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Certainty over Uncertainty: A Search for an Endemic Amphibia in Indo-Burma Hotspot Guided by a Predictive Distribution Modeling Approach

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Abstract: Conservation of tropical endemic amphibians largely suffers from Wallacean shortfall, a gap to which predictive species distribution models have contributed significantly to bridge by delineating probable distribution and the underlying suitable habitat within their distributional range. However, rarely is a prediction model ground-truthed to evaluate their predictive performance. Here we present a species distribution modeling approach using maximum entropy algorithm corrected for smaller sample size, in guiding explorative surveys aimed at optimizing survey effort and discovering unrecorded populations of *Zhangixalus suffry*, a rhacophorid tree-frog endemic to the northeastern part of the Indian subcontinent along with the factors limiting their distribution. With only 16 established historical locality data to model for (after spatial thinning to reduce autocorrelation) and a set of environmental predictors (climatic, topographic, and landscape composition), our model prediction enabled the successful discovery of seven new population records from unreported landscapes, extending its southernmost distributional limit over a considerable distance. The final composite distribution model combining all the locality records (n=23) predicted similar core areas of suitable habitat consistent with the known geographic distribution of the species but showed poor representation under existing coverage of Protected Area (PA) network in the Region with only 7% representation of suitable habitat under protection. Habitat suitability of a site was significantly governed by factors related to precipitation (precipitation seasonality and precipitation of the warmest quarter) and topographic factors that can influence it (elevation and aspect). This corroborates with the known ecology of Rhacophorid frogs, especially concerning their seasonal explosive reproductive strategy and foam nest-building behavior. Through this study, we propose explorative surveys guided by species distribution models to expedite unknown population discovery of rare, tropical endemic amphibians and using such taxa as surrogates in identifying conservation priority zones that can be directly applied to reserve design and conservation and management planning.

Keywords: maximum entropy; species distribution model; ground validation; endemic; tree-frog; protected area; biodiversity hotspot

Introduction

    Amphibians are imperiled globally, largely plagued by the so-called *Linnean* (knowledge gaps in species taxonomy) and *Wallacean* (knowledge gaps in species distribution) shortfalls (Hortal *et al*., 2015). Extensive inventory surveys coupled with an integrative taxonomic approach have catered much to bridge the knowledge gap of the former shortfall evident from the unprecedented rise of species descriptions in the last two decades (see Frost, 2021); however, the latter shortfall is still shrouded in uncertainty and skewed, being heavily biased to surveys across easily accessible areas and that too for only a few charismatic or flagship species. This *Wallacean* shortfall is even more acute for tropical countries in South and Southeast Asia with significant forest cover and topographic relief having largely remote and inaccessible regions (Bini *et al*., 2006), despite being hotspots of amphibian diversity and endemism (Stuart *et al*., 2008). To bridge this growing disparity among the two above-mentioned pitfalls, conservationists' are increasingly relying upon predictive distribution models to

ascertain the geographic distribution of amphibian species (see Barbosa *et al.*, 2012), a knowledge that is a prerequisite parameter for effective management and conservation plan.

Species distribution models (hereafter SDM) are prediction based modeling approaches used for refining distribution data and works on the underlying principle of estimating the fundamental niche of a species (the environmental suite of conditions within which a species can persist) from known samples of occurrences (absence data being seldom used because of its credibility), by establishing a relationship between the associated environmental variables found therein and then projecting it back into the geographical space to identify areas that could be a potentially suitable site (ecologically conducive areas) for the species concerned (Peterson *et al.*, 2011; Anderson, 2012). Being robust in nature, SDMs' have found wide ecological applications ranging from investigating climate change-induced impact assessment to identifying and delineating conservation priority areas as well as studying underlying evolutionary processes in speciation (Peterson & Soberon, 2012). However, their predictive potential has found limited usage in guiding explorative surveys of rare, endemic, and at-risk amphibians largely owing to the availability of few occurrence records (but see Bourke, Busse & Böhme, 2012; Groff, Marks & Hayes, 2014), hitherto failing to produce accurate niche models (Pawar *et al.*, 2007). Moreover, the tests evaluating the predictive performance of very limited occurrence records to yield reliable predictions of distribution have mostly centered around using discrimination-based test statistics (Fielding & Bell, 1997) and the "jackknife" validation approach (Pearson *et al.*, 2007). But, rarely are these predictive models ground-truthed to evaluate their predictive performance or remodeled incorporating newly discovered localities guided by the model's prediction with change detection approach (Rebelo & Jones, 2010). Thus, our objective was to assess the potential of SDM based on few occurrence records in guiding surveys aimed at identifying unrecorded populations of *Zhangixalus suffry* (Bordoloi *et al.*, 2007), endemic to one of the most biodiversity hotspot region of the world– the Indo-Burma Region (Myers *et al.*, 2000). We also intend to identify the suite of environmental factors that limits the distribution of *Z. suffry* in the region and evaluate the coverage performance of the current protection level existing in the form of Protected Area (PAs) in its predicted potential distribution range. We hypothesize that the environmental cues influencing the habitat suitability of amphibians will strongly reflect their biphasic mode of life.

