

## Article

# Bioclimatic Envelopes for Two Bat Species from a Tropical Island: Insights on Current and Future Distribution from Ecological Niche Modeling

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**Abstract:** Bats perform critical ecosystem functions, including the pollination, seed dispersal, and regulation of invertebrate populations. Yet, bat populations are declining worldwide primarily due to habitat loss and other anthropogenic stressors. Thus, studies on bat ecology, particularly on environmental determinants of bat occupancy, are paramount to their conservation. High mobility, nocturnal behavior, and roosting site selection of bats make conventional surveys challenging. Moreover, little is known about geographic distribution, habitat suitability, and responses to climate change among tropical bat species. To bridge these research gaps, we applied ecological niche modeling to two Ceylonese bat species, *Kerivoula malpasi* and *Kerivoula picta*, to map their geographic distribution. Seasonal variations in temperature and precipitation were critical environmental predictors of bat distribution in general. Southwestern lowland forests contained the most optimal habitats for the relatively wide-ranging *Kerivoula picta*, while the central highlands provided the most suitable habitats for the narrow-ranging *Kerivoula malpasi*. No tangible changes in the highly suitable habitats were evident in response to projected climate change for either species. Yet, the optimal ranges of *K. malpasi* can become fragmented in the future, whereas the most optimal habitats for *K. picta* are likely to become spatially contiguous in the future. Habitat availability or fundamental niche alone is insufficient to reliably forecast species persistence, thus we caution against considering these two bat species as resilient to climate change. Our findings will enable the conservation authorities to initiate preemptive conservation strategies, such as the establishment of landscape-scale habitat connectivity and management of buffer zones around conservation lands. We also encourage conservation authorities to employ ecological niche models to map potential species distributions and to forecast range shifts due to climate change.

**Keywords:** *Kerivoula picta*; *Kerivoula malpasi*; MaxEnt; climate change; ecological niche modeling

## 1. Introduction

Given their ability to fly, bats have inherited a unique position in the mammalian phylogeny [1,2]. Among mammals, global-scale species diversification (~1400 species) of bats is only second to rodents [3]. Flight and echolocation are among the key adaptive traits underlying their success and cosmopolitan biogeography [4]. While certain chiropteran lineages (e.g., leaf-nosed bats) have undergone remarkable niche specializations following adaptive radiation [5], recent evidence also suggests multiple instances of convergent evolution [6]. Bats are often considered environmental indicators given their heightened sensitivity to deforestation and damage to other terrestrial ecosystems, disturbances at

roosting sites, broad-spectrum pesticides, and resource depletion [7–10]. They also play crucial ecosystem services in pollination, seed dispersal, forest regeneration, suppress arthropod populations in both natural and agricultural landscapes, and nutrient and energy redistribution [11–13].

Bats are declining worldwide, which can be linked to both habitat loss (e.g., deforestation, expansion of commercial farmlands, urbanization) and anthropogenic disturbances (e.g., visitations at roosting sites, pesticide applications) [9]. Implementing conservation measures to counter these declines warrants information on species distribution, habitat suitability, and species responses to global change [14]. However, due to their nocturnal behavior and the incomplete sampling of roosting sites, field surveys may underestimate their true distribution [12]. Given taxonomic crisis, the identification of bats to the species level with gross morphological features alone is challenging and can result in improper estimations of their geographic distribution [15]. Although theoretical developments in soundscape ecology [16], automated recording devices, and machine-learning models [17] offer promising alternatives for conventional field sampling. Implementing such passive surveys across broader geographies can be prohibitively expensive. Hence, there is a pressing need to develop alternative methods to map the current and future distribution of bats. Herein, predictive geospatial models that piggyback on environmental covariates of species occupancy and limited georeferenced data on species presence, known as habitat suitability models (species distribution models or ecological niche models, hereafter ENMs), can provide reliable solutions. This modeling approach is applicable for both mapping current distribution and forecasting future range shifts in response to global environmental change [14,18].

Successful applications of ENMs depend on the selection of biologically meaningful proxies and spatial characteristics that correlate with the probability of species occupancy [14]. The ENMs strike an empirical relationship between observed species distribution and spatially explicit environmental variables [14,18], and thereby predict species occurrence across geographies, forecast future distribution ranges in response to changing environment, and help prioritize conservation targets [19,20]. The ENMs have been widely utilized to address questions pertaining to biogeography, conservation, evolution, hindcast historical species distributions, and estimate the magnitude of climate change on species geographic ranges [21]. Seasonality and climate are critical drivers of habitat selection by bats, as is evident from their variable roosting-site selection across seasons [22,23]. Life-history stages of bats, such as mating, parturition, lactation, postnatal care, and peak food-availability (e.g., such as insect swarms), are tethered to seasonality [10,18,24]. Both resource acquisition and energy conservation by bats are also climate-mediated [25]. Therefore, bioclimatic variables are useful environmental proxies to model the fundamental niche of bats.

Due to logistical and financial constraints, there is a paucity of island-wide bat surveys in Sri Lanka, and thus the current geographic ranges of bats remain unresolved. Although ENMs can at least partly address these knowledge gaps, such applications are considerably limited in certain tropical biodiversity hotspots. For instance, in the Indian-oceanic island of Sri Lanka, ENMs are uncommon in ecological and conservation research [26–28]. A scholarly search across numerous (PubMed, BioOne, ProQuest, Web of Science, Dimensions) databases did not reveal any research on ENMs targeting Ceylonese bats.

