# Uncertainty in blacklisting potential Pacific plant invaders using species distribution models

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## Abstract

1. Invasive alien species pose a growing threat to global biodiversity, necessitating evidence-based prevention measures. Species distribution models (SDMs) are a useful tool for quantifying the potential distribution of alien species in non-native areas and deriving blacklists based on establishment risk. Yet, uncertainties due to different modelling decisions may affect predictive accuracy and the robustness of such blacklists. We thus aim to assess the relevance of three distinct sources of uncertainty in SDM-based blacklists: species data, environmental data and SDM algorithms.
2. Focusing on 82 of the most invasive plant species on the Hawaiian Islands, we built SDMs to quantify their establishment potential in the Pacific region. We considered two different species datasets (native vs. global occurrences), two environmental predictor sets (climatic vs. edapho-climatic), and four different SDM algorithms. Based on SDM predictions, we derived blacklists using three distinct blacklisting definitions and quantified the variance in blacklist rankings associated with each source of uncertainty.
3. On average, SDMs showed fair predictive performance. SDM algorithm choice resulted in the largest variation in blacklist ranks while the relevance of species and environmental data was lower and varied across blacklist definitions. Nevertheless, using only native occurrences led to a clear underestimation of the establishment potential for certain species and to lower predictive performance, including high-ranking species on blacklists.
4. SDMs can serve as a robust decision support tool to plan preventive management strategies. To establish robust model-aided blacklists, we recommend ensemble models using multiple SDM algorithms that rely on global rather than native occurrences only. The relevance of environmental predictors additional to climate should be carefully considered and weighed against spatial coverage of those data to ensure sufficiently large sample sizes and predictive accuracy. We advocate for explicit

assessment of uncertainty to increase confidence in blacklists and allow more reliable decision-making.

**Keywords**

Blacklisting, ecological niche, ensemble predictions, habitat suitability models, islands, plant invasions, uncertainty

## Introduction

Invasive alien species have been identified as a major direct driver of native biodiversity loss on a global scale, and a threat to human health and ecosystem services (IPBES, 2023; Pyšek et al., 2020). The magnitude of these impacts is predicted to increase rapidly, as the breakdown of biogeographic barriers continues to be facilitated by the worldwide expansion of trade and transport (Seebens et al., 2021). To slow down the accumulation of alien species, evidence-based efforts in implementing effective management strategies, specifically targeting the prevention of biological invasions, are urgently needed (Seebens et al., 2017; Simberloff et al., 2013). In light of limited resources, such as financial and time constraints, priority-setting is key for planning adequate prevention measures and maximising expected conservation benefits (Bellard et al., 2017; Ziller et al., 2020). For this purpose, blacklists have proven to be an effective policy tool to regulate introductions by providing a ranked priority list of alien species that pose a high risk of becoming naturalised and invasive (Cerri et al., 2022; Ziller et al., 2020). Importantly, such blacklists should rely on objectively quantified invasion risks of species to serve as a robust decision tool (Gallien et al., 2019; Pili et al., 2024).

Correlative species distribution models (SDMs) have become a widely used decision-support tool for risk analysis (Li & Wang, 2013; Peterson et al., 2011). These models statistically relate observed species

occurrences or abundances to current environmental conditions and can be used to predict a species' potential distribution in non-native areas. SDMs are comparably easy to use as they have low data requirements and the availability of such data is constantly increasing (Wüest et al., 2020). However, if SDMs are to serve as a decision-support tool, a thorough analysis of uncertainties related to methodological and fundamental limitations is essential (Barbet-Massin et al., 2018; Buisson et al., 2010; Sittaro et al., 2023). Several previous papers have studied the uncertainty of different SDM algorithms that can lead to large variations in spatial and temporal predictions and is of particular concern for making predictions under global change scenarios (Buisson et al., 2010; Thuiller et al., 2019). To overcome this challenge and enhance the robustness of species distribution predictions, the use of an ensemble modelling approach was proposed, i.e., considering multiple algorithms and capturing the range of predictions that emerge from model uncertainty (Araujo & New, 2007). Strictly, however, ensemble models should also consider other sources of uncertainty, such as those related to the choice of input data. Yet, the sensitivity of prediction outcomes to species and environmental input data have received comparably less attention, although these could be of particular relevance when modelling distributions of potentially invasive species (Beaumont et al., 2009).

The choice of species input data is non-trivial for alien species. SDMs are usually calibrated on native species occurrences, which represent their realised ecological niche (Beaumont et al., 2009; Gallien et al., 2010). However, alien species require a more differentiated consideration of their realised niche. While a species' realised niche reflects the environmental (abiotic and biotic) conditions within its geographical range of current occurrences, evidence suggests that different realised niches could emerge when a species is introduced to a new geographical area (Arlé et al., 2024; Guisan et al., 2014). Possible reasons are associated with changes in the abiotic and biotic conditions promoting release from biotic constraints, changes in biotic interactions, or rapid genetic adaptation (Gallien et al., 2010; Guisan et al., 2014). These differences between native and non-native regions can ultimately lead to distinct realised

104 niches, violating the underlying key assumption of niche conservatism in SDM applications (Barbet-Massin
105 et al., 2018). The reduced model transferability when extrapolating into new regions can therefore result
106 in an underestimation of the species' naturalisation or invasion potential (Beaumont et al., 2009). To
107 address this issue, it has been suggested to include all available species occurrences from native and non-
108 native areas together, to provide a more comprehensive estimation of the realised niche (Beaumont et
109 al., 2009; Gallien et al., 2012; Liu et al., 2022). Of course, the use of global data is only possible if substantive
110 numbers of non-native occurrences have been recorded.

111 Another source of uncertainty is selecting environmental input data to serve as meaningful
112 predictor variables. Environmental predictors should aim to capture the ecological requirements of a
113 species to ensure a high quality of predictions (Descombes et al., 2020). Climate predictors are widely used
114 to determine species distributions, presumably due to their recognised role as a primary driver and the
115 high availability of digital data (Guisan et al., 2017). But particularly for plants, the complementary
116 consideration of soil properties in SDMs, such as soil pH and nitrogen content can significantly improve
117 prediction quality (Dubuis et al., 2013), suggesting that these could also be of relevance for predicting
118 non-native plant distributions (Lázaro-Lobo et al., 2021; Sittaro et al., 2023). Although these sources of
119 uncertainty (algorithm choice, species data, environmental data) have been studied separately, their
120 relative importance for deriving blacklists of potentially invasive species has not been evaluated yet.