Study area

Northeast (NE) India, with a spatial coverage of 256,083 km^2 (extending from 88°E to 97°E and 22°N to 29°30'N), covers a significant portion of both the Himalaya and the Indo-Burma biodiversity hotspots (Myers *et al.*, 2000, Figure 1). It presents characteristic features of the Eastern Himalayan Ranges in the north with significant topographic relief (above 7000 m), the northeast hill ranges aligned in the north-south direction offering a much lesser imposing relief feature (with Manipur and Naga hills varying between 900-2100 m, while the Mizo hills rarely rising above 900 m) merging with the Meghalaya-Karbi plateau through the intervening Garo, Khasi, Jaintia and Barail Hill Range (1300-1800 m). These orographic features encircle the low-lying river valleys– the Brahmaputra and the Barak Valley (around 100 m.s.l. on an average), endowing the region with substantial environmental gradients (Pawar *et al.*, 2007). Lying close to the Tropics, NE India enjoys a subtropical climate characterized by hot humid summers and heavy precipitation clustered around four summer months from June to September, largely contributed by the moisture-laden southwest monsoon winds coming from the Bay of Bengal (Jain, Kumar & Saharia, 2013). With a mean annual rainfall of 2068 mm, this region (marked by a steep 1,200 m high escarpment of the Shillong plateau) receives some of the highest rainfall in the world with only a few pocket areas receiving rainfall below 1500 mm, being located in the rain shadow regions of the mountain range (Jain *et al.*, 2013). Recorded mean annual temperatures vary considerably across the region with a stark contrast between the valleys (15°-28° C), the adjoining mountainous region (9°-21° C) and the upper reaches in the Eastern Himalayan Region (6°-20° C), while the mean relative humidity remains high (70-85%) for most of the year (Dikshit & Dikshit, 2014). With all these factors contributing to diverse habitats (Champion & Seth, 1968) fostering rich diversity, its strategic position as a "gateway" bridging the Indian

subcontinent with the rest of Asia have enabled dispersal and subsequent diversification of various anuran lineages creating high species-level regional endemism (Pan *et al.*, 2017).
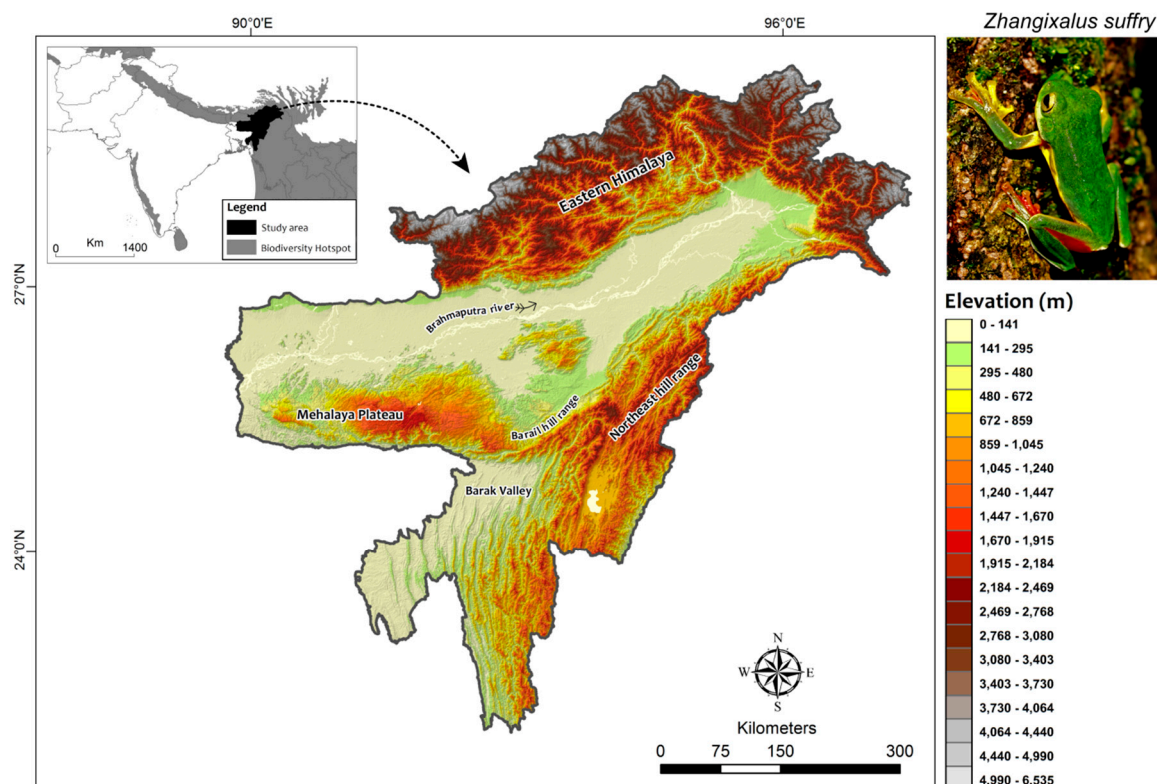
Figure 1. Map of the Northeast India delineating the elevation range of the study area. Insetleft: location of the study area within Biodiversity Hotspot regions of the world. Inset top right: shows live individual of *Zhangixalus suffry* near Barak Reserve Forest, Assam, India (Photographed by Samrat Sengupta).

Study species and Occurrence Data

Zhangixalus suffry was described based on collections from a tea garden (Suffry Tea Estate, Assam) in the Brahmaputra Valley of NE India (Bordoloi *et al.*, 2007). Originally described as *Rhacophorus suffry*, this frog was recently placed under the genus *Zhangixalus* (Jiang *et al.*, 2019). The species is a medium-sized, green dorsum, red webbed tree frog, without any dark black spots on the flanks, which are its prominent distinguishable characters that make field identification relatively easy. Among the green dorsum tree frogs of the genus *Zhangixalus* found to be having overlapping geographical range, *Z. suffy* is very similar to *Z. smaragdinus*; however, the latter is differentiated from the former by the absence of red-colored webbings and much larger body size. Besides, from the other species of *Rhacophorus* (sensu lato) having red-webbings like *R. bipunctatus*, *R. rhodopus*, and *R. subansiriensis*, *Z. suffry* can be differentiated by the absence of dark black spots on the flanks (Figure 1 inset).

Post its description, it has been reported from the Brahmaputra Valley (2 localities), the Eastern Himalayas and its adjoining hill range (10 localities), and northeast hill ranges (1 locality) extending its range of occurrence to a few kilometers away from its type locality (summarised in Saikia, Nanda & Sinha, 2017). Subsequently, it was also reported from Mizoram and Meghalaya (Lalremsanga, 2017, Mukhim *et al.*, 2017). All these verified occurrence records within the study area (16 localities) were gleaned from published literature (surveys conducted during 2007-2017) and were used to generate SDM. To reduce the effect of spatial autocorrelation between two adjacent locations (Hampe, 2004; Luoto *et al.*, 2005), the presence localities were spatially thinned (using the package spThin, Aiello-

Lammens *et al.*, 2015) into a 1-km² grid cell to retain only one presence point per grid cell (Brown, Bennett & French, 2017).