Tropical islands, such as Sri Lanka, can be physiologically stressful environments characterized by disturbances emerging from frequent tropical storms, which can negatively impact bat populations [9]. Episodic extreme climate events (e.g., typhoons, hurricanes, or extended drought), put island bats at an elevated risk of catastrophic population declines [29]. Climate change can compound the psychological stress encountered by insular bats. For instance, rising global average air temperatures elevate the metabolic rate (i.e., Arrhenius effect) [30], whereas the frequency and intensity of extreme climate events (e.g., heat waves, tropical storms) are also likely to heighten in the tropical realm due to global warming [31]. Together, these phenomena impose physiological stress on endotherms such

as bats [30]. As warming trends escalate, geographic ranges can shift into cooler climates, either towards higher altitudes or higher latitudes [32,33]. Nevertheless, these adaptive relocations are untenable for island bats (such as those of Sri Lanka) given geographic isolation, limited dispersal opportunities, and smaller island size. Hence, understanding how climate change impacts island bats is crucial for conservation planning. Yet, how Ceylonese bats respond to climate change remains understudied. Collectively, these scientific deficiencies impede conservation and management actions in Sri Lanka as well as other tropical islands [4]. To fulfill this research gap and applied needs, in this study (1) we developed ENMs for two Ceylonese bat species under both current and future climate change scenarios and (2) estimated their extent of occurrence (EOO) and area of occupancy (AOO) to re-evaluate their national conservation status. The ENMs we developed will map both the current and future (in response to climate change) geographic ranges of two Sri Lankan bat species. Our efforts in mapping the potential distribution will pave pathways to develop similar applications for other bat species, both in Sri Lanka and other tropical islands.

## 2. Materials and Methods

### 2.1. Focal Species

Sri Lanka is home to 31 species of bats (8 families), of which 18 are listed as threatened [3,34]. The genus *Kerivoula* (Family Vespertilionidae; subfamily Kerivoulinae, woolly bats) comprises seven species distributed across Paleotropics, particularly in south and southeastern Asia, Australasia, as well as Sub-Saharan Africa [3]. *Kerivoula* congeners are interior forest-dwellers that roost in foliage or tree cavities, and forage in high-clutter (i.e., with dense vegetation) environments [35]. Only two *Kerivoula* congeners are known in Sri Lanka: the Painted bat (*K. picta*) and the Sri Lankan Woolly bat (*K. malpasi*) [3,36–38] (Figure 1).



Figure 1. Cont.



**Figure 1.** (a) Painted bat (*Kerivoula picta*) (Male) (Photo credit—Gayan Edirisinghe) and (b) Sri Lankan Woolly bat (*Kerivoula malpasi*) (Male) (Photo credit—Madhava Botejue), both species roosting on Banana fronds.

*Kerivoula picta* is broadly distributed across the Indo-Malayan region [3,10] and listed as “Near threatened” in both the Global and Sri Lankan Red Lists [34,39]. The Sri Lankan endemic *K. malpasi* is nationally categorized as “Critically Endangered” [3], while its Global status remains unassessed [3,34]. The existing distribution records of *K. picta* are scattered throughout the Sri Lankan lowlands (<600 m), although they have been infrequently recorded in higher elevations (up to 1372 m). In contrast, *K. malpasi* is only known from very few localities of the central highlands (up to 1260 m), and southwestern and northeastern Sri Lanka [3,40] (Figure 2).

## 2.2. Distribution Records

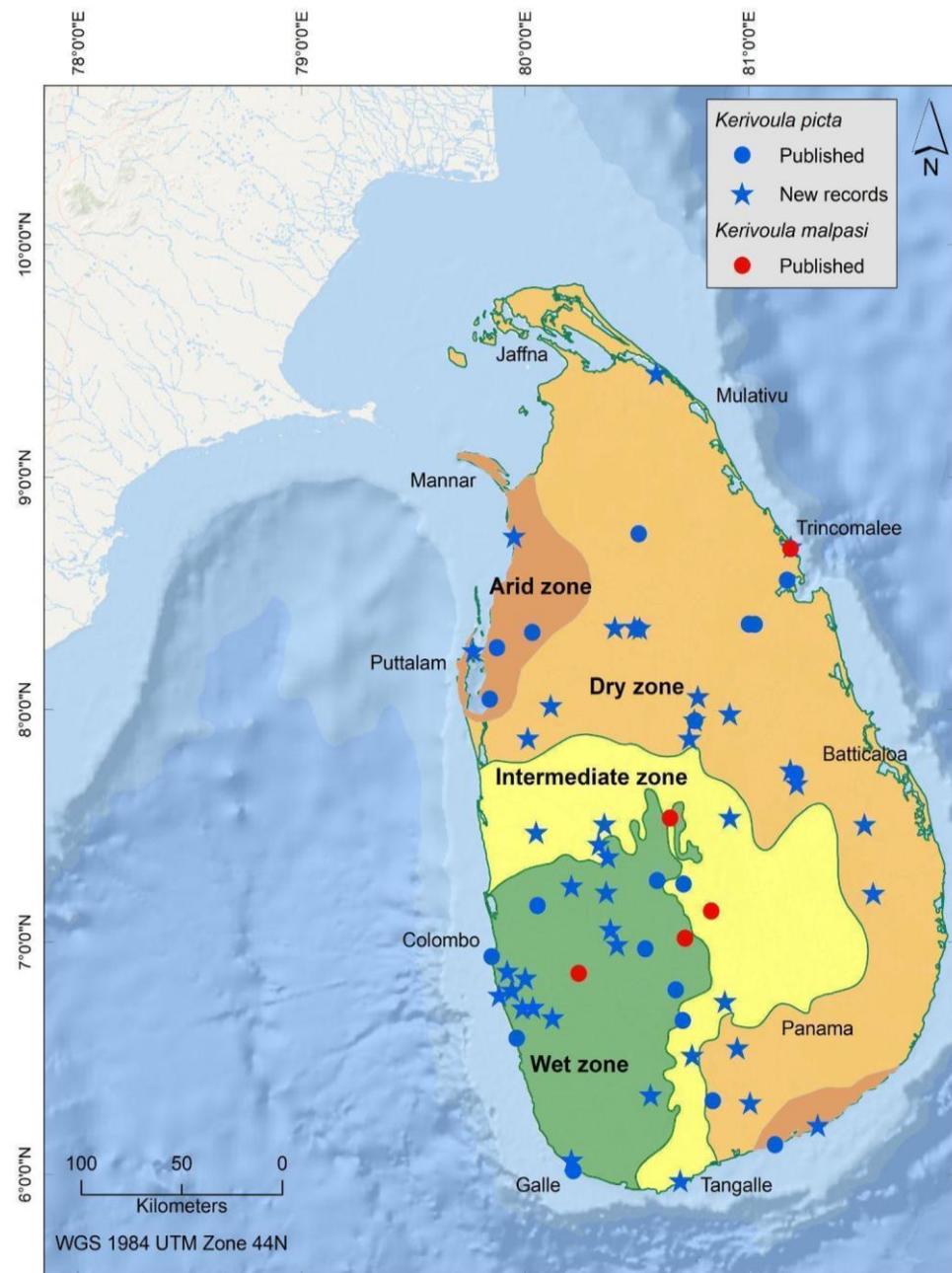
Species occurrence records were obtained for both focal species within Sri Lanka from (1) unpublished opportunistic observations by field biologists updated from 2016 to 2020; (2) published historical accounts [3,10,36,40–47]; (3) the Global Biodiversity Information Facility [48]. Although distribution of *K. picta* is not limited to Sri Lanka, since our focal area is Sri Lanka, we did not use distribution records outside Sri Lanka. Species–habitat relationships vary throughout their biogeography, thus interpolating *K. picta*’s environmental proxies from its overall geographical range to map its distribution in Sri Lanka may lead to spurious results. Since our historical records (beyond 2000) were not georeferenced, the coordinates for those observations correspond to the nearest town at the reported elevation. Since our historical records predate the year 2000, we cross-validated the historical records against field observations to confirm contemporary species presence.