121 To better understand the uncertainties linked with SDMs and their implications for blacklisting
122 potentially invasive species, the Pacific region represents an ideal study system. The Pacific Islands have
123 rich biodiversity and high levels of endemism that are highly threatened by biological invasions. Compared
124 to other regions of the world, the Pacific region demonstrates the steepest regional relationship between
125 alien plant species and area meaning that the fastest increase in alien plant species worldwide is found on
126 the Pacific islands (van Kleunen et al., 2015). The Hawaiian Islands, in particular, are exceptionally invaded,
127 with nearly as many alien as there are native plant species. However, at this time, a large majority of the

128 Pacific alien plant species are still spatially restricted to a few island groups (Wohlwend et al., 2021),
129 suggesting that the adverse effects of biological invasions to much of the Pacific can be tackled by
130 implementing preventive measures such as blacklists. Additionally, most of the Pacific alien plant species
131 have also naturalized elsewhere in the world, making them a particularly useful study system to test the
132 effects of species input data vis-à-vis environmental data and algorithm choice on prediction and
133 blacklisting uncertainty.

134 Here, we aim to construct Pacific-wide blacklists based on SDMs while explicitly considering
135 uncertainty introduced by different species input data, environmental input data, and SDM algorithms.
136 We focus on 82 of the most invasive species present on the Hawaiian Islands according to the PIER
137 database (Pacific Island Ecosystems at Risk; http://www.hear.org/pier/), which could potentially spread to
138 other Pacific island groups. Our study objectives were threefold: 1) to quantify the relative importance of
139 the uncertainty factors on the blacklist ranking, considering differences in species data (native vs. global
140 occurrences), environmental data (climatic vs. edapho-climatic predictors), and SDM algorithm
141 (regression-based and machine-learning), 2) to analyse variation in uncertainty between three different
142 blacklist definitions, and 3) to analyse resulting differences in predictions of unrealised colonisation
143 potential.

## 144 Methods

145 The general workflow involves fitting SDMs on opportunistic species occurrence data that
146 represent the native or global niches of these species, using different sets of environmental predictors and
147 SDM algorithms, in line with current best practice standards (Araújo et al., 2019). From the predicted
148 habitat suitability maps, we derived blacklists using three approaches. Additionally, we compared our
149 predictions to independent data on species occurrence at the island group level. Following the ODMAP
150 protocol (Zurell, Franklin, et al., 2020), we detail all data preparation and modelling steps in Supplementary
151 Material C.

## *Species and environmental data*

### *Species data*

We focused on an initial subset of the 122 most invasive plant species, occurring on at least one of the Hawaiian Islands, whose invasive status is recognised by the PIER database. The well-established commercial ties with much of the Pacific suggest that these species might spread to other Pacific Islands. The initial subset was derived from Wohlwend et al. (2021), containing information on the presence of non-native species on the different Pacific island groups. This dataset encompassed 50 island groups, defined both by political and geographic borders. These groups included islands located from 40°N to 40°S, ranging in size from 1 km² to 66,141 km². The delineation of the studied Pacific region was primarily based on biogeographic factors, as specific island features, such as geographic isolation and size, contribute to a particular vulnerability to the non-native establishment (Reaser et al., 2007). Therefore, we did not consider large archipelagos such as New Zealand, Japan, the Philippines, Indonesia, and Papua New Guinea along, nor small islands located near the American and Australian Pacific coasts, nor islands belonging to Japan and South East Asia west of Bonin/Palau. The presence of non-native species at the island group level, as documented by Wohlwend et al. (2021), also served as independent test data for our blacklist predictions. For training SDMs, we additionally required spatially-explicit occurrence data and thus derived two different species datasets: one containing only native occurrences and another containing both native and introduced (i.e., global) occurrences. These data were obtained from two databases, GBIF (Global Biodiversity Information Facility; https://www.gbif.org/) and BIEN (Botanical Information and Ecology Network; https://bien.nceas.ucsb.edu/bien/). We cleaned the coordinates by excluding occurrences with erroneous time stamps and coordinates (Zizka et al., 2019) and removed duplicate records within 1 km² cells for each species to obtain a target spatial resolution of 1 km.

To compare SDMs fitted with native or global species data, we determined the biogeographical status of plant occurrences as native or introduced. We therefore consulted the following sources: the

176 World Checklist of Vascular Plants (WCVP, https://powo.science.kew.org) at the base resolution of tdwg
177 level 3 (Brummitt, 2001), the Global Inventory of Floras and Traits (GIFT; Weigelt et al., 2020), and the
178 Global Naturalized Alien Flora (GloNAF; https://glonaf.org). The final biogeographical status was
179 determined by merging the assignment information of all three sources. In the simplest case, all available
180 source information agreed on the native or introduced status of each occurrence. When sources provided
181 conflicting status assignments but referred to areas of different sizes, we assigned the status from the
182 source referring to the smaller area. If an occurrence with conflicting sources referred to the same area
183 size, we classified it as having a contradictory status. Overall, our final status assignments classified species
184 occurrences as native, introduced, contradictory, or unknown.

185 Because our resulting species occurrence data only contained presence data but most SDM
186 algorithms require background data to identify areas with unsuitable environmental conditions, we
187 derived pseudo-absences or background data for all study species (Barbet-Massin et al., 2012). For this,
188 we randomly selected background points within a buffer distance of 200 km from the presences while
189 excluding the presence locations. We chose this buffer distance to account for the dispersal limitations of
190 species. Following previous recommendations (Barbet-Massin et al., 2012), we used a
191 presence-background ratio of 1:10 for the regression-based SDM algorithms and 1:1 for machine-learning
192 algorithms. Lastly, to avoid spatial autocorrelation, all presences and background data of the species were
193 thinned using a 3 km threshold (Aiello-Lammens et al., 2015).

194 For the final species selection, we set a lower limit of 40 native occurrences per species to avoid
195 overfitting for species with a low sampling effort (Breiner et al., 2015). An additional criterion tested for a
196 minimum difference of 40 between native and global occurrences to ensure the consideration of two
197 different niches in the species input data. Species that, contrary to the information from Wohlwend et al.
198 (2021), showed native records on the Hawaiian Islands, were also excluded. The species selection process
199 resulted in a final list of 82 species that were considered in further analyses (Supplementary B Table S1).