Data acquisition

Environmental variables

There has been a global unison of amphibian distribution in an area to be influenced by temperature and precipitation (reviewed in Buckley & Jetz, 2007, Cunningham *et al.*, 2016) with members representing the Rhacophorid group depending equally on topographic features and habitat matrix quality living close to water sources (Khongwir, Hooroo & Dutta, 2016; Zheng & Natuhara, 2020). With this rationale, we assembled a dataset of 27 environmental variables in our SDMs (Table 1) to model the potential distributional range of *Z. suffry* in NE India. The model covered 19 bioclimatic variables obtained from WorldClim (http://www.worldclim.org), relative humidity (%) from CHELSA (http://chelsa-climate.org/), while the rest of environmental predictors covered general aspects of topography (slope, aspect, and elevation), land-use land-cover (LULC) pattern, normalized difference vegetation index (NDVI for the first and second quarter) and night light as a surrogate measure of anthropogenic impact (habitat fragmentation and urbanization), all readily downloaded from within R (see details of acquisition and processing in Table 1).

All variables were projected to the World Geodetic System 1984 (WGS84) datum and resampled to a 1 × 1 km spatial resolution for further analyses using cubic convolution (cc) approach in R program (v.3.6.2) (RCore Team, 2020).

Table 1. Description of environmental variables used to build the MaxEnt model with details of source, default resolution, method of extraction and processing. All the Bioclimatic variables were resampled to a working resolution of 30 arc-sec (~1 km) for further analysis (see Methods section).

Data	Source	Default resolution	Extraction and Processing
Elevation	Aster DEM-Earth Data	30 m	Using "Raster" and "sp" package in R (Hijmans *et al.*, 2015; Pebesma *et al.*, 2012)
Aspect	Same as above	30 m	Analysis of aspect using terrain function in raster package in R
Slope	Same as above	30 m	Analysis of slope similar to aspect
Land use and land cover (LULC)	USGS-Landsat 8	30 m	Extraction using "getSpatialData" package (Kwok, 2018) and classification using "terra" package (Hijmans *et al.*, 2021)
Normalized difference vegetation index (NDVI)	MODIS	250 m	Analysis using Modistsp and Raster package in R (Busetto & Ranghetti, 2016)
Bio-climatic variables	BIOCLIM (consisting of 19 variables)	1 km	Using getData function trough raster package in R
Relative humidity	CHELSA	1 km	same as above
Night light	DMSP/OLS	1 km	same as above

Data analysis

Model approach

The highly non-systematic and opportunistic nature of faunistic surveys in the past has resulted in datasets with geographic sampling bias for distribution modeling approaches (Hortal *et al.*, 2008). Thus, we employed the Maximum entropy method (MaxEnt; Phillips, Anderson & Schapire, 2006) which have proved to be more efficient for predictive modeling approaches with presence-only data, that too when constrained with sparse occurrence records (Hernandez *et al.*, 2006; Pearson *et al.*, 2007; Tsoar *et al.*, 2007; Wisz *et al.*, 2008).

MaxEnt evaluates the species' probability of occurrence in a site based on the environmental constraints (Elith *et al.*, 2011), and thus the suite of environmental predictors considered during the modeling approach can have a profound effect on the probability distribution. In this study, variable retention was based on "data-driven" variable selection to identify the least correlated and most parsimonious model (Vignali *et al.*, 2020). This was achieved through a two-step method which firstly involves using the *"varSel"* function (in SDMtune package) to identify and remove all highly correlated variables (r > 0.75) from the initial set of 26 predictors (LULC being the only categorical variable). Subsequently, for model parsimony, the "*reduceVar*" function retained a subset of the most important variables (S-Table 1) using a threshold set to 5 % permutation importance (see Groff *et al.*, 2014).

Models were trained by "maxnet" implementation (Phillips *et al.*, 2017) through SDMtune package (Vignali *et al.*,2019) and run with default settings enabling the application of any feature class combination (i.e., linear, quadratic, product and hinge) and suitable regularization multiplier. With a random sample of 1000 "background" locations to represent the varying environmental condition in the study area, models were run for 500 iterations including the selected environmental variables and available locality records described earlier (Phillips & Dudík, 2008; Elith *et al.*, 2011; Warren & Seifert, 2011).

Post prediction survey

To ground validate the SDM (Max$_I$) generated using published historical records (n=16), regional clusters of suitable predictions sites were first selected "*a posteriori*" (within the two river valleys and the Meghalaya plateau), narrowing down to specific survey sites within these clusters that apparently had favorable tree-frog habitats with the help of Google Earth imagery. We directed our survey efforts mainly to private lands (tea gardens) and community-owned forests, as they were less likely to have been previously surveyed.

Field surveys were carried out in 43 such sites between March and June 2018 (after the first monsoon rain) using extensive visual encounter surveys (VES) in shallow, vegetated areas near water sources (63 days of field sampling, about 500 m in each site). The primary focus was to record the presence of *Z. suffry* individuals and egg mass detection, with each encountered individual identified following Bordoloi *et al.* (2007), photographed and geo-located using Garmin eTrex map 62 GPS. Findings of these surveys were incorporated to create a final composite distribution model (Max$_F$) and evaluated for any change in predictions by calculating a two-tailed Wilcoxon-signed rank test using each model's corresponding species presence cell values (between Max$_I$ and Max$_F$). Additionally, we calculated pairwise linear regressions of the model's logistic output values for only localities where *Z. suffry* is known to occur. The species data frame with occurrence records, geographic layers consisting of the selected environmental variables, and a background spatial mask of NE India for clipping the geographic layers was created, and based on this mask the environmental raster layers were re-projected.