## 2.3. Data Sources and Modeling Approach

Following a maximum entropy approach, we built the ENMs using georeferenced locations of both bat species (63 and 5 locations for *K. picta* and *K. malpasi*, respectively) with the MaxEnt software version 3.3 (<http://www.cs.princeton.edu/~schapire/maxent/> (accessed on 20 February 2022)) [20]. Maximum Entropy (MaxEnt) is a machine-learning approach to ENMs that uses environmental variables and georeferenced locations of species presence to predict both the current and future distribution ranges with weighted habitat suitability [19].

Although our sample size for *K. malpasi* is small, MaxEnt can deliver reliable distribution models even for sample sizes as small as five [49,50]. We screened records of *K. picta* for spatial autocorrelation using SDMtoolbox in ArcMap (ver. 10.8.1) to remove correlated georeferenced species-occurrence points [51], and subsequently extracted 58 spatially independent (on average, 18 km between any two nearest occurrence points) georeferenced points for the ENM. Since the georeferenced points for *K. malpasi* were limited and spatially

dispersed (on average, 35 km between any two nearest occurrence points), we did not perform any autocorrelation diagnoses.



**Figure 2.** Updated distribution map of *K. picta* and *K. malpasi* in Sri Lanka. Published records were extracted from the literature [3,10,36,40–48]. New records are from unpublished data from personal observations of the authors and personnel communications with expert field biologists.

As predictor variables, we used WorldClim bioclimatic variables, elevation, and land-cover geospatial data layers. The land-cover data was obtained from the Copernicus Global Land Cover (CGLC) dataset produced by the Land Monitoring Service at 100 m spatial resolution [52]. This global-scale dataset identifies a total of 23 land-use and land-cover types [52,53], which includes different types of forest types (evergreen, deciduous, mixed vegetation types as well as both open and closed forests), shrublands, herbaceous vegetation, herbaceous wetlands, moss and lichen, bare/sparse vegetation, croplands, permanent water bodies, and built-up land surfaces. The CGLC data were developed

from Sentinel-2 imagery (collected in 2019) and has been validated and used in geospatial analyses [54].

The bioclimatic data were obtained from WorldClim database (<http://www.worldclim.org/bioclim.htm> (accessed on 4 January 2022)) [55,56] at a 1 km spatial resolution. The elevation data were derived from NASA's shuttle Radar topography mission, aggregated to 1 km spatial resolution, using the median value. This elevation dataset has undergone postprocessing to correct for no-data voids via interpolation techniques [57,58]. The original data for WorldClim bioclimatic variables were assembled from a variety of weather stations (e.g., Global Historical Climate Network Dataset) using monthly precipitation, mean temperature, and minimum and maximum temperature data within a large climatic stations network. Bioclimatic variables were derived from the monthly temperature and precipitation measurements to generate more biologically relevant variables suitable for ENMs. These bioclimatic variables represent annual (e.g., mean annual temperature, annual precipitation) as well as seasonal (e.g., annual range in temperature and precipitation) trends and extreme conditions (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters).

#### 2.4. Bioclimatic Variable Selection

We downloaded all 19 bioclimatic variables from WorldClim, which were derived from the past 30 years (1970–2000), and future averages over 20 years (2041–2060) [57,58] (Table 1). Both current and forecasted bioclimatic variables were available for the full geographic extents of Sri Lanka. The bioclimatic data was converted to the BIL raster files, and the data were clipped to Sri Lanka's geographical boundary (9.9433°–5.8681° N, 79.3125°–82.2285° E) using ArcGIS 10.8.1. These bioclimatic variables express annual trends and seasonality and are critical determinants of bat life histories and their fundamental niche [18]. Bioclimatic variables have been used in the ENMs to map the current distribution, as well as to forecast future ranges in response to climate change [59,60].