*Environmental data*

Similar to the species data, we built two different predictor datasets, one containing only climatic data and one containing climatic and edaphic data. These environmental predictor variables were obtained at a resolution of 1 km, matching the species data. Climate predictor variables were acquired from CHELSA (Climatologies at High Resolution for the Earth Land Surface Areas; version 2.1; Karger et al., 2017, 2018), including 15 bioclimatic variables. We excluded bioclimatic variables that combine temperature and precipitation data to avoid artefacts leading to discontinuities in interpolated surfaces (Booth, 2022). A set of 14 edaphic variables was obtained from SoilGrids (https://www.soilgrids.org), containing soil physical and chemical properties as well as soil water contents at different pressure heads (version 2.0). The soil property maps were downloaded for three standard depth intervals from the surface to a depth of 30 cm and were afterwards averaged over these depths (Descombes et al., 2020). The spatial coverage of the edaphic data was lower than that of the climate data, which mostly affected the maps of predicted occurrence probabilities. This lower spatial coverage was mainly attributable to urban areas and water surfaces. For predictions, we only included island groups with a representative spatial data coverage of ≥ 50 % for all variables. The island group of Tuvalu was not considered in any predictions due to its small size relative to the 1 km resolution used. Hence, we made predictions based on purely climatic data for 49 Pacific island groups, and predictions incorporating both predictor variable types for 25 island groups (Fig. 1; Supplementary B Table S2).

In accordance with our study objectives, the two types of species data (native vs. global occurrences) were intersected with the two types of environmental data (climatic vs. edapho-climatic predictors) resulting in four input datasets: 'natclim', which describes the combination of the native niche and purely climatic data, 'natclim+eda', which considers the native niche and edaphoclimatic data, and 'globclim' and 'globclim+eda', which describe the analogous input datasets regarding the global niche (Supplementary A Fig. S1).

*Species distribution models*

For each of the four SDM input datasets per species, the four most important and weakly correlated predictor variables were identified prior to model building. To achieve this, we identified highly correlated pairs of variables with Spearman correlations $|r| > 0.7$ and only retained the most important variable (Dormann et al., 2013). Variable importance was determined using univariate generalised linear models (GLM) and a 5-fold cross-validation approach (Zurell, Zimmermann, et al., 2020). The univariate GLMs were fitted with binomial error distribution and second-order polynomials, and with equal weight given to the sum of presences and background data. We then assessed the univariate predictive performance for each variable by cross-validation using the Boyce index (Hirzel et al., 2006). For SDMs that used both types of predictor variables, the two climatic and two edaphic variables that were ranked most important in the list of weakly correlated predictors were considered for model building (Supplementary B Table S3).

SDMs were fitted using four different statistical algorithms with intermediate model complexity: GLM, generalised additive models (GAM), random forest (RF) and boosted regression trees (BRT). GLMs were estimated with linear and quadratic terms and GAMs were estimated with non-parametric cubic smoothing splines with up to four degrees of freedom. RF models were fitted with 1,000 trees and a minimum node size of 20. Finally, we fitted BRTs using a tree complexity of 2 and a bag fraction of 75 % and optimised the learning rate to obtain tree numbers between 1,000 and 5,000 (Elith et al., 2008). For the regression-based methods (GLM, GAM), we used all background data with a presence-background ratio of 1:10 and presences and background were equally weighted in model building. For the machine-learning methods (RF, BRT), we used ten replicate sets of background data in a ratio of 1:1 to the presences, resulting in 10 models each that were subsequently averaged (Barbet-Massin et al., 2012; Dullinger et al., 2017).

247 For all models, SDM performance was evaluated using a 5-fold cross-validation by computing the
248 area under the receiver operating characteristic curve (AUC), true skill statistic (TSS), sensitivity, specificity,
249 and the Boyce index. A model would be judged to have fair predictive performance of AUC > 0.7 and TSS
250 > 0.5 (Guisan et al., 2017). Since the threshold-dependent performance measures TSS, sensitivity and
251 specificity require binary predictions, the threshold that maximises the sum of sensitivity and specificity
252 was applied (maxSSS; Liu et al., 2013). Cross-validated predictions for models based on regression methods
253 used prior defined equal weights of the sum of presences and background, while for machine-learning
254 algorithms SDM performance in cross-validation was averaged over the ten replicate models (Barbet-
255 Massin et al., 2012; Dullinger et al., 2017). Ensemble models were constructed using the arithmetic mean.
256 The ensemble model performance was assessed based on the averaged cross-validated model predictions
257 of all algorithms using the same input dataset. To guarantee equal contributions of the four considered
258 model algorithms, the cross-validated predictions derived from the ten models of each machine-learning
259 algorithm were averaged beforehand (Dullinger et al., 2017).

260 *Blacklisting*

261 We predicted occurrence probabilities and binary predictions of the potential presence and
262 absence of all study species using the same procedure described above. Predicted presences were
263 interpreted as indicating environmental conditions that define suitable habitats for the species. Based on
264 these predictions we constructed blacklists to identify species with the highest potential for establishment
265 across the Pacific. We used three different definitions for blacklists (Supplementary A Fig. S1): First, the
266 total suitable habitat fraction across the Pacific region considered the establishment potential across the
267 entire Pacific region independent of individual island group sizes. It was derived by summing up the
268 predicted suitable area across island groups and dividing it by the total area of all island groups. Then,
269 species were ranked according to their total predicted suitable habitat fraction, with the species with the
270 highest habitat fraction receiving rank 1. Second, the blacklist based on the mean suitable habitat fraction

271 across all Pacific island groups puts more emphasis on local establishment risk, highlighting the variability
272 of establishment risk on different island groups. It was calculated by dividing the predicted suitable area
273 per island group by the area of that island group and then averaging the suitable area fractions across all
274 island groups. Species were then ranked according to their mean habitat fraction across all island groups,
275 with the species with the highest mean fraction receiving rank 1. Third, the blacklist based on the number
276 of island groups with suitable habitats does not consider habitat fraction per island group but simply uses
277 a binary measure of whether suitable habitat is or is not found within an island group. An island group is
278 considered to be potentially suitable if the fraction of potentially suitable habitat is greater than 0. Species
279 were then ranked according to the number of island groups where they could establish. If species were
280 predicted to have suitable habitats on the same number of island groups (regardless of their suitable
281 habitat fraction on those island groups), they received the same rank. All blacklist definitions relied on the
282 quantified absolute area of predicted suitable habitat in $km^2$ and the total area covered by data in $km^2$ at
283 the island group level. For subsequent uncertainty analyses, we separately constructed a blacklist for each
284 combination of species input data, environmental input data and SDM algorithm. Additionally, we derived
285 final blacklists with ensembles of SDM algorithms, to highlight how the choice of input data and blacklisting
286 procedure would affect practical decision-making.