Model performance and validation

Model performance was evaluated using a threshold independent statistic (ROC plots, Fielding & Bell, 1997) as well as a threshold dependent statistic ('leave-one-out' jackknife evaluation, Pearson

et al., 2007). ROC plots with a respective area under curve (AUC) provide a measure of the model's predictive performance with values above 0.9 suggesting highly efficient discrimination. However, the jackknife 'leave-one-out' evaluation approach requires model reclassification into binary maps (presence/absence) using a critical threshold, defined based on trade-offs between omission and commission errors while training a model (Hernandez *et al.*, 2006). The threshold value (probability value above which a species presence is predicted to be positive) in our study was set to a 10 percentile training presence logistic threshold which in turn, rejected the only lowest 10% of all the predicted values (see Bean, Stafford & Brashares, 2012). Subsequently, each observed locality was removed once from the set of data and a model is built using the remaining n – 1 localities. Predictive performance (success rate) was then evaluated for each model based on its ability to predict the single locality excluded from the training data as suitable according to the presence 'threshold' described above and generating a *P-value* using a program (pValueCompute) for Windows OS, suggesting the model's predictive performance (Pearson *et al.*, 2007). Apart from this, we calculated sensitivity and specificity and true skill statistics (TSS) for both the SDMs (Allouche, Tsoar & Kadmon, 2006).

The model results and predictions were interpreted through response curves, variable importance (accessed through percentage contribution in maxEnt model), and maps of predicted relative probability of species occurrence where anything above the chosen logistic threshold (0.19) was classified into low (0.19-0.29), moderate (0.29-0.49) and high (>0.49) probability zones of occurrence.

Efficiency of Protected area coverage

To evaluate the efficiency of the existing network of Protected Area (PAs) in terms of spatial coverage over the predicted potential distribution of the species in the study area, we superimposed the predicted distributional range over the boundaries of the PA network of NE India made available online through the Protected Planet website featuring a comprehensive database on Protected Areas of the World (WDPA) (http://www.protectedplanet.net).

Results

Predicted distributional range

The potential distribution of *Z. suffry* modeled based on historical presence-only data and a set of environmental variables (Max₁) presented a diffused distribution of suitable habitat within the study area (Figure 2a). All the historical occurrence records used for modeling have been superimposed over it and are summarised in S-Table 2.
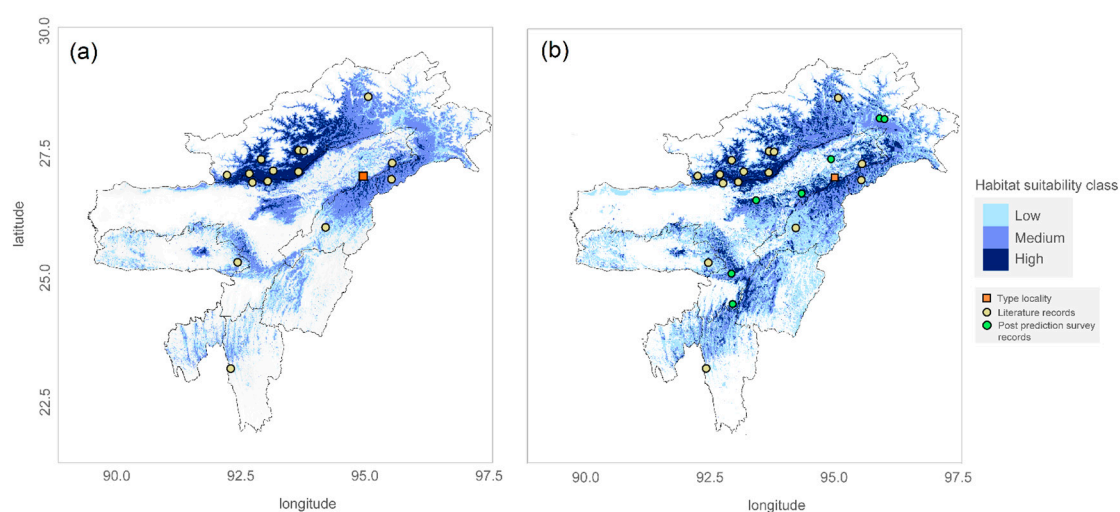
Figure 2. The species distribution model of *Z. suffry* showing the predicted probability of occurrence within Northeast India based on maximum entropy modelling approach corrected for small sample

size. **a)** Max_I represent SDM based on only historical records available in existing literatures, **b)** Max_F represent SDM based on the historical records as well as incorporating the new distributional records guided by model predictions during *ground-truthing* process. Habitat suitability classes in discrete scale: lowest: cyan blue, medium: cobalt blue highest: navy blue. Point markers, yellow round: historical database records; green round: new locality records (present study); red square: type locality (Suffry Tea Estate, Assam).

Prior to this work, the population of *Z. suffry* reported from Meghalaya and Mizoram (Mukhim *et al.*, 2017; Lalremsanga, 2017) was considered as two disjunct groups that appeared to be isolated from the main range. However, our MaxEnt modeling predictions suggest that these isolated populations could be linked to the main range via suitable habitats all along the Barail Hill Range and the low elevation hill ranges of Manipur and Mizoram (Figure 2a). Later, subsequent exploration guided by the model predictions revealed new distributional records from seven previously unrecorded localities, suggesting connectivity between the ranges (forming a continuous distribution) corroborating our model predictions.

We observed one sub-adult male on a private land (Khasi punji) near Barak Reserve forest on 17th March 2018, along a forest trail running parallel to a small stream. The observed individual was identified by its distinct red webbings without any dark black spots on the flanks which set it apart from its congeners. Subsequently, the species presence was also recorded from six other unrecorded sites spanning across both river valleys and adjoining hill ranges (S-Table 3). However, no reproductive behavior could be recorded in any of these sightings. While survey efforts in and around the Meghalaya plateau did not yield any sighting of *Z. suffry*, these new occurrence records (7 localities) confirms the presence of the species at altitudes as low as 100 m to an upper altitude limit of 2000 m (S-Table 3).

