias affects both presences and absences, so the effect of bias cancels out (Phillips et al, 2009). Sampling bias correction is the main challenge when fitting presence-only models (Merow et. al. 2013).

Geographic bias itself is not automatically harmful. It becomes a problem when it is related to specific environmental conditions, which is usually the case when a geographic bias occurs (Phillips et al., 2009). By default, MaxEnt models assume that all locations on the landscape are equally likely to be sampled, regardless of their spatial pattern - in environmental space (*vidi raksturojošā telpā*), rather than geographical space (Merow et. al., 2013). If sampling bias (*paraugošanas piepūles novirzes (no nejaušības)*) is not taken into account, the model can overestimate the importance of some variables (Phillips et al., 2009) and hide the ecologically meaningful relationships between species occurrence and the environment (Barber et al., 2022). Therefore, models that are not adjusted for sampling bias often produce distributions and response curves that mirror the sampling effort (*paraugošanas piepūle*), rather than representing the true distributions of species (Ranc et al., 2016). To illustrate this (and other points made later), examples of two bee species will be used, for each of which four models with different bias correction methods were created. An example of how much the relative importance of variables can change is depicted in Fig 1. The relative importance is consistently low for some variables (e.g., EGV 1 to 4) , but for others it varies greatly between biased models and models with different correction methods (e.g., EGV 5 to 7).