287 Generally, the area of suitable habitat and area of island groups were calculated based on rasters
288 with 1 km resolution. Thus, the calculated areas partly deviated from the true sizes of island groups,
289 particularly those composed of numerous small-sized or thinly-shaped islands. Regarding the area of island
290 groups, we considered the area covered by data instead of true island group sizes, as island groups with a
291 data coverage of ≥ 50 % were included in SDM predictions. Due to differences in the spatial coverage of
292 the environmental predictor datasets, resulting in differing numbers of considered island groups
293 depending on the predictor type used, the ranking could only be compared when considering the same
294 island groups. Thus, all final blacklist rankings were based on the 25 Pacific island groups covered by both

295 predictor variable types (climatic and edaphic). Additionally, as a sensitivity analysis, we generated
296 blacklists using purely climatic data considering prediction results for all 49 island groups covered by
297 climatic data. This allowed for a more extensive analysis in terms of included island groups but did not
298 allow us to assess environmental input data as a source of uncertainty in the resulting blacklists.

299 *Uncertainty analysis*

300 We quantified three relevant sources of uncertainty in blacklisting potentially invasive species
301 using SDMs: the species input data (native vs. global occurrences), the environmental input data (climatic
302 vs. edapho-climatic predictors), and SDM algorithms (GLM, GAM, RF, BRT). To quantify the relative
303 importance of these uncertainties for blacklisting, we used a random forest approach to relate blacklist
304 ranks to categorical variables representing the choice of input data and algorithms (Liaw & Wiener, 2002).
305 Sources of uncertainty were quantified separately for each blacklist definition. Finally, we estimated the
306 importance of each uncertainty factor, measured as the mean decrease in model accuracy when
307 randomising the variables, which we normalised to add up to 100 %.

308 *Unrealised colonisation potential*

309 Finally, we quantified the potential for the species to establish on island groups beyond their
310 current non-native range and how these predictions varied across input datasets. For this, we calculated
311 the Pacific-wide predicted unrealised colonisation potential per species and input dataset using ensembles
312 of SDM algorithms. Colonisation potential was defined as the False Positive Rate per island group (FPR =
313 FP/(FP+TN)), which compares how many island groups that are hitherto unoccupied by a species would
314 provide suitable habitat for that species. Reported presences at island group levels were taken from the
315 independent dataset gathered by Wohlwend et al. (2021) (Supplementary B Table S4). A predicted
316 presence on an island group was considered if the suitable habitat fraction was greater than zero. If a non-
317 native species was unreported on an island group (absence) in the independent dataset but the model

predicted a presence, then this prediction was considered a False Positive (FP), whereas non-native species that were neither reported nor predicted to occur were classified as True Negative (TN). In a final step, the FPR over all island groups was calculated for each study species. FPR ranges between 0 and 1, with 1 indicating that all island groups are unoccupied although providing suitable habitat, and 0 implying that none of the unoccupied island groups is predicted to provide suitable habitat for the studied species. In our main analyses, we considered the 25 island groups for which climatic and edaphic data availability allowed a comprehensive uncertainty assessment but also repeated the analyses for the 49 island groups for which only climatic data were available.

For all analyses and visualisations, R 4.3.1 (R Core Team, 2023) was used, along with the following packages: *terra* (Hijmans, 2023), *tidyverse* (Wickham et al., 2019), *sf* (Pebesma & Bivand, 2023), *sfheaders* (Cooley, 2023), *ecospat* (Broennimann et al., 2023), *mgcv* (Wood et al., 2016), *randomForest* (Liaw & Wiener, 2002), *dismo* (Hijmans et al., 2023), *PresenceAbsence* (Freeman & Moisen, 2008), *gbm* (Greenwell et al., 2022), *viridis* (Garnier et al., 2023) *maps* (Becker et al., 2022) and *ggplot2* (Wickham, 2016).

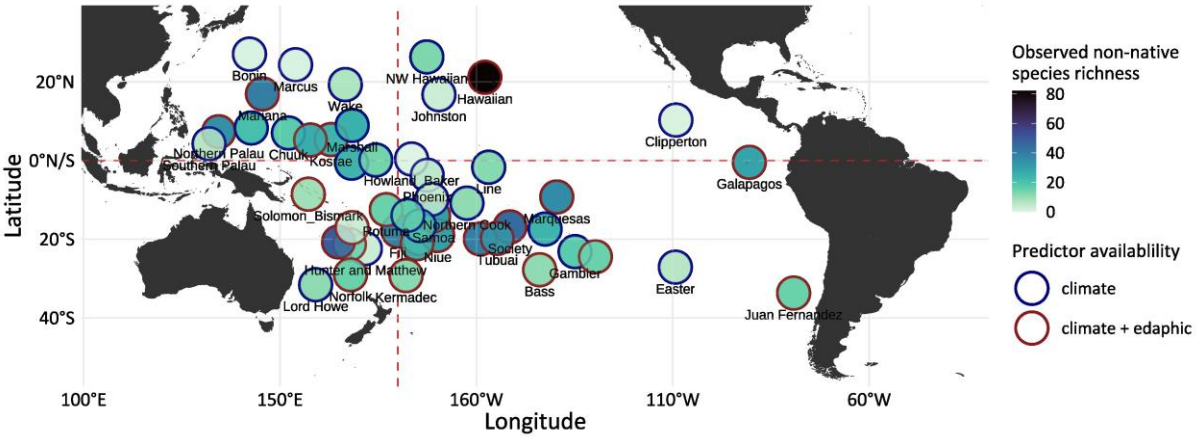


**Figure 1: Study region.** The location of Pacific island groups included in the study, each represented by a circle for easier visualisation. The circle shading shows the observed non-native species richness per island group, considering all studied non-native plant species (n = 82). Additionally, the availability of climatic and edaphic predictor variables per island group is indicated by the border colour, with a predictor type considered available if a representative spatial data coverage of ≥ 50 % per island group was achieved. Due to space limitations, not all island group labels are displayed. The circles are positioned at the central coordinates of each island group. The red dashed lines represent the equator (horizontal line) and the prime meridian (vertical line).