The final composite SDM (Max_F) built using the new distributional and the historical records (23 localities in total) also predicted similar core areas of suitable habitat (spatial coverage, Figure 2b). The percentage of study areas predicted to be in the low suitability class was fairly consistent among the two models. However, areas predicted as moderate to high suitability class increased in spatial coverage (extent of area) post inclusion of these new records (Table 2). Interestingly, one opportunistic sighting of *Z. suffry* from Jokai Botanical Garden, Dibrugarh comes from an area predicted to be under low habitat suitability class.

Table 2. Percent of study area predicted by each maximum entropy model corrected for small sample size (Max_I and Max_F) according to four habitat suitability classes: unsuitable, low suitability, moderate suitability and high suitability based on the chosen 10th percentile training presence logistic threshold.

Models (n)	Percent of study area			
	Unsuitable	Low	Moderate	High
Max_I (n=16 localities)	59.85	25.6	8.28	6.28
Max_F (n=23 localities)	45.63	25.5	19.11	9.77

Statistical comparison of model prediction (species presence cell values) showed no significant difference even after the addition of new location records (Median values: Max_I=0.74, Max_F=0.76; Wilcoxon test, W=242; p=0.64) which suggest similarity in prediction pattern (median box-whisker plot given in Figure 3a). Further, linear regression analysis showed a positive relationship between the models' species presence cell values revealing consistency with the known geographic distribution of the species (R^2= 0.34, scatter-line plot given in Figure 3b).
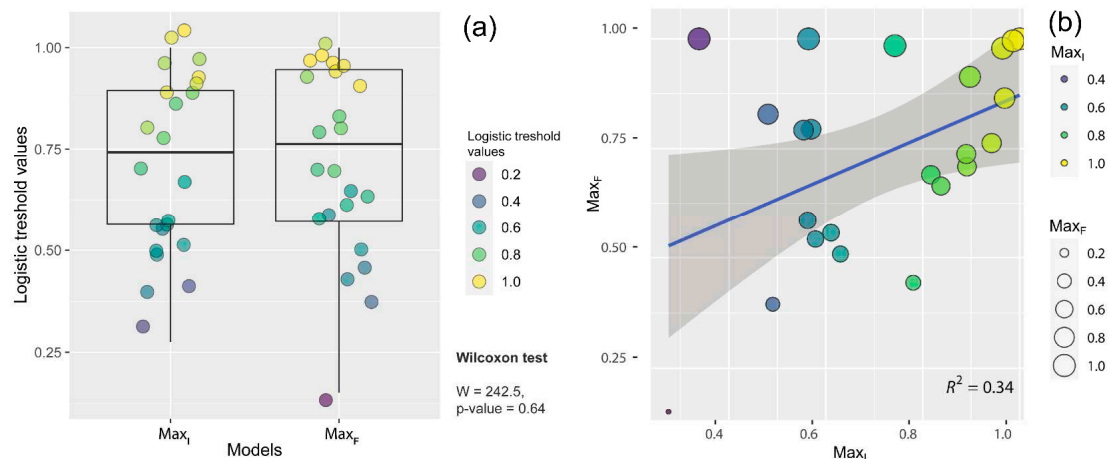
Figure 3. Comparison between each model's corresponding species presence cell values where *Z. suffry* is known to occur. **a)** median box-whisker plot representing overlapping confidence intervals and Wilcoxcon test shows insignificant difference (*p*=0.64), **b)** linear regression model showing positive relationship between two models (R²=0.34). Model abbreviations given in *materials and methods*.

Model evaluation and validation

Model performances of Max_I (run using hinge feature combinations and a regularization multiplier of 1.0) resulted in statistically robust predictions (Max_I: AUC = 0.89 ± 0.082 SD, S-Figure 1a). Here, the model classified a site as a suitable habitat with one having probability values greater than the lowest 10% of all probability values (~0.19).

Jackknife (leave-one-out) validation test (corrected for small sample size) for Max_I produced a moderately high success rate at 62% (p= 0.0042) and was statistically significant when compared to a random assignment of the excluded localities. This corresponds with a 38% omission rate where 10 model runs were able to predict the excluded locality successfully.