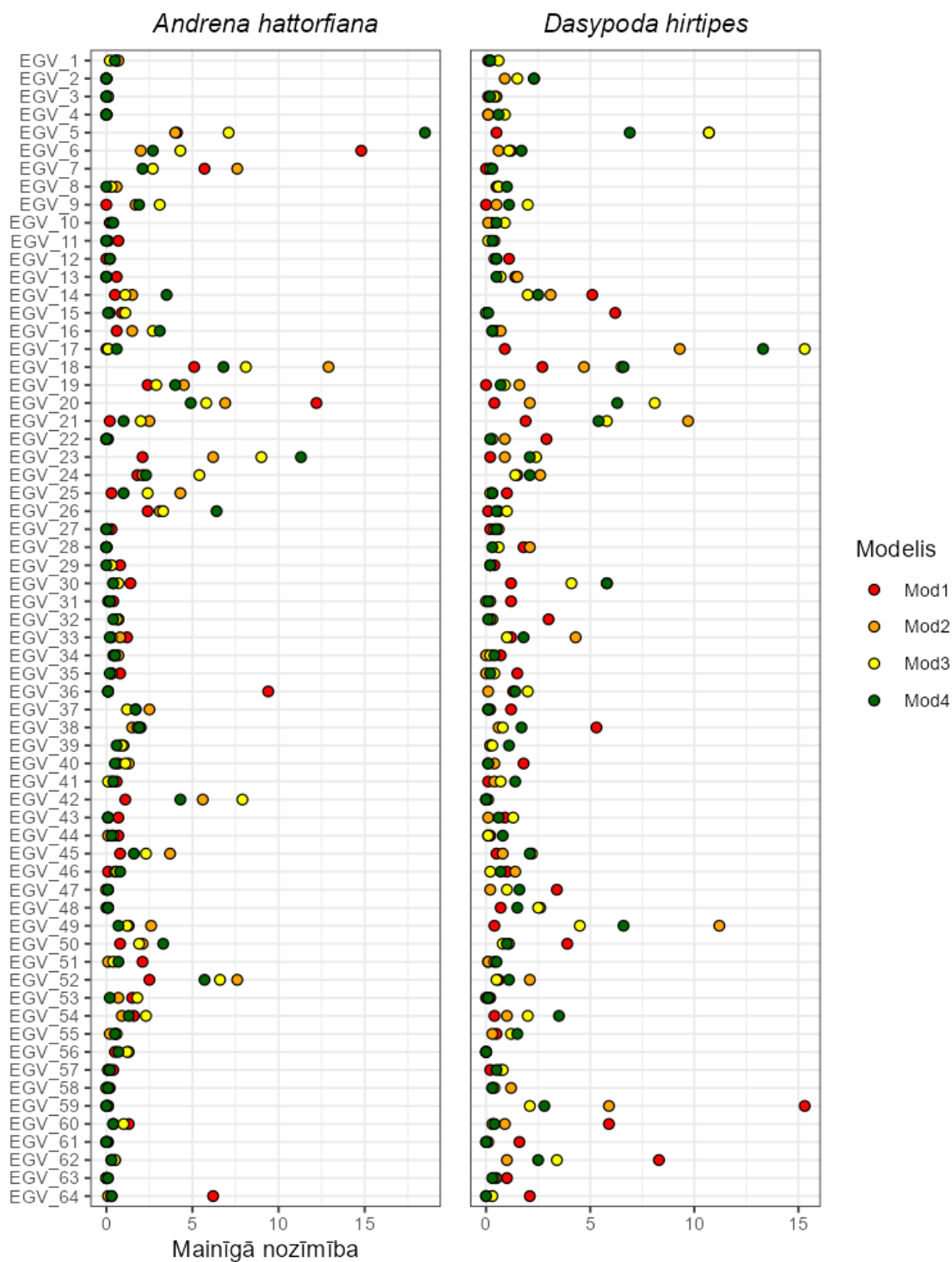


Fig. 1. The relative importance of environmental variables in models with different sampling bias control methods. Mod1 – no bias control; mod2 – spatial filtering; mod3 – spatial filtering + bee-specific bias layer; mod4 - spatial filtering + species-specific bias layer.

Despite all of the limitations of using opportunistic occurrence data in presence-only modelling, it is still a very important and useful data source. Ecologists should just be cautious and modest in their expectations for inference (Yackulic et al. 2013) and keep in mind that the results should primarily be used for exploratory analyses, e.g., to formulate hypotheses about the species or inform structured survey strategies (Merow et al. 2013). The reliability of a model's output is directly connected to the degree to which the model assumptions are met - despite this, the sampling bias is ignored in a large part of research where MaxEnt is used (Yackulic et al., 2013). In most cases, a justified attempt to correct the sampling bias will bring the result closer to the true estimation of the sampling effort and therefore offer a distribution that is more similar to the true species distribution (Barber et al., 2022) and is therefore strongly recommended (Merow et al., 2013, Yackulic et al., 2013).

Sampling effort bias corrections can be divided into three main approaches - occurrence filtering (*novērojumu filtrēšana*), background manipulation (*fona punktu manipulācija*), and model manipulation (*modeļu manipulācija*, Ranc et al. 2016). In research where sampling effort corrections have been introduced, two of often used methods are the **target-group approach** (*mērķa grupas pieeja*, background manipulation) and **spatial filtering** (*telpiskā filtrēšana*, occurrence filtering). Other methods are also sometimes used, such as radius-restricted background (background manipulation), which limits the area that the algorithm uses to determine environmental variability (Barber et al., 2022). Some studies implement covariates of sampling effort in their models (model manipulation), such as human density maps or road networks (Barber et al., 2022) or data filtering in environmental space (*novērojumu filtrēšana vidi raksturojošā telpā*, Varela et al., 2014). These methods are employed less often, mainly because of their limitations, as well as because the methods are more difficult to justify and are often found to be less effective (Barber et al. 2022). The terms background points (*fona punkti*) and pseudo-absences (*pseudo-iztrūkumi*) can be used as synonyms in most cases (Guissan et al. 2017), although background points could be considered a wider term.

Target-group approach

The target-group approach is based on the way that the background points are selected or treated in the model. In MaxEnt, pseudo-absences do not necessarily imply the absence of the species, but rather just represent the environmental conditions available in the sampled space (Phillips et al. 2009). In many other SDM algorithms, pseudo-absences are treated as true absences nevertheless (Guisan et al., 2017). By contrast, in MaxEnt, these background points are not interpreted as absences, but as a sample of the environmental distribution, against which presence records are contrasted (Phillips & Schapire 2004). If the assumption of evenly and representatively sampled space holds, the pseudo-absences can be drawn randomly from the whole study region. But, as mentioned earlier, this is seldom the case. The true sampling effort is usually also not known, since the collection of records is not based on a specific sampling design. In any case, if the exact sampling effort is known, it is generally advisable to use presence-absence models to effectively utilize all the available information (Elith et al., 2011).