**Table 1.** Bioclimatic variables from WorldClim 2.0 used to predict the current and future distribution of two Sri Lankan bat species.

Code	Variable	Description	Unit
bio1	Annual mean temperature	The average temperature for each month	°C
bio2	Annual mean diurnal range	Measure of temperature change over the course of the year using monthly maximum temperatures and monthly minimum temperatures	°C
bio3	Isothermality	Derived by calculating the ratio of the mean diurnal range (bio 2) to the annual temperature range (bio 7, discussed below), and then multiplying by 100	%
bio4	Temperature seasonality (Standard Deviation)	The amount of temperature variation over a course of the year, based on the standard deviation (variation) of monthly temperature averages	%
bio5	Max temperature of warmest month	The maximum monthly temperature occurrence over a given year (time series) or averaged span of years (normal)	°C
bio6	Min temperature of coldest month	The minimum monthly temperature occurrence over a given year (time series) or averaged span of years (normal)	°C
bio7	Annual Temperature range	A measure of temperature variation over a given period. (bio 7 = bio 5 – bio 6)	°C
bio8	Mean temperature of wettest quarter	Mean temperatures that prevail during the wettest season	°C
bio9	Mean temperature of driest quarter	Quarterly index approximates mean temperatures that prevail during the driest quarter	°C
bio10	Mean temperature of warmest quarter	Quarterly index approximates mean temperatures that prevail during the warmest quarter	°C

**Table 1.** Cont.

Code	Variable	Description	Unit
bio11	Mean temperature of coldest quarter	Quarterly index approximates mean temperatures that prevail during the coldest quarter	°C
bio12	Annual precipitation	Sum of all total monthly precipitation values	mm
bio13	Precipitation of wettest period	The total precipitation that prevails during the wettest month.	mm
bio14	Precipitation of driest period	The total precipitation that prevails during the driest month	mm
bio15	Precipitation seasonality (Coefficient variable)	Measure of the variation in monthly precipitation totals over the course of the year	%
bio16	Precipitation of wettest quarter	Total precipitation that prevails during the wettest quarter	mm
bio17	Precipitation of driest quarter	Total precipitation that prevails during the driest quarter	mm
bio18	Precipitation of warmest quarter	Total precipitation that prevails during the warmest quarter	mm
bio19	Precipitation of coldest quarter	Total precipitation that prevails during the coldest quarter	mm

The multiple bioclimatic variables we used from WorldClim can be highly correlated [55]. High collinearity among bioclimatic variables may lead to model overfitting, and thereby overestimate distribution ranges [61,62]. We performed a Pearson correlation test via the Species Distribution model toolbox v2.5 (SDM toolbox) in ArcMap (ver. 10.8.1) to diagnose multicollinearity. After removing highly correlated variables (i.e., Pearson correlation coefficient  $\geq 0.90$ ), we selected 12 bioclimatic variables (bio1–10, bio15, and bio17) to develop ENMs.

For the future species distribution model, we used the bioclimatic variables for the year 2050 (the midpoint for the 2041–2060 period) based on two different climate projections, namely Geophysical Fluid Dynamics Laboratory climate model version 3 (GFDL-CM3) [63] developed by the National Oceanic and Atmospheric Administration and the Norwegian Earth System Model 1-medium resolution (NorESM1-M) [64,65] developed by the Norwegian Climate Center [66]. The 12 bioclimatic variables we used for modeling current distribution were also used for the future ENMs (Table 2 and Table 3). Both GFDL-CM3 and NorESM1-M best captured the mean precipitation and mean temperature observed in the Indian subcontinent, thus suitable for forecasting climate projections in Sri Lanka [67,68]. Land cover and elevation were retained as additional predictor variables for future ENMs as well.

**Table 2.** Estimates of percent contribution (PC) and permutation importance (PI) of bioclimatic and environmental predictor variables of the MaxEnt habitat suitability modeling for the current and future (2050) distribution based on GFDL-CM3 and NorESM1-M of *Kerivoula picta* in Sri Lanka.

Variable	Current		GFDL-CM3		NorESM1-M	
	PC	PI	PC	PI	PC	PI
bio1	0.2	0	0.2	1.5	2.4	3.5
bio2	5.3	1.7	0.2	0	5	3.7
bio3	2.8	4.4	1.4	2.1	1.1	1.3
bio4	39.6	17.3	36.5	20.7	30.1	19.9
bio5	3.3	0.7	8.7	7.2	7.2	5.3
bio6	2.6	16.2	0.6	0.7	0.1	0.1
bio7	1.9	0.2	4.1	9.1	0.8	1.2
bio8	0.2	0.3	2.2	7	0.7	0.6
bio9	0	0	1.6	5.7	0	0
bio10	0.1	0.5	8.3	7.1	0.4	0.2
bio15	9.5	16.8	5.9	5.6	21.8	23.6
bio17	9	7.7	18.5	8.3	19.9	20.4
land-use	18.8	14.4	5.6	6.5	4.4	5
elevation	6.7	19.9	6.3	18.6	6.1	15.4

**Table 3.** Top three variable contributors based on percent contribution (PC), permutational importance (PI) and jackknifing (JK) to the Maxent models for current and future ecological niche models based on GFDL-CM3 and NorESM1-M.