The performance however increased substantially when new distribution records from unrecorded localities were incorporated (7 new localities). The consolidated model outperformed (Max_F: AUC = 0.93 ± 0.05 SD, S-Figure 1b) the previous model. Jack-knife validation test resulted in a rate of 77% success (p=0.0016). However, six localities were consistently excluded in both cases when tested with the fixed (10%) threshold method with one of these localities reporting the frog from a cave entrance (Figure 4, S-Figure 2). We additionally assessed the models using True Skill Statistic (TSS) which confirmed the latter one to be a more robust model (Max_I = 0.69, Max_F = 0.73).
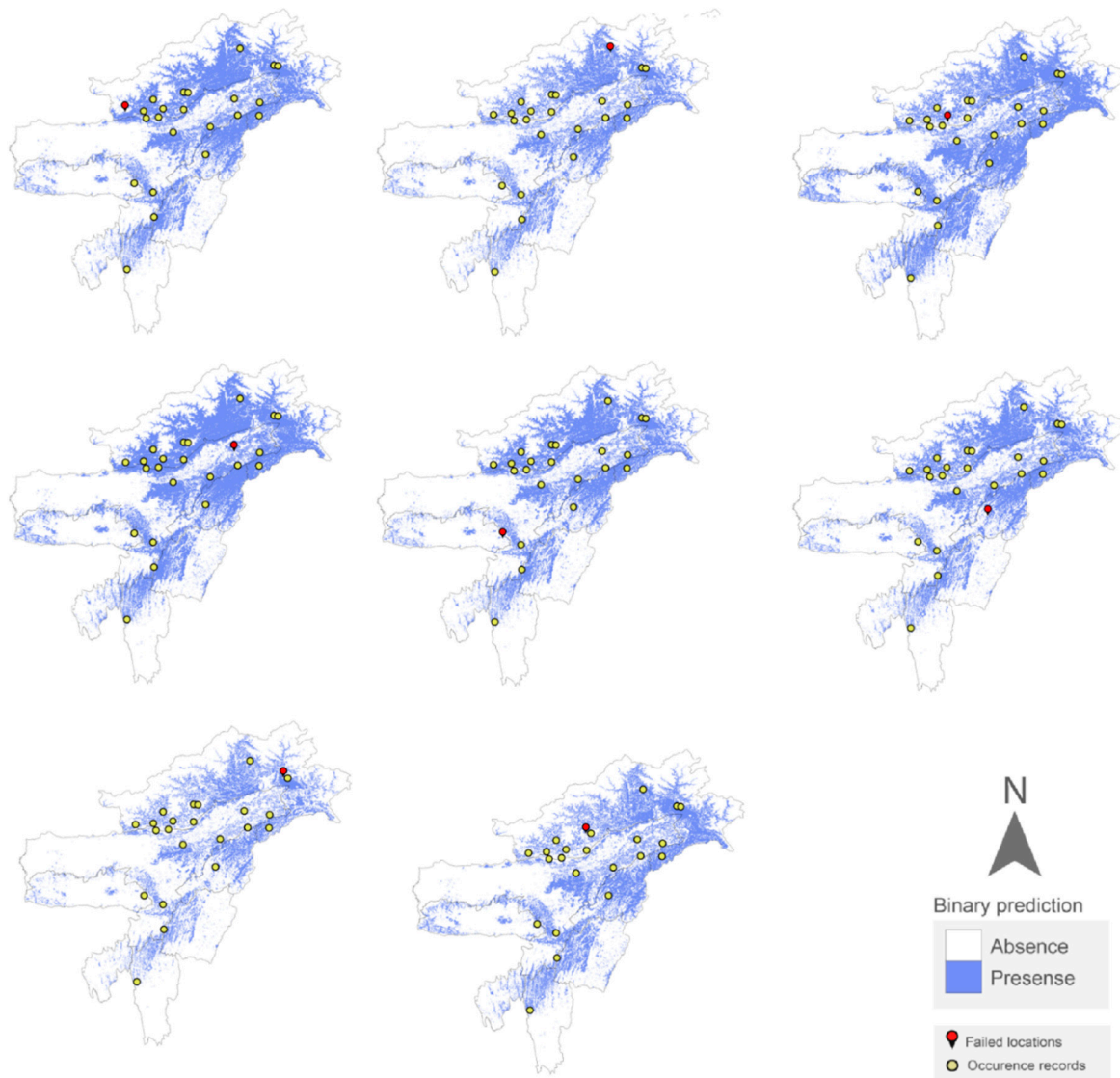
Figure 4. Projected distribution of *n-1* different models of *Z. suffry* using MaxEnt following the Jackknife approach (eight failed prediction models).

Environmental variable contribution

Maxent jackknife test for variable contribution (Max$_F$) shows precipitation related predictors to be the most important bioclimatic variable explaining the probability of occurrence of *Z. suffry* with precipitation of the warmest quarter and precipitation seasonality (40.6 % and 12.7 % respectively) along with aspect (19.6 %) accounting altogether for more than 72 % contribution (S-Figure 3).

Apart from these strong predictors, elevation and vegetation quality (NDVI) contributes significantly to the model. These results are somewhat consistent under model permutation with the same set of predictors contributing the most to the model. However, precipitation seasonality gained relatively disproportionate importance in this analytic approach (Table 3).

Table 3. Contribution of the environmental variables to the MaxEnt model (Max_I and Max_F). The percentage contribution assesses the model's gain through each environmental variable, while the model is built. The permutation importance value is the drop of the AUC value based on the final MaxEnt model, when randomly permuting the values of the variable among the training points. .

	Variables	Percent contribution	Permutation importance
	Precipitation of Warmest Quarter	24.7	18.4
	NDVIQ2	21.8	17.3
Max_I	Aspect	15.9	7.9
	Precipitation Seasonality	13.1	23.9
	Slope	12.8	20.1
	Isothermality	11.8	12.4
	Precipitation of Warmest Quarter	40.6	35.7
	Aspect	19.6	16.2
Max_F	NDVIQ2	17.4	21.3
	Elevation	9.7	1.7
	Precipitation Seasonality	12.7	25.1

Precipitation of the warmest quarter displayed a strong peak response curve suggesting high occurrence probability in areas receiving between 1300 and 2000 mm rainfall during the warmest part of the year. Elevation and aspect both impacted the frog's distribution pattern, with their respective response curves pointing towards decreasing suitability as elevation increases, being mostly confined to the shade side (North and North-East) of mountains and steep valleys of the region (S-Figure 4).

Efficiency of Protected area coverage

Overlaying the current protected area network over the predicted distribution of the frog revealed just 7 % (about 1774 km²) coverage over its high occurrence probability zone, with many large patches of high suitability zones outside the protected areas network (Figure 5). Among the seven states of Northeast India, Arunachal Pradesh followed by Assam presents a fair coverage of high suitable zones under legal protection (Table 4).

Table 4. Extent of coverage of the predicted potential distribution of *Zhangixalus suffry* under the existing Protected Area (PA) network in the study area.

Levels	AR	AS	ML	MN	MZ	NL	TRPA	coverage (km²)	NE coverage (km²)
<10% threshold	5052	2035	520	55	324	193	244	8423	116853
Low	1929	1768	319	137	280	68	310	4811	65258
Moderate	1897	688	53	25	247	8	55	2973	48940
High	1038	662	7	8	29	9	21	1774	25032
Total area	9916	5153	899	226	880	278	629	17981	256083