The target-group (TG) approach is based on a collection of presence records of a taxonomic group that is assumed to have a similar sampling effort as the species that is being modelled. This assumption is made because, for example, a person who has observed a specific bird species in different regions is likely to pay attention to other birds, too, but will probably not record observations of insects. Using observations of a specific organism group essentially lets the model highlight the more sampled areas (by using the TG species observations as a proxy for the sampled area) and therefore the habitats the species occupies in the sampled space, not in all the environmental conditions available in the region.

The information on sampling effort can be incorporated into MaxEnt in two strategies: by a weighting of the given set of randomly selected background points, or by using the sampling effort as a bias/weights in the selection of the background points (Phillips et al., 2009). Most studies use biased background selection, as this is the default implementation by the MaxEnt software when a bias layer is provided. To create the bias layer, it is common to use kernel density estimates of all target-group observations (Barber et al., 2022), with the application of an ecologically meaningful bandwidth (*joslas platums*, Ranc et al., 2016). An example of a resulting bias layer for bees (utilising all bee species observations available and using kernel density estimate with a bandwidth of 5 km, representing a rough estimate for the bee flight range) is provided in Fig. 2. This layer is then used to randomly select background points, where the

selection is weighted by the estimated sampling bias – i.e., the lighter areas will have more background points. The value given to the background (areas with no known observations) also greatly impacts model results (Kramer-Schadt et. al., 2013), so the choice of the value should be based on inference about the expected sampling effort.

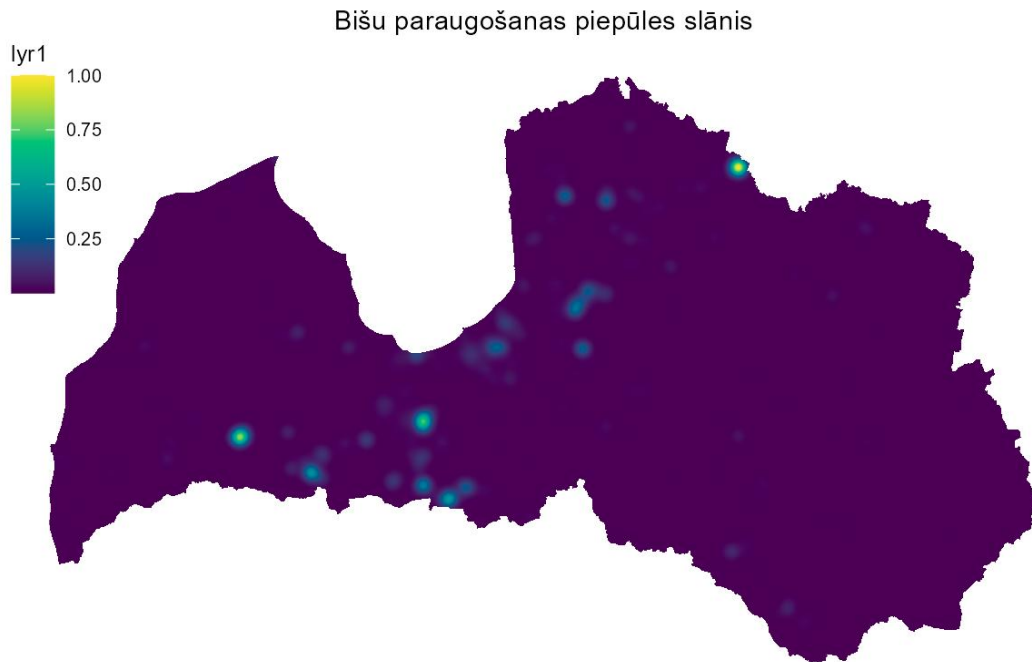


Fig. 2. Sampling bias layer for bees, developed using the target-group approach.