Species	Current			GFDL-CM3			NorESM1-M		
	PC	PI	JK	PC	PI	JK	PC	PI	JK
<i>K. picta</i>	bio4	elevation	bio4	bio4	bio4	bio15	bio4	bio15	bio15
	land use	bio4	bio15	bio17	elevation	bio4	bio15	bio17	bio4
	bio15	bio15	bio17	bio5	bio7	bio17	bio17	bio4	bio17
<i>K. malpasi</i>	bio15	bio15	bio15	bio15	bio15	bio15	bio15	bio15	bio15
	bio2	bio2	bio9	bio2	bio2	bio17	bio2	bio2	bio2
	land use	land use	bio2	bio17	bio9	bio2	land use	bio9	elevation

The Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report sets climate projections based on variable greenhouse gas (GHG) concentrations following four Representative Concentration Pathways (RCPs) [69]. Each RCP defines variable heat energy generated ( $\text{Wm}^{-2}$ ) via radiative forcing due to GHGs. We selected RCP 8.5, which follows the highest possible radiative forcing by GHGs for 2100 expected due to high population growth and a lower rate of technology development (worst-case climate change scenario). The monthly values for these climatic variables were averaged over 20-year timeframes (2021–2040, 2041–2060, 2061–2080, 2081–2100) [70,71]. For this study, we selected averaged climatic projection data for 2041–2060.

According to the National Physical planning policy of Sri Lanka, numerous major land-cover transformations (new expressways, an east–west economic corridor, and several large metropolitan regions) are expected by 2050. Therefore, to model the future distribution, we simulated land-cover change for Sri Lanka for the year 2050 following the National Physical Plan, as described below [72]. First, we converted the CGLC raster dataset into a vector format and then edited the CGLC layer to incorporate both the east–west economic corridor (that links southwest to northeastern coasts) and five metropolitan regions (located in the northern, southeastern, south central, and southwestern coastal Sri Lanka) by manually digitizing these new land uses. Next, we classified both the economic corridor and the metropolitan areas as built-up land surfaces. These edits increased the urban areas in Sri Lanka by 31%. We assumed the rest of the land areas in Sri Lanka to remain unchanged.

### 2.5. Model Building and Evaluation

MaxEnt combines species-presence point data with spatially referenced, grid-scale environmental variables, where species presence is confirmed to estimate the suitability of specific areas for the species of interest. Then, utilizing a machine-learning approach, the MaxEnt model assesses how similar the environmental conditions (i.e., climate, elevation, land-use) of other regions are to the environments required by the focal species on a continuous scale from 0 to 1 (most dissimilar to most similar, respectively). The latter is a proxy of habitat suitability for a defined spatial extent with regard to the focal species (0: unsuitable, 1: optimal) [20,67,68,73]. However, the estimation of species suitability may be reduced if sampling is incomplete across the landscape [74].

For each species, we constructed the models under current and future climatic scenarios with 15 replicates, 500 iterations, and 10,000 background points while using default MaxEnt settings [75]. Species occurrence information was divided into training (75% of total occurrence records) and test sets (25% of total occurrence records) for model calibration [76]. To evaluate the predictive performance of the model, we calculated the maximum true skill statistics (TSS) [77] of presence–absence by the predicted values in addition to the AUC (area under the receiver operating characteristic curve). MaxEnt model prediction performance was assessed using the AUC, TSS, sensitivity, specificity, and overall accuracy. Spatially explicit predictions (such as ENMs) are liable to omission (false negatives, omitting known distributional areas from the predicted distribution) and commission errors (false positives,

including unsuitable areas into the predicted distribution) [78]. The True Skill Statistic (TSS) evaluates the predictive accuracy of an ENM and calculates the sensitivity + specificity – 1, which ranges from –1 to +1. MaxEnt automatically generates background predictions from background points (i.e., pseudoabsences), and sample predictions from species occurrence. We used the 10th percentile training presence logistic threshold (i.e., 0.344 for *K. picta* and 0.489 for *K. malpasi*) to calculate the overall accuracy, sensitivity, specificity, and TSS, using the logistic suitability outputs to evaluate the predictive performance of the MaxEnt model. Overall accuracy is the rate of correctly classified pixels. Sensitivity is the probability that the ENM correctly classifies a presence. Specificity is the probability that the ENM correctly classifies an absence.

We used two default metrics provided by MaxEnt percent contribution, permutation importance, and a Jackknife test to determine the importance of environmental variables in the final model [20]. Percent contribution was calculated by MaxEnt during model training. The permutation importance of each variable was computed by randomly permutating each predictor variable during model training. Through MaxEnt's built-in Jackknife test (suitable for small sample (4–23 presence points) sample sizes) [50], each environmental variable was sequentially dropped, the remaining variables were refitted, and the model gain was computed to estimate the contributions from the dropped variable to the model fitting [79]. Finally, the model gains in each step were compared to determine the relative importance of each variable.

The MaxEnt output maps were exported to ArcMap 10.8.1 for subsequent processing. Habitat suitability on the predicted map was binned into four intervals based on probability values [80]: unsuitable 0–0.2, less suitable 0.2–0.4, moderately suitable 0.4–0.6, and highly suitable 0.6–1.0. These habitat-suitability categories were adopted from MaxEnt-derived habitat classifications [81,82].

### 2.6. Extent of Occurrence and Area of Occupancy

We used the Geospatial Conservation Assessment Tool (GeoCAT—<http://geocat.kew.org/> (accessed on 5 February 2022)) [83] to calculate the EOO and AOO, thereby assessing the IUCN status of the focal species (May 2021). GeoCAT is a web-based, open-source application that determines the IUCN Red List status by plotting georeferenced species presence data on the Google Maps interphase, and therefrom calculates both EOO and AOO following IUCN Red List categories and criteria [84].