All areas are in **km²·**
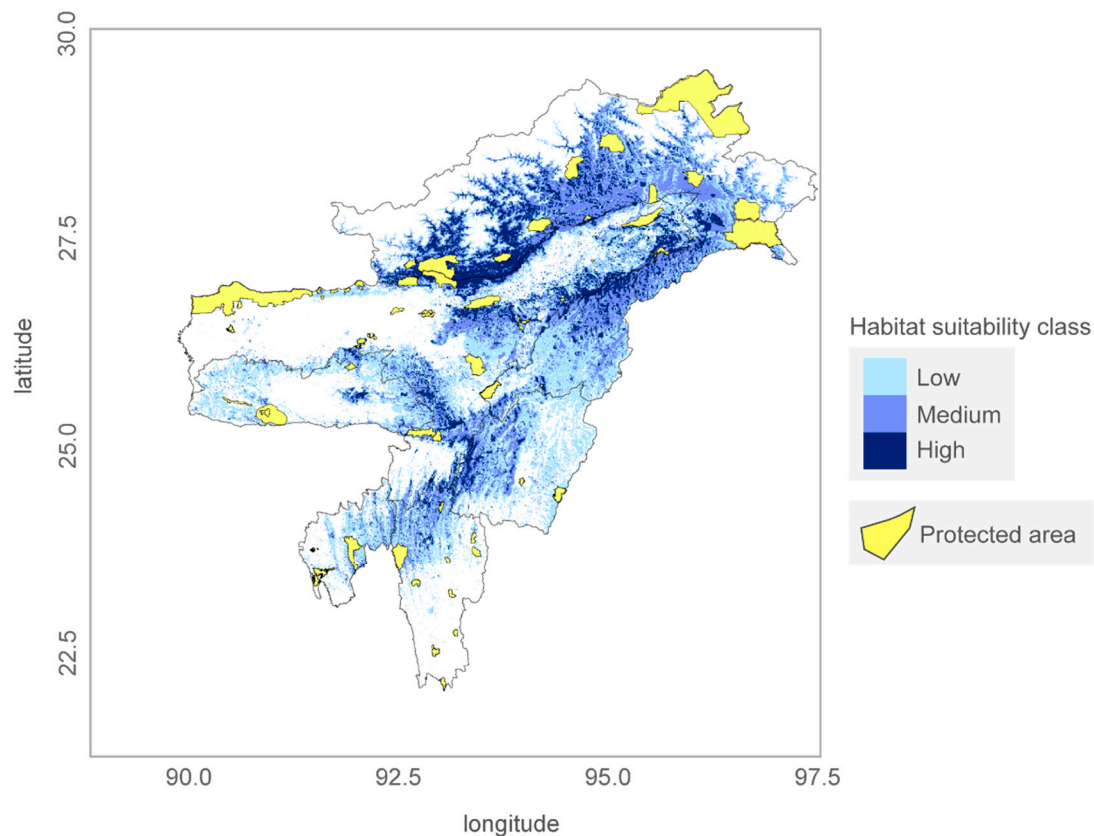
Figure 5. Predicted distribution map of *Z. suffry*, showing the Protected Area (PA) network in the study area.

Discussion

Species distribution models (SDMs) rely on the concept of niche theory that underpins predictive model(s) of species occurrences along the suitable environmental gradients. This enables one to make generalizations from point locations to larger scales, forming the cornerstone of effective species conservation plan (Austin, 2002; Chase & Leibold, 2003).

Our model prediction with 16 occurrence records projected a diffused distribution of suitable habitat, invariably predicting the empirically known localities of *Z. suffry* as suitable. Despite predicting a tight distribution of moderate and high suitability zones clustered around known localities, it successfully facilitated exploratory surveys leading to the discovery of seven new populations from previously unrecorded locations, which was our primary objective in the first place. The usage of the MaxEnt's default regularization parameter(s) which is known to produce models that overfit the input data (Anderson & Raza, 2010; Warren & Seifert, 2011), might have resulted in the concentration of suitable habitats around known localities of the species resulting in a 23% omission rate in our model evaluation process.

The new locality records extend the known distributional range significantly over both the river valleys and also revealed a continuous distribution across the study area giving an impression that the species could be much more widely distributed than previously assumed. Importantly, the new populations recorded near Barak Reserve Forest and Barail Wildlife Sanctuary re-establishes the southernmost distributional range of the species, which extends up to Mizoram (Lalremsanga, 2017). It also asserts the bio-geographic importance of the Barail Hill Range acting as a dispersal corridor for various mid-elevation faunal elements (Pawar *et al*., 2006). This hill range, a south-western extension of the Patkai Range, connects to the Jaintia Hills of Meghalaya where another report of *Z. suffry* exists. However, the study's failure to record any sightings in the Meghalaya Plateau

(commission error) where suitable habitat was predicted should not be ruled as "true absence," as such assertions require extensive ground probing, which was a constraint in this study.

Furthermore, non-detection of the target species when surveyed beyond its 'explosive reproductive' time period could be due to our limited understanding of its microhabitat (see Khongwir *et al.*, 2016) coupled with restricted access to private lands and sacred grooves in Meghalaya. This could be also attributed to the inherent characteristics of niche models, which do not account for biotic interactions, the presence of geographic barriers, and anthropogenic influences (Peterson, 2001; Anderson, Lew & Peterson, 2003). We refrain from postulating local extinction to be a plausible factor as such speculative assertions need proper and long-term monitoring.

Surprisingly five existing literature records of the species constantly failed to be predicted as suitable through our model evaluation, even with a final composite model that incorporates the new locality records.   These localities centered around parts of the Eastern Himalayas, and thus formed the highest elevation records for *Z. suffry*. In contrast, nearly every new distributional record of this species found in the present study comes from low to mid-elevation areas (see S-Table 2).

These finding creates an interesting avenue and the possibility that *Z. suffry* might not be a high mountain taxon, warrants a further investigation dealt with a molecular approach to authenticate the identification of the species. While taxonomic identification of *R. bipunctatus* seems easy (see Species Description section), it's the presence of similar red webbings in sub-adults of *Z. maximus (*now *Z. smaragdinus)* (Wildenhues *et al.*, 2010) which might have led to erroneous identification obscuring their representation in geographic space. Also, the ecological requirement of both the species is quite similar with largely overlapping distribution in the entire study area.

Its occurrence in a habitat predicted to be less suitable (locality record no. 18, S-Table 2) shows that some areas predicted to be under low suitability class in our model prediction may hold remnant populations of the species, which might have been overlooked in the present study. Their occurrence in less suitable habitats could suggest the high tolerance of *Z. suffry* or could simply imply a relict population holding up in these habitats where conditions might have been conducive in former times. We, therefore, recommend surveys in search of other populations at lower altitudes which can have considerable implications in their conservation status (Bordoloi *et al.*, 2008).