A very important assumption of the TG approach is that all the data have been collected using the same methods, so that an estimate of the sampling effort for each member of the group is represented by the occurrences (Phillips et al., 2009). In addition, this method assumes that the species probability of detection does not vary across sites and is the same for all TG species (Yackulic et al., 2013). Attention should also be paid to the scope of the selected TG and the amount of species observations in it, because using a small group of species and therefore few locations can match the occurrences of the modelled species too closely and therefore dampen the relationships between occurrences and variables (Merow et. al., 2013). When using the TG approach, attention should also be paid to species richness patterns in the study region - heterogeneous species richness can also cause a bias (i.e., it is more likely for a species from a TG

to be observed if there is a higher species richness in the area). Therefore, while often helpful, the TG approach does not always provide a robust proxy for the effective sampling bias, so authors advise against applying it in an uninformed and automatic manner (Ranc et al., 2016). Using the TG approach has been proven to produce results almost as good as when the true sampling effort is used (Ranc et al. 2016, Barber et al. 2022). It is strongly recommended that users always report information and support for the assumptions and approximations of the inferred sampling effort (Merow et. al. 2013).

A notable number of studies have turned to using virtual species to evaluate the effects of a sampling bias and its correction methods in a more detailed manner, as in these cases, the ground-truth is known (i.e., the true probabilities and sampling bias). It must be kept in mind, though, that simulated sampling bias might be too simplified and might not represent the more complex patterns in real datasets (Barber et al. 2022). In the study of Ranc et al. (2016), when comparing true and predicted (model with true sampling bias, TG-corrected bias, and biased models) probabilities, the largest differences (measured by niche overlap) tend to be located in areas with low sampling intensity, especially when compared against biased models. In these areas, biased SDMs tend to severely underestimate species' probability of presence, whereas bias-corrected SDMs usually show slight overestimation. This mismatch explains why biased models can also sometimes achieve higher model quality evaluation metric (*modeļa kvalitātes metrikas*) scores than corrected ones - in biased models, large, unsampled regions can be incorrectly predicted as unsuitable. As a result, biased SDMs sometimes appear to perform better in terms of discrimination metrics like Area Under the Curve (*telpa zem uztvērēja līknes*, AUC, Veloz, 2009).

The usefulness and relative importance, and improvement of bias corrections by the TG approach are largely dependent on the study area, specifically, the extent of high versus low sampling areas. Modellers are therefore more likely to see improvements in cases where large unsampled regions contain unsampled environmental conditions relevant to the species (Ranc et al., 2016). It has also been shown that the usefulness of the corrections depends on the range and niche breadth of the species, as well as the sample size of presences. Wide-ranging species and species with large niche breadth (generalists) and a high amount of observations are more vulnerable to bias and usually benefit more from corrections (Ranc et al., 2016).

Spatial filtering

Sometimes, there is no justifiable way to reconstruct the sampling effort in the study region. In cases like these, spatial filtering (SF) is described as the most suitable method to correct the sampling bias, as it is simple to apply and requires no prior knowledge (Fourcade et al., 2014). Some authors note that this method performs consistently better over other methods, including background manipulation (Fourcade et. al., 2014; Kramer-Schadt et. al., 2013), but Fourcade et al. (2014) also note that the usefulness of a specific correction method is not universal and should be chosen based on the type and intensity of the bias.

Spatial filtering (SF) refers to the thinning of occurrence records in geographical space to reduce the effect of oversampling in certain regions. By reducing spatial clustering, SF can also lessen the associated bias in environmental space. In addition, SF may help to address issues of small-scale spatial autocorrelation in species distribution data (Moudrý et al., 2024). Models with SF show better performance and lower overfitting (*pārpielāgošanās (ievades datiem)*) than unfiltered models (Boria et al., 2014), and minimise omission and commission errors (Kramer-Schadt et. al., 2013). In the study by Kramer-Schadt et al. (2013), the area predicted as suitable increased substantially when spatial filtering (SF) was applied. The authors note that sampling was heavily concentrated in one region of the study area, causing occurrence records to be strongly associated with climatic variables that lacked an obvious ecological explanation. As a result, the same type of theoretically suitable habitats only received high predicted suitability values in the highly sampled region. After the bias correction, however, the same land-use categories were predicted as suitable across a much larger part of the study area. To rule out the chance that the effects of SF are mainly due to reduced sample size, the authors of Boria et al. (2014) also conducted a random thinning. This resulted in models that were slightly better than unfiltered models but had very similar predictions, likely because a larger dataset reinforced the spatial biases.