## Results

### *Model performance*

The predictive performance of the SDMs varied considerably among the species studied, ranging from poor to excellent. However, on average, fair performance scores over all models were achieved (TSS, mean ± SD: 0.55 ± 0.14; Boyce, mean ± SD: 0.93 ± 0.09; AUC, mean ± SD: 0.84 ± 0.07; Fig. 2; Supplementary A Fig. S2; for detailed information on model performance see Supplementary B Table S5).

Predictive performance also varied across SDM algorithms, with models based on the RF algorithm generally outperforming those based on the GLM, GAM, and BRT algorithms. This is demonstrated by an average TSS value of 0.7 ± 0.06 for all RF models, whereas average TSS scores of models based on the other algorithms were lower, ranging from 0.47 ± 0.12 to 0.52 ± 0.12 (Fig. 2a). Similarly, RF models achieved an average Boyce index value of 0.98 ± 0.04 which was considerably higher than those achieved by the other algorithms (GLM, mean ± SD: 0.92 ± 0.1; GAM, mean ± SD: 0.93 ± 0.09; BRT: mean ± SD: 0.86 ± 0.12; Fig.

2b). Ensemble models generally achieved fair performance accuracies (TSS, mean ± SD: 0.58 ± 0.09; Boyce, mean ± SD: 0.97 ± 0.05; AUC, mean ± SD: 0.87 ± 0.04; Fig. 2; Supplementary A Fig. S2).

Overall, the use of different input datasets resulted in smaller differences in predictive performance than the choice of SDM algorithm (Fig. 2; Supplementary A Fig. S2). Still, all models, including ensembles, achieved slightly higher model performances when trained on global rather than native occurrences. Also, the Boyce index showed markedly better model performances when considering global occurrences instead of native occurrences, with average values of 0.95 ± 0.07 and 0.90 ± 0.12 respectively (Fig. 2b).

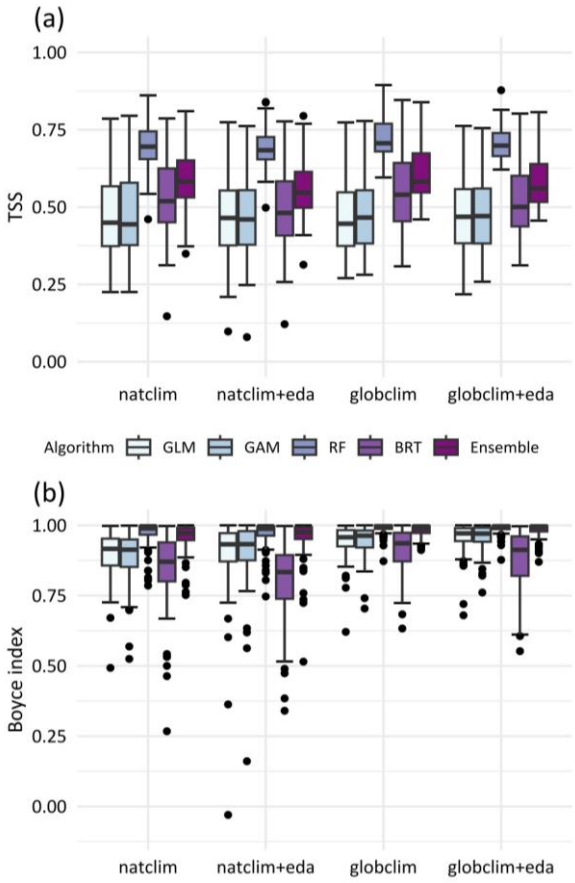


**Figure 2: Model validation in terms of TSS (True skill statistic) and Boyce index.** For all studied non-native plant species (n = 82), the range of performance measures for the four applied model algorithms and the averaged ensemble model along the four different input datasets are displayed as boxplots (a-b). Models were validated using 5-fold cross-validation. (GLM: generalised linear model; GAM: generalised additive model; RF: random forest; BRT: boosted regression tree; natclim: models based on native occurrences and climate data; globclim: models based on global occurrences and climate data; eda: models additionally considering edaphic data)

353 *Uncertainty analysis*

354 Using the SDMs, we constructed blacklists based on predictions of suitable habitat on 25 Pacific
355 island groups and assessed differences in blacklist ranking in relation to species input data (native vs. global
356 occurrences), environmental input data (climatic vs. edapho-climatic predictors), SDM algorithm, and
357 blacklist definition. The choice of SDM algorithm was the biggest source of uncertainty (explaining 54.5 %
358 to 88.4 % of the variation in ranking) although the relative importance of uncertainty sources markedly
359 varied across blacklisting definitions (Fig. 3). The set of environmental predictors and species occurrence
360 data demonstrated strongly diverging patterns across the different blacklist definitions. Specifically, the
361 set of environmental predictors only affected the rankings based on the total suitable habitat fraction and
362 the mean suitable habitat fraction with variable importance values of 11.6 % and 20.3 % respectively.
363 Conversely, the type of species data solely affected the blacklist ranking based on the total number of
364 suitable island groups (explaining 45.5 % of the variation in ranking).

365 As a sensitivity analysis, we predicted suitable habitat based on climate-only models for 49 Pacific
366 island groups. The uncertainty patterns identified in this climate-only assessment showed largely similar
367 results as those of the assessment of 25 island groups. When using total habitat fraction or mean habitat
368 fraction for species ranking, the choice of SDM algorithm was most important. Again, species data input
369 only affected the blacklist based on the number of suitable island groups, and its variable importance even
370 surpassed that of algorithm choice (Supplementary A Fig. S3).

371

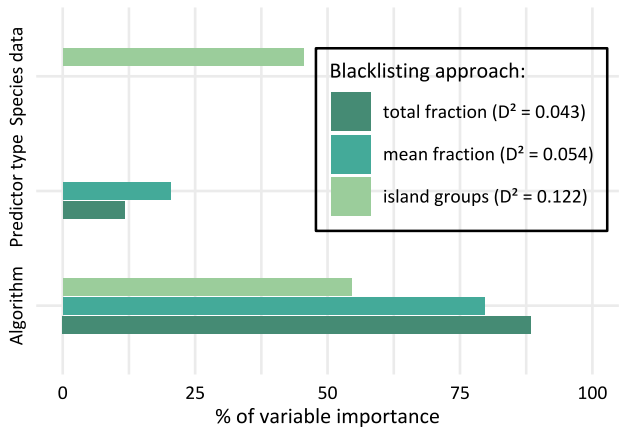


**Figure 3: Quantification of investigated uncertainty sources based on analysis of 25 Pacific island groups**. The bars display the influence in the choice of three different sources of uncertainty on the blacklist ranking outcome: species data (global vs. native occurrences), the environmental data (climatic vs. edapho-climatic predictors), and the SDM algorithm (GLM, GAM, RF, BRT). Variable importance was estimated with a random forest model relating the differences in blacklist ranking to uncertainty factors. The values of variable importance per blacklisting approach were standardised to sum up to 100 %. The explained deviance $D^2$ of the models is noted in the legend. The models include blacklisting results of all studied non-native plant species (n = 82) based on predictions to 25 Pacific island groups covered by climatic as well as edaphic data.