We obtained the current EOO by calculating the area contained by the minimum bounding geometry of the convex hull drawn encircling all georeferenced points. We calculated the current AOO by summation of 1 km<sup>2</sup> grids within the species-present localities. In addition, using GeoCAT (an open-source geospatial conservation assessment tool), we calculated both AOO and EOO from ENM generated current and future distribution maps for the high habitat suitability (with >60% probability of species presence) class. Herein, we reclassified the high suitability class as category 1 and all other classes as no data. Next, we converted the raster to points, generated a CSV file for highly suitable localities, and imported the CSV file into GeoCAT to compute both EOO and AOO (within a 1 km square grid).

## 3. Results

### 3.1. Habitat Suitability Modeling

#### 3.1.1. Evaluation of the Model and Analysis of Variable Contribution

The model accuracy for *K. picta* can be considered “good”, since the average training AUC values were  $0.714 \pm 0.012$ ,  $0.755 \pm 0.001$  and  $0.751 \pm 0.009$  for the current and future distributions, respectively. Models for *K. malpasi* showed a high accuracy, with average AUC values for current and future distributions being  $0.937 \pm 0.019$ ,  $0.938 \pm 0.019$  and  $0.953 \pm 0.023$  for the current and future distributions, respectively (Table S1). These values indicated that the distribution patterns characterized by the selected bioclimatic and environmental variables are highly satisfactory. The overall accuracy for *K. picta* ranged from 0.5 to 0.6, while *K. malpasi* ranged from 0.9 to 1.0 for the current and future predictions,

respectively. The TSS values for both species are under the threshold of 0.20–0.40 and slightly variable among current and future predictions.

### 3.1.2. Variables of Importance for *Kerivoula picta*

MaxEnt model projections based on percent contribution indicated that temperature seasonality (bio4) was the most important predictor, followed by land-use, precipitation seasonality (bio15) and precipitation of the driest quarter (bio17) (Table 2). For the GFDL-CM3 future scenario, temperature seasonality (bio4) best explained the future distribution, followed by precipitation of the driest quarter (bio17) and maximum temperature of warmest month (bio5) (Table 2). Based on the NorESM1-M future scenario, temperature seasonality (bio4), precipitation seasonality (bio15) and precipitation of the driest quarter (bio17) contributed to explain the future distribution (Table 2).

When permutation importance was considered, elevation had the highest impact on the current distribution, followed by temperature seasonality (bio4), precipitation seasonality (bio15) and minimum temperature of the coldest month (bio6). Temperature seasonality (bio4), elevation and annual temperature range (bio7) showed a higher permutation importance for the GFDL-CM3-based future distribution (Table 2). The future distribution modeled from the NorESM1-M dataset identified precipitation seasonality (bio15), precipitation of the driest quarter (bio17), temperature seasonality (bio4) and elevation as variables with relatively high contributions (Table 2).

The Jackknife test that assessed the relative contributions of the predictor variables for modeling the current distribution showed temperature seasonality (bio4), precipitation seasonality (bio15) and precipitation of the driest quarter (bio17) with the highest gains, whereas precipitation seasonality (bio15), temperature seasonality (bio4) and precipitation of the driest quarter (bio17) showed the highest contributions when modeling the future distribution for both GFDL-CM3 and NorESM1-M datasets (Table 3; Figure S1).

### 3.1.3. Variables of Importance for *Kerivoula malpasi*

Concerning the percent contribution to model the current distribution, precipitation seasonality (bio15) was the most important predictor, followed by annual mean diurnal range (bio2) (Table 3). In the future distribution model based on GFDL-CM3 dataset, precipitation seasonality (bio15), annual mean diurnal range (bio2), precipitation of the driest quarter (bio17) and land-use emerged as the variables with the greatest contributions (Table 3). For the NorESM1-M dataset, precipitation seasonality (bio15), annual mean diurnal range (bio2) and land-use had the highest contributions (Table 4).

**Table 4.** Estimates of percent contribution (PC) and permutation importance (PI) of bioclimatic and environmental predictor variables of the MaxEnt habitat suitability modeling for the current and future (2050) distribution based on GFDL-CM3 and NorESM1-M of *Kerivoula malpasi* in Sri Lanka.