There are several ways that SF can be conducted. One example is the removal of localities that are within a certain distance from each other, keeping the most localities possible (Boria et al. 2014) or keeping the most informative observations, for example, ones with the greatest observation precision (Kramer-Schadt et. al., 2013). Another approach is making a grid and keeping only one observation per each grid cell (Fourcade et al., 2014). The optimal geographic

distance of spatial filtering for an organism or system should be determined by the mobility of the species or by conducting filtering experiments (Boria et al., 2014).

Spatial filtering is applied in geographical space, where clustered occurrences are removed to reduce spatial sampling bias. However, this approach has been criticised because unique environmental conditions may also be eliminated in the process (Varela et al., 2014). To address this, Boria et al. (2014) recommend replacing spatial filtering with filtering in environmental space. This means the removal of repeated occurrences from similar environments that have been extensively sampled, which can reduce the overweighting of particular conditions. Still, environmental filtering is not always justified or beneficial and should be applied with caution (Gábor et al., 2020). This is because environmental clustering does not necessarily indicate sampling bias - it may instead reflect the species' true niche, which is precisely what we aim to model. Conversely, if observations cluster in environments that lack ecological justification (e.g., near cities, if the species is known to also often occur elsewhere), this may suggest a sampling bias, and environmental filtering could then be appropriate. Ultimately, environmental filtering should not be applied blindly and without evidence (Gábor et al., 2020). The decision is subjective and depends on current ecological knowledge of the species as well as the known or suspected sampling bias in the dataset.

Another concern with SF is that it further reduces the amount of available occurrences, which can be a problem if the data is already limited (Barber et al. 2022). It is known that reducing the number of observations, especially if the amount of environmental layers is larger than the presence records, affects model performance, more so in complex models (Warren & Seifert, 2011). To maximise the performance of spatial filtering, it is important to evaluate the trade-off between sampling bias corrections and the reduction of information (Fourcade et al. 2014). Another potential problem that the authors note is that the clustering of observations is not necessarily always a sampling bias - it might occur because of ecological reasons, for example, population structure.

The effects of SF can depend on the type and intensity of the sampling bias, as well as on the species being modelled, and it is not always the most appropriate method of bias correction (Fourcade et al., 2014). The same way as in background manipulation, SF has more effect in models made for wide-ranging generalist species (Kramer-Schadt et al., 2013).

SF can also improve the model in ways that might not be clearly detectable by metrics or visual evaluations. Most studies aim to improve and assess model generalisation (*vispārināšanās spēja*), with k -fold cross-validation being the most common approach. In k -fold cross-validation, the presence data are divided into k subsets (folds). For each iteration, the model is trained on $k-1$ folds and evaluated on the remaining fold. This procedure is repeated k times so that each fold serves once as the test set and $k-1$ times as part of the training set (Guisan et al., 2017). In addition, some studies use an independent test dataset for more robust model evaluation, applied only after model training. Ideally, this independent dataset is completely separate from the data used in cross-validation, but in practice, it is often just a subset of the original presence records. If a sampling bias is present, the independent test set will typically be affected by the same bias, which can artificially inflate performance metrics. The spatial aggregations of observations can cause autocorrelation in model residuals. To mitigate these effects, it has been recommended to remove spatial clusters of occurrence localities, which is precisely the goal of SF (Veloz, 2009).