372 *Final blacklisting and unrealised colonisation potential*

373 As SDM algorithms appeared as the most important source of uncertainty, we provide final
374 blacklisting results for the studied species based on ensemble predictions averaging across SDM
375 algorithms. Although the rankings of most species were in close agreement, several species displayed large
376 discrepancies depending on species input data and predictor type (Fig. 4). Ranking positions varied by 13
377 ± 12 (mean ± SD) in blacklists based on the total suitable habitat fraction and by 13 ± 13 (mean ± SD) in
378 blacklists based on the mean suitable habitat fraction. Furthermore, variations of up to 14 positions were
379 found when evaluating blacklist rankings using the number of suitable island groups as the blacklisting
380 approach.

381 Focusing solely on rank order shifts towards leading blacklist positions, the non-native species
382 *Echinochloa esculenta*, *Tecoma stans*, and *Tithonia diversifolia* exhibited the largest ranking differences,
383 exceeding 50 ranks. These shifts were attributable to variations in species data input from native to global
384 occurrences. The same species also showed the highest shifts towards leading blacklist positions in our

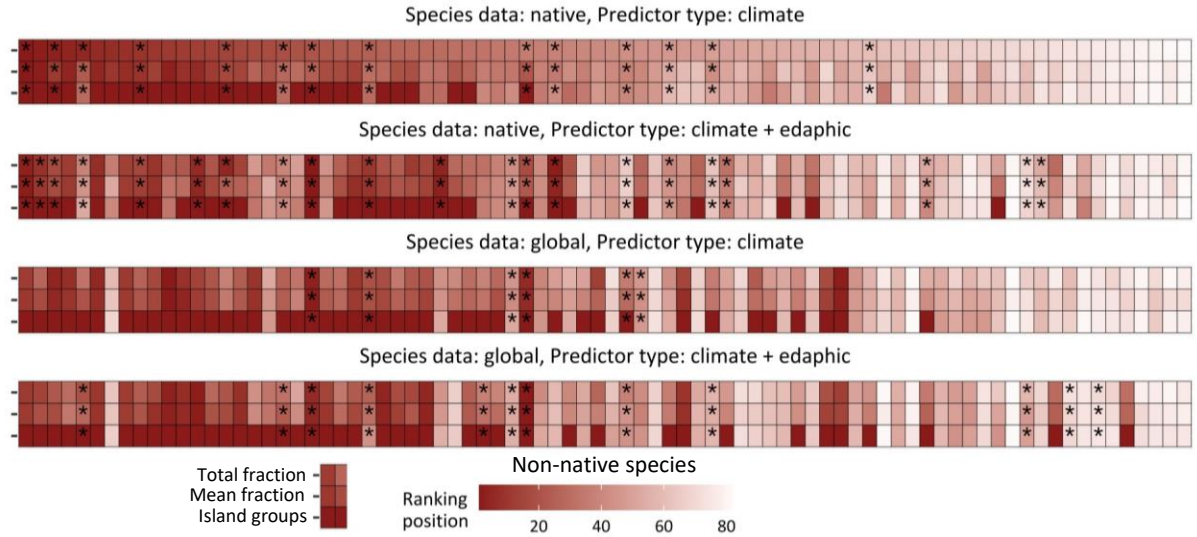


**Figure 4: Final blacklisting based on analysis of 25 Pacific island groups.** The final blacklisting results of all three blacklisting approaches over the four different input datasets are displayed. Final ranking positions are based on the predictions of ensemble models to 25 Pacific island groups covered by climatic and edaphic data. Every non-native plant species (n = 82) is depicted along a vertical line of cells. The horizontal lines of cells per input dataset represent the three blacklisting approaches, with cell colour intensity indicating the ranking position of each study species. To enhance visual (dis)similarities of ranking positions using the number of suitable island groups as a definition, positions were recalculated incorporating gaps equivalent to the number of tied ranks. Predictive performance values of ensemble models below a TSS (True Skill Statistic) score of 0.5 are marked with an asterisk.

sensitivity analyses considering climate-only models and predicting habitat suitability for 49 Pacific island groups (Supplementary A Fig. S4).

Notably, species with leading blacklist positions showed poor predictive performance (TSS < 0.5) when the ensemble models used only native occurrences as species data. This indicates that the choice of species occurrence data can considerably affect model uncertainty and through that confidence in blacklists. Final blacklists based on SDMs fitted with global occurrence data and edaphoclimatic predictors and covering all three approaches to blacklisting are provided in Supplementary B Table S6.

From the ensemble predictions, we also assessed unrealised colonisation potential, i.e., the proportion of the 25 Pacific island groups with suitable habitats that have not yet been colonised by the current Hawaiian non-native species. We found that the choice of species data led to markedly different predictions. With an average of 0.73 ± 0.32, the unrealised colonisation potential was notably lower when only considering native occurrences. In comparison, when global occurrences were considered, the

397 unrealised colonisation potential yielded an average value of 0.79 ± 0.32. The difference between
398 occurrence datasets is largely due to the higher number of island groups that are predicted to harbour
399 suitable habitat for Hawaiian non-native plant species (Fig. 5). This was also true when making predictions
400 to more island groups based on climate-only models (Supplementary A Fig. S5).