According to our model, changes and variability in precipitation values (Precipitation Seasonality and Precipitation of the Warmest Quarter) and the factors that can modulate it (e.g. elevation and aspect) were key climatic and topographic determinant for habitat suitability of the species, restricting their distribution to moist areas largely coinciding along the mountains and hill ranges with local changes in aspect (shade side), capturing additional variation typical of tree frog habitats.

This is also reflected in most SDM studies of cold-blooded amphibians where precipitation related variables have received more weight than temperature (Dolgener *et al.*, 2013; but also see Gül, Kumlutaş & Ilgaz, 2018) with extreme values (e.g., precipitation of driest month, precipitation of the warmest quarter) likely to be more influential than averages or range values (reviewed in Carey & Alexander, 2003; Corn, 2005; Soares & Brito, 2007; Henle et al. 2008; Qian, 2010; Baselga *et al.*, 2012). However, this apparent generalization might vary with the geographical location of the study site as well as with the eco-physiology of the target species being modeled. For a study site having a subtropical climate like ours, high seasonality of rainfall pattern can potentially restrict the breeding phenology of Rhacophorid frogs to a narrow window of time (March-April) by affecting the hydro-period of water sources in their environments (Walls, Barichivich & Brown, 2013; Khongwir *et al.*, 2016).

This was evident in the response curve obtained for precipitation seasonality showing high seasonality drastically reducing the suitability of the site for *Z. suffry*. This is not surprising considering that Rhacophorid anurans (tree frog) life history are characterized by the presence of a unique behavioral adaptation to built foam nest which appears to have evolved mainly for egg or tadpole protection against desiccation and predator avoidance (Duellman & Trueb, 1986). Our study establishes the critical interplay of not only the pattern and timing of rainfall events (precipitation seasonality) but also of ambient temperature (both air and water) during these rainy months

(precipitation of warmest quarter) in influencing the distribution pattern of amphibians in tropical countries, especially in relation to their seasonal explosive reproductive strategy. The sharp orographic features and the time of arrival of moisture-laden monsoon winds in this region from the Bay of Bengal, which acts as a critical checkpoint controlling the attainment of maximum temperature (warmest quarter) across the study area plays a pivotal role in the habitat suitability of Rhacophorid anurans like *Z. suffry*.

On comparing the ecological preferences of *Z. suffry* with its closest sibling species (*Z. burmanus)* studied with MaxEnt in the same area, a similar pattern of biotope utilization mostly confined to moist and humid terrestrial habitats such as banks of ponds and ephemeral forest streams with shaded overhanging vegetation was evident (see Sengupta, Das & Ahmed, 2016). We are of the opinion that topography (only when accessed on a finer scale) and preferred microhabitat features if and when classified and incorporated, can have the potential to define a species' presence within that range (Mazerolle & Villard, 1999; Guerry & Hunter, 2002; Buskirk, 2005).

Species with restricted ecological niches have smaller geographic ranges (such as endemics) providing more robust and precise niche distribution models (Stockwell & Peterson, 2002, Tsoar *et al.*, 2007). The occurrence records reviewed, collected, and used in our modeling approach however present an uneven geographic sampling regime with much more extensive sampling covering the Eastern Himalayan Region and their adjacent hills. Not to mention the level of accuracy associated with some of the historical locality data of species being in the form of textual descriptions rather than pinpoint geographical coordinates. In addition, our study area lacks a dense weather station network, and it provides only a generalized picture of the climate with only 30 weather stations (Dikshit & Dikshit, 2014), which could not well represent actual climatic conditions on ground (Hijmans *et al.,* 2005). On top of it, the environmental dataset assembled for the modeling purpose had a temporal discrepancy (1950-2000 data) not congruent with the occurrence record (post-2007 data). Albeit all these drawbacks, our MaxEnt distribution model for *Z. suffry* had robust evaluation metrics with AUC value of 0.93, where values > 0.9 are suggestive of substantial predictive performance (Elith, 2002; Merow, Smith & Silander, 2013). Thus, various studies (including ours involving the "*ground-truthing*" approach) vindicates MaxEnt successful implementation to identify suitable habitat and potential distribution of rare and endemic amphibians across various bio-geographic realms when having very few occurrence localities (for < 20 records, see Bourke *et al.*, 2012; Groff *et al.*, 2014; Fernandez *et al.*, 2009).

In conclusion, we argue that the predicted suitable habitat and potential distribution range delineated in our study can help in developing conservation strategies, land use management, and habitat restoration around these existing populations. Though PAs are widely advocated as successful management tools for *'in-situ'* conservation of biodiversity in natural ecosystems, they have a poor spatial coverage (less than 15%) globally (Protected Planet Report 2018), coupled with inadequate biodiversity representation (Brooks *et al.*, 2004, Rodrigues *et al.*, 2004). Our results corroborate these lacunae as > 90% of the predicted distribution area of *Z. suffry* falls outside of the limits of the PA network in the Region, where it is reported to be endemic.

Rhacophorid amphibians with limited dispersal abilities, being largely restricted to breeding migrations before and after spawning to nearest water sources can be severely impeded by fragmentation, intensification of agriculture, and linear infrastructure intrusion into pristine habitats (Collins & Storfer, 2003; Cushman, 2006; Holderegger & Di Giulio, 2010). Evidence of these potent threats is rampant in the study area reeling under tremendous agronomic pressure, resulting in fragmentation of contiguous distribution of wildlife species creating isolated populations prone to local extinctions (Sharma, Madhusudan & Sinha, 2014). Future thrust areas in research and modeling approaches should investigate privately owned lands, especially Tea Gardens as our survey efforts were hindered by our inability to access such private lands. Also, with a continuous decline of monsoon precipitation over the Region since the 1950s (Preethi *et al.*, 2017), the impact of different climate change scenarios in the distributional pattern of suitable habitat for endemic amphibians should be addressed to develop climate change-adapted conservation strategies.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

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