Model evaluation and the choice of bias control method

It is important to note that there is no universal best method for every situation. Authors advise to first evaluate the bias type and intensity to choose a method, or to simply apply several correction methods and evaluate the results (Fourcade et al., 2014). Even if the available information about sampling effort is vague and indirect, a justified inclusion results in a better model, especially regarding the predictions in a new environment (Boria et al., 2014; Kramer-Schadt et al., 2013).

AUC is the statistic most commonly used to evaluate model performance in SDMs. It is originally intended to classify presences versus absences, but in MaxEnt the statistic is actually classifying presences versus background points (Yackulic et. al., 2013). Therefore, the value can essentially be interpreted as the probability that a randomly chosen presence location ranks higher than a background point (Merow et. al., 2013). Naturally, we can infer that providing the model with randomly selected background points (i.e., environments that were not sampled, but for which we have no information about the species' occurrence) in cases when sampling bias is present will inflate the AUC, as having background points in unsampled environments makes the model better at classifying presences versus background points. Consequently, employing the TG approach can

cause the prediction strength to decrease (Phillips et al., 2009). Moreover, if the detection probability is variable across sites, the AUC is effectively classifying detections versus background points, which means it reflects how well the model predicts observed records rather than the species' true distribution (Yackulic et al., 2013). The reduction of AUC values after sampling bias correction implementation has been shown in other studies (e.g., Fourcade et al., 2014) as well as in the examples with the two bee species (Table 1) and can lead to wrong inferences regarding the performance of bias-corrected SDMs. In addition, it is known that the same models can produce different AUC values depending on factors like species prevalence, spatial scale, and cross-validation strategy (Abrego and Ovaskainen, 2023). This leads to the conclusion that AUC and other evaluation metric values should not be used as the only means of model evaluation, as a higher AUC value does not necessarily mean that the model is more ecologically accurate.

Table 1. Model-independent test describing metrics. AUC – Area under the operator receiving Curve, TSS – True skill statistic. Mod1 – no bias control; mod2 – spatial filtering; mod3 – spatial filtering + bee-specific bias layer; mod4 - spatial filtering + species-specific bias layer.

	<i>Andrena hattorfiana</i>		<i>Dasypoda hirtipes</i>	
	AUC	TSS	AUC	TSS
Mod1	0.896	0.711	0.904	0.740
Mod2	0.863	0.771	0.863	0.575
Mod3	0.860	0.718	0.711	0.344
Mod4	0.872	0.748	0.708	0.333

In addition to metrics such as AUC and TSS, visual evaluations can also provide useful information, which includes both the response curves and model projections (Fourcade et al., 2014). It is important to note that, even though metrics can be misleading, visual evaluations should be paired with metrics and a general context of the modeling procedure so readers can accurately evaluate the modeled relationships (Yackulic et al., 2013). Unfortunately, thorough evaluations are rarely provided in SDM studies, as most researchers only focus on a particular aspect or do not provide enough information so that the study is reproducible (Yackulic et al., 2013).

The importance of making choices informed by combining various evaluations is illustrated in Figs 3 and 4. *Dasypoda hirtipes* is a bee species that digs nests in soil in areas of sparse vegetation. Therefore, it also inhabits anthropogenic sites, such as roadsides and quarries. Mod2 has been created with observation filtering as the bias control method (Fig. 3). The projected habitat suitability clearly highlights some cities as one of the most suitable habitats. Given our knowledge of the species' ecology and the fact that most observations come from a citizen science website, it is reasonable to assume that the resulting maps do not represent the true species distribution. It is likely that the information we provide to the model by using the observations available mostly just shows where the species occurs in the space that is easily sampled, i.e., cities and roads, but does not necessarily the niche of the species, and the employment of spatial filtering does not compensate for this, so the chosen sampling bias control method is not very helpful in this case. In mod4 (Fig. 4), observation filtering is paired with a species-specific sampling bias layer, and the projections of this model do not show high suitability area clustering around cities. This is because the sampling bias layer helped to identify the environments with a higher sampling intensity (likely variables linked to cities), so the effect was removed. Clustering of higher suitability habitats around cities is also often observed in biased models, which is usually resolved by the application of bias correction methods (Barber et al., 2022).