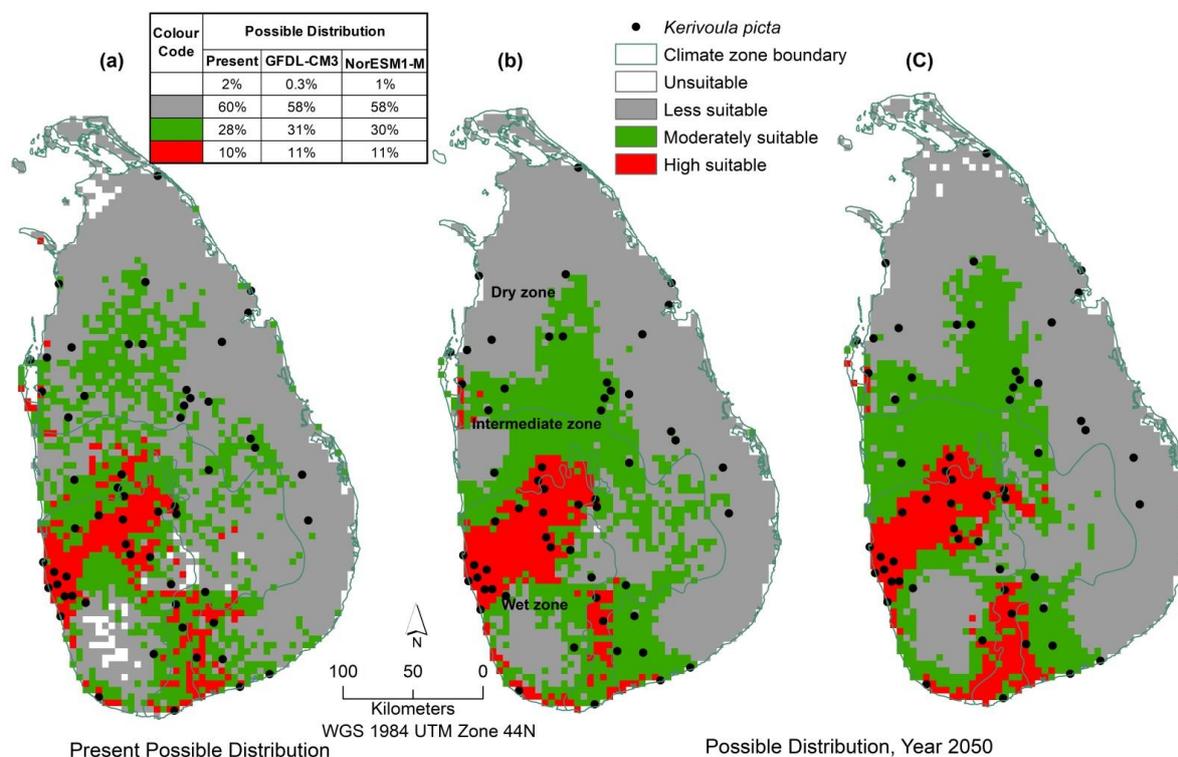
Variable	Current		GFDL-CM3		NorESM1-M	
	PC	PI	PC	PI	PC	PI
bio1	0	0	0	0	0	0
bio2	31.3	35.3	32.1	32	28	28
bio3	0	0.4	0	0	0	0
bio4	0.1	0	0.3	3.3	0	0.1
bio5	0	0	2	0	1.4	0.4
bio6	0	0	0	0	0	0
bio7	0.2	0	0	0	0	0
bio8	0	0	0	0	0	0
bio9	0	0	0.9	7	0.2	4.1
bio10	0	0	0.6	0	0.3	0
bio15	63.6	46.6	40.7	57.6	51.6	67.4
bio17	0	0	15	0.1	8.2	0
land-use	3	15.5	8.5	0	9.8	0
elevation	1.8	2.2	0	0	0.4	0

Based on permutation importance, precipitation seasonality (bio15), annual mean diurnal range (bio2) and land-use ranked highest in the current distribution model (Table 3). Under future scenarios based on GFDL-CM3 dataset, precipitation seasonality (bio15), annual mean diurnal range (bio2) and mean temperature of driest quarter (bio9) had the highest permutation importance (Table 3). Based on NorESM1-M dataset, precipitation seasonality (bio15) and annual mean diurnal range (bio2) ranked the highest in terms of the greatest permutational importance (Table 4).

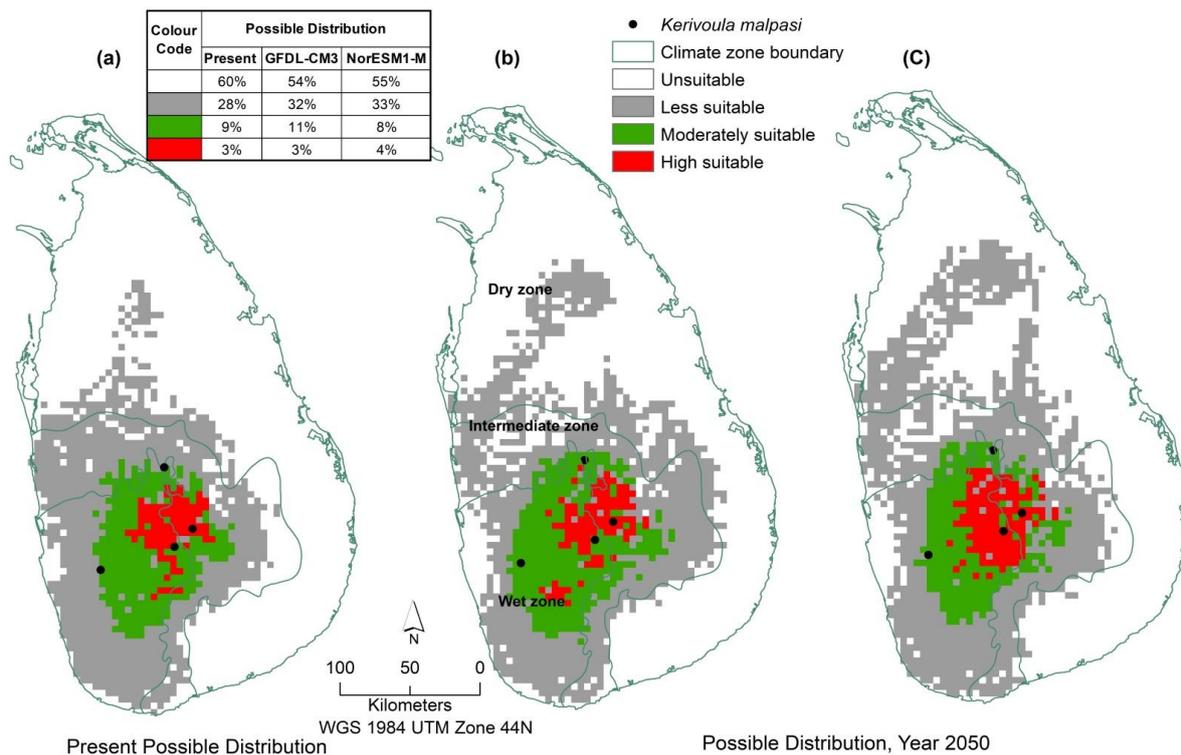
The variables with highest gain for modeling the current distribution as revealed by the Jackknife tests were precipitation seasonality (bio15), mean temperature of the driest quarter (bio9) and annual mean diurnal range (bio2). Precipitation seasonality (bio15), precipitation of the driest quarter (bio17) and annual mean diurnal range (bio2) showed the most gains in the future distribution model when the GFDL-CM3 dataset was used, while precipitation seasonality (bio15), annual mean diurnal range (bio2) and elevation had the highest gains when the NorESM1-M dataset was used (Table 3, Figure S2).