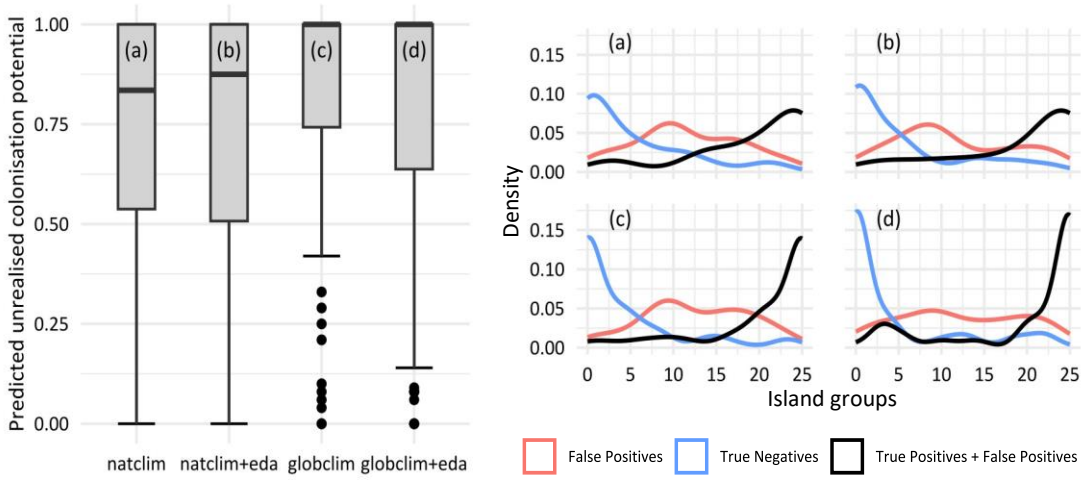


**Figure 5: Predicted Pacific-wide unrealised colonisation potential based on analysis of 25 Pacific island groups.** On the left, the predicted unrealised colonisation potential for all studied non-native plant species (n = 82) is displayed as boxplots, based on the ensemble predictions of 25 Pacific island groups covered by edaphic and climatic data along all four input datasets (a-d; natclim: models based on native occurrences and climate data; globclim: models based on global occurrences and climate data; eda: models additionally considering edaphic data). The predicted unrealised colonisation potential per species represents the False Positive Rate defined as the number of island groups that are hitherto unoccupied by the non-native species but predicted as suitable divided by the total number of island groups where the species is currently absent. On the right, the density of island groups with false positives (predicted but absent; red line), true negatives (blue line), and all predicted presences (black line) is depicted for all study species using the same ensemble predictions (a-d).

401 **Discussion**

402 In this study, we quantified the relative importance of three distinct sources of uncertainty in
403 SDM-based blacklist rankings by studying 82 of the most invasive plant species occurring on the Hawaiian
404 Islands and assessing their establishment potential across the Pacific region. Our insights can serve as
405 guidance for developing robust SDM-based blacklists. As blacklists can be constructed in different ways
406 and depending on the scale of the study, we considered three different approaches to blacklisting

407 potential invasive species by varying the emphasis on regional vs. local habitat suitability. Our results
408 highlight the choice of the SDM algorithm as being the largest source of uncertainty in blacklisting,
409 independent of the blacklist definition. The relevance of species data and environmental data was overall
410 smaller. Yet, when considering only native occurrences in SDMs, models of the top-ranked species on the
411 blacklists had poor predictive performances, which means that they might be overlooked if following
412 accepted modelling standards. Also, SDMs based only on native occurrences predicted lower suitable
413 habitat in the Pacific, potentially resulting in an underestimation of unrealised colonisation potential.
414 Based on the comprehensive uncertainty analyses, we derive recommendations for robust model-aided
415 blacklisting.

416 Our uncertainty analysis identified the choice of the SDM algorithm as the main source of
417 uncertainty in all three approaches to blacklisting potentially invasive plant species, reflecting the known
418 issue of variability in model outputs stemming from different algorithmic choices. Multiple studies have
419 reported such contrasting predictions arising from the use of different SDM algorithms, primarily in the
420 context of climate change predictions (Buisson et al., 2010; Thuiller et al., 2019). Inconsistencies among
421 models may stem from differences in model complexity and flexibility, particularly in the estimated
422 species-environment relationships, which become even more pronounced when extrapolating into new
423 niche spaces (Buisson et al., 2010). While highly complex models often provide a close fit to the observed
424 data, potentially capturing valuable ecological processes, their applicability to new times and places might
425 be limited compared to more simple models (Brun et al., 2020; Merow et al., 2014). Here, we purposefully
426 restricted the model complexity of the more flexible machine-learning algorithms at intermediate levels
427 but still found strong effects of algorithm selection on blacklisting. This emphasises that ensemble SDMs
428 are also needed to provide more robust model predictions and decision support for potentially invasive
429 plant species (Araujo & New, 2007).

The uncertainty stemming from species and environmental data in blacklist ranking was comparably less pronounced. Still, the choice of species occurrence data and environmental predictors affected the amount of habitat predicted to be suitable for the establishment of non-native plant species, which resulted in differences in the predictions of unrealised colonisation potential and some ranking differences on the blacklists. Using global occurrences, as opposed to native occurrences, led to higher predicted numbers of suitable island groups across species and larger areas of predicted suitable habitat. Larger predicted areas of suitable habitat by SDMs considering global occurrences indicate that some of the species may exhibit expansion of the realised niche when considering non-native regions, rather than conserving the realised niche from their native range (Guisan et al., 2014). Previous studies have shown that niche differences between native and non-native ranges and niche expansion are common in invasive plant species (Barbosa et al., 2013; Beaumont et al., 2009; Gallagher et al., 2010). Invasive species have also been used as test cases for assessing the transferability of SDMs and accuracy in predicting ongoing invasions (Barbet-Massin et al., 2018; Jones, 2012). We highlighted some species for which the regional establishment potential was strongly underestimated when only considering native species occurrences. This could indicate niche expansion, e.g., due to competitive release. To verify this assumption, additional analyses would be necessary that specifically compare environmental niche overlap between native and non-native ranges (Gallien et al., 2012; Guisan et al., 2014). It is also important to note that using only native occurrences in SDMs resulted in models with poor predictive performance for some of the top-ranked species on the blacklists. When strictly following the suggested modelling standards (Araújo et al., 2019), these models would not be used for making predictions to new times and places. Therefore, these species might never be blacklisted for a specific region although they may have a high establishment potential.