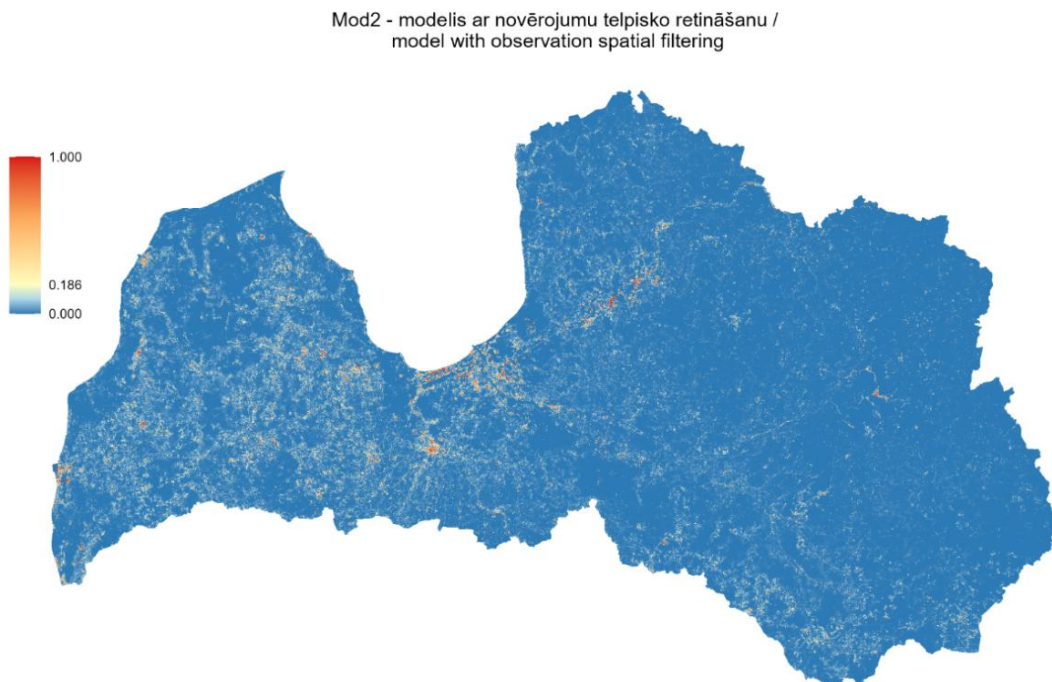


Fig. 3. Model projection for *D. hirtipes* model with observation spatial filtering (mod2).

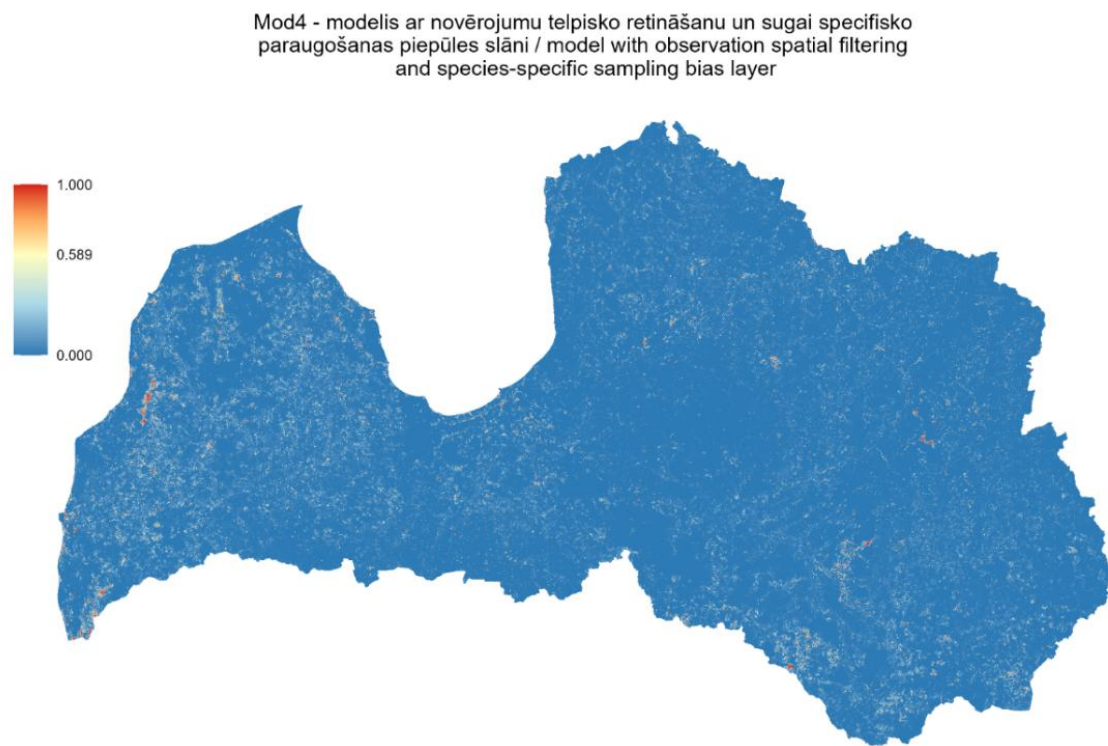


Fig. 4. Model projection for *D. hirtipes* model with observation spatial filtering and species-specific sampling bias layer (mod4).

Background point amount

In order to adequately reflect information about the environment in the study region, a decision must be made regarding how many background points should be sampled. More background points make it more likely that the environment will be well represented; however, increasing the number of points requires more computational power to run the models.

There are no strict guidelines for how many background points should be selected. It seems that in general, the amount of 10 000 points has been accepted, which is also the default setting in the MaxEnt software. It has been shown before that increasing the amount over 10 000 does not significantly improve the performance of a model (Phillips and Dudik 2008). However, it has to be kept in mind that bioclimatic variables are the most commonly used predictor type in the models (e.g., Boria et al. 2014, Ranc et al. 2016). These are only sometimes supplemented with

topographic variables and occasionally with land use variables (Valavi et al. 2022) or remotely sensed vegetation structure data, such as Normalized Difference Vegetation Index (NDVI, Fourcade, 2014). By nature, bioclimatic variables have higher autocorrelation and relatively smooth spatial gradients, and therefore 10 000 background points, as recommended by Phillips and Dudik (2008), are usually enough to represent all the gradients in the environment (or sampled space, if a bias layer or other restriction methods are used).

MaxEnt models built on variables that describe habitats rather than climate have a few important differences. Firstly, habitat-describing variables are typically more heterogeneous and can vary sharply over small spatial scales. Secondly, to informatively capture habitat structure, more variables are often required, which in turn increases the dimensionality of the predictor space and the number of possible environmental combinations. This all leads to the insight that, in habitat-based models, a larger number of background points may be necessary to represent the environmental conditions adequately. Therefore, increasing the background sample size helps stabilize model estimates and better represent fine-scale habitat variation. For these reasons, several authors recommend using substantially more background points, even up to 50 000 (e.g., Valavi et al. 2022) when modelling species distributions with complex habitat variables, especially when high-resolution raster layers or many predictors are involved. Ultimately, the optimal number of background points depends on the spatial resolution, heterogeneity, and extent of the study region, and should be assessed in combination with model performance and computational cost.

In addition, it is important to consider the available number of presence locations. In general, model performance greatly decreases when the number of presences falls below 30 (Guisan et al. 2017), although the exact threshold can vary depending on the number and type of variables used. When many predictors are included, each presence record contributes proportionally less information to the estimation of the species' environmental niche, which can increase the risk of overfitting and unstable parameter estimates. Conversely, with fewer broader-scale variables, even relatively small sample sizes may still provide enough information. One small-scale study found that models with many land use variables were only selected as best in cases when more than 150 presence points were available (Ficetola et al. 2014). This interaction between sample size and predictor complexity means that models with limited presence data must be built more cautiously.

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