The selected predictor type had minimal effects on SDM performance and relatively little importance for blacklist uncertainty. This suggests that climate predictors generally capture regional

habitat suitability well. Previous studies found that including edaphic variables improved SDM predictive accuracy and thus play a crucial role in shaping plant distributions (Dubuis et al., 2013). However, these studies fitted SDMs at much finer spatial resolutions and focused on smaller spatial extents, underlining the importance of considering edaphic data when assessing plant habitat suitability more locally. Studies conducted at regional scales support our findings, highlighting climate as the overwhelming driver of plant species distributions (Beauregard & Blois, 2014; Syphard & Franklin, 2009). This demonstrates that small-scale variations of soil properties become less noticeable across broader regions or continents, while climate strongly determines the range margins of plant species distributions. Also, the lower importance of edaphic variables for the study of invasive plant species suggests that successful invaders may be generalists in terms of soil properties. Still, small-scale environmental factors such as pH levels in the soil could limit the establishment of plant species, and their inclusion in SDMs should thus be carefully considered or tested. Additionally, as spatial coverage of environmental predictor variables may vary, we also recommend to explicitly test the effect of data coverage on blacklisting results.

Our approaches to blacklisting potentially invasive plant species were designed to test the sensitivity of blacklists to habitat suitability with varying spatial emphasis. The ranking based on the total suitable habitat fraction reflects a broad, region-wide perspective, while the ranking based on the mean suitable habitat fraction takes a more localised view, highlighting the variability of establishment risk on different island groups. The third blacklisting approach, which considers the number of island groups with suitable habitat, focuses on the presence or absence of suitable habitat, emphasising the potential reach of potentially invasive species regardless of the predicted extent of suitable habitat within each island group. These approaches are not exhaustive of potential blacklist definitions but nevertheless reflect a range of spatial objectives for blacklisting. Our results indicated that different species and environmental input data could lead to large discrepancies in ranking positions for all three blacklisting approaches. However, substantial ranking differences were attributable to only a few species, while the majority of

478 blacklist rankings were robust. This indicates that despite differences in defining establishment risk, similar
479 inferences can be drawn for blacklists. Nevertheless, we recommend that the approach to blacklisting
480 potentially invasive species should be carefully adapted to the management objectives, which may vary
481 depending on the spatial focus.

482 Our analyses show that many non-native species present on the Hawaiian Islands have a high
483 colonisation potential across the Pacific island groups. Blacklists should prioritise species likely to establish
484 (i.e., those identified in this study), that have also proven invasive in Hawaii and are not yet widespread in
485 the Pacific. For instance, the Australian native *Grevillea banksia* is invasive in Hawaii (Simpson et al., 2022)
486 and in other countries, including Madagascar and South Africa. Our results indicate that this species
487 has a high potential to spread from the four island groups it currently occupies to all 25 island groups in
488 the Pacific, making it a critical target for prevention. *Psidium guajava*, originally introduced as a fruit tree
489 in Hawaii, and many other regions, is now recognised as a major pest that aggressively displaces native
490 species worldwide (Richardson & Rejmánek, 2011). In our study, *Psidium guajava* ranks high for all three
491 blacklisting definitions. However, the window for effective prevention of this species may have passed, as
492 it is already established on 22 island groups in the Pacific.

493 *Limitations and perspectives*

494 We highlighted crucial factors contributing to uncertainties in blacklisting potentially invasive
495 species based on SDMs. However, it is important to recognise that various aspects of SDMs can further
496 contribute to uncertainty, as reflected by the low explanatory power of our random forest regression
497 models. For instance, model parameter settings (Guisan et al., 2017), the thresholding approach (Liu et al.,
498 2013), and sample size (Wisz et al., 2008) are additional factors that may affect model accuracy and
499 subsequently lead to variation in spatial predictions. Moreover, potential biases associated with the
500 underlying data could also have influenced the estimation of the species' niches. To reduce such biases,
501 we designed a number of data filtering steps and used several complementary data sources to build a

502 robust framework for obtaining occurrence data and assigning their biogeographical status. Another factor
503 influencing our results could be the limited availability of edaphic data, which substantially reduced our
504 region of predictions (25 instead of 49 island groups). However, we are confident that our results are
505 representative of the Pacific region as our climate-only sensitivity analysis, which included almost twice as
506 many island groups, yielded similar results. In the context of our study objectives, we assessed the
507 establishment potential for all species as equivalent, based on the predicted suitable habitat identified by
508 the fitted SDMs. If such information is available, blacklists could also consider additional factors relevant
509 for establishment potential, for example, trait similarity with native flora (Denslow, 2003) or dominance
510 capacity (Gallien et al., 2019). Another important consideration is the initial selection of species. Here, we
511 focused our initial species selection on the PIER database and extracted all species listed as invasive on the
512 Hawaiian Islands. However, depending on how often such databases are updated, blacklist applications
513 intended to inform preventive measures may need to tap additional information sources to include the
514 most current and comprehensive list of potential invasive species relevant to the region under study.

515 *Conclusions*

516 While using ensembles of SDM algorithms is common and recommended for biodiversity
517 assessments and decision-making (Araújo et al., 2019), the uncertainty associated with the underlying
518 data, i.e., species occurrence and environmental data, is rarely acknowledged or tested, particularly in the
519 context of prediction accuracy and blacklist construction for non-native species. Overall, we recommend
520 using global occurrence data within an ensemble framework to construct robust blacklists for non-native
521 plants. Additionally, the consideration of environmental predictors in addition to climate, e.g., soil data, is
522 recommended but may depend on the spatial coverage of those data. In this regard, our results provide
523 reassurance that pragmatic decisions that prioritise higher data coverage are indeed warranted.
524 Specifically, when the available sample size of global occurrences is already limited and further restricted
525 by low coverage of edaphic data, we recommend fitting climate-only models to yield more reliable

blacklisting results by maximising the species occurrence data. Non-climatic predictors may be more important for determining species distributions at smaller spatial scales, such as identifying suitable habitats on a specific island. Overall, explicitly considering these sources of uncertainty can considerably improve confidence in blacklists and the reliability of model-aided management decisions.

**Author contributions:**

Valén Holle and Damaris Zurell conceived the ideas and designed the methodology; Valén Holle, Anna Rönnfeldt and Katrin Schifferle prepared the data; Valén Holle analysed the data; Valén Holle led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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**Conflict of Interest:**

The authors declare that they have no conflict of interest to disclose.

**Data availability statement:**

The code used for the biogeographic status assignment can be accessed at https://github.com/UP-macroecology/StatusAssignment/releases/tag/v1.0.0, and the code for the uncertainty analyses at https://github.com/UP-macroecology/Holle_PacificPlantInvaders_BlacklistUncertainty_2023/releases/tag/v1.0.0.

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