### 3.1.4. Potential Distribution Analysis

Model projections in both current and future climatic scenarios revealed that the southwestern part of the lowland wet zone which encompasses the tropical wet evergreen rainforests to be the most suitable area for *K. picta* (Figure 3). However, the optimal habitat areas for both the current and future distributions for *K. picta* are spatially constrained to a smaller portion of the island (10%). The acreage of highly suitable habitats for *K. picta* is unlikely to change dramatically between current and future distribution ranges. Nonetheless, highly suitable habitats of *K. picta* within its current range seemed to be scattered in both the southwestern wet zone and the intermediate zone. In contrast, the highly suitable habitats of its future distribution range appear to be rather continuous and consolidate across the northernmost parts of the lowland wet zone (Figure 3). Our projected models also suggest a minor increase (2–3%) in moderately suitable habitats for *K. picta* (Figure 4, Table S2).



**Figure 3.** MaxEnt-based habitat suitability maps for current (a) and future (2050) distribution ranges based on GFDL-CM3 (b) and NorESM1-M climate change forecasts (c) for *K. picta* in Sri Lanka. Table tallies proportional changes in distribution acreage between current and future scenarios.



**Figure 4.** MaxEnt-based habitat suitability maps for current (a) and future (2050) distribution ranges based on GFDL-CM3 (b) and NorESM1-M climate change forecasts (c) for *K. malpasi* in Sri Lanka. Table tallies proportional changes in distribution acreage between current and future scenarios.

Both current and future predictions exhibit highly suitable areas for *K. malpasi* within wet as well as intermediate bioclimatic zones (Figure 4, Table S2). Our models did not detect any dramatic changes in either the highly or moderately suitable habitats between the current and future distribution ranges of *K. malpasi* (Figure 4, Table S2). However, the highly suitable habitats of *K. malpasi* in its future distribution appeared to be fragmented, with considerable differences in the spatial and geographic configuration compared to the current distribution. The habitat area with the greatest suitability for *K. malpasi* is a single contiguous range across the wet and intermediate zones in its current range. In forecasted ranges, a substantial degree of fragmentation (i.e., the number of fragments) is evident among its highly suitable habitats. Sri Lanka's dry zone appeared to be unsuitable for *K. malpasi* in both the current and forecasted distributions.

### 3.2. AOO and EOO

Based on georeferenced locations of *K. picta*, the AOO and EOO were 62 km<sup>2</sup> and 55,374 km<sup>2</sup> (0.09% and 84.4% of overall land acreage of Sri Lanka, Table 5), respectively. According to our ENMs for the current scenario, the AOO and EOO (when areas with >60% probability of occupancy were considered) were 291 km<sup>2</sup> and 31,580 km<sup>2</sup> (0.44% and 48.13% of overall land area), respectively. The AOO for both future models (324 km<sup>2</sup>, 348 km<sup>2</sup>) will remain approximately the same as the current AOO, while the EOO (19,339 km<sup>2</sup>, 21,908 km<sup>2</sup>) is predicted to incur a modest decline. The AOO and EOO calculated from georeferenced records for *K. malpasi* were 5 km<sup>2</sup> and 5340 km<sup>2</sup> (0.01% and 8.08% of overall area), respectively, while the equivalent, ENM-derived figures for the current scenario were 91 km<sup>2</sup> and 3266 km<sup>2</sup>; (0.14% and 5% of total land area), respectively. Both the AOO and EOO of *K. malpasi* in Sri Lanka are expected to undergo little to no change in response to future climate scenarios.

**Table 5.** The extent of occurrence (EOO) and area of occupancy (AOO) of *K. picta* and *K. malpasi* in both current and future distribution scenarios as predicted by the ENMs in comparison with the same metrics calculated by the georeferenced points following IUCN criteria.

Model	Distribution Range Metrics	Species	
		<i>K. picta</i>	<i>K. malpasi</i>
Without ENMs	EOO	55,374 (84.40)	5340 (8.14)
	AOO	62 (0.09)	5 (0.01)
Current	EOO	31,580 (48.13)	3266 (5.00)
	AOO	291 (0.44)	91 (0.14)
GFDL-CM3	EOO	19,339 (29.48)	4420(6.74)
	AOO	324 (0.49)	96 (0.14)
NorESM1-M	EOO	21,908 (33.39)	4035 (6.15)
	AOO	348 (0.53)	123 (0.19)

#### 4. Discussion

The ENMs offer effective tools to understand how environmental variables affect distribution and their response to climate change [18,85,86]. MaxEnt based ENMs are particularly effective at predicting geographic ranges from minimal presence only ground referenced data [49], and hence are applicable to map distribution of range restricted species that are challenging to document via field surveys (such as bats). Despite an impressive increase in ENM based studies to map species geographic ranges, bat-focused ENM applications are infrequent in the Indo-Malayan realm [85]. MaxEnt ENMs use bioclimatic, topographic, and land cover variables that influence species physiological optima, their life histories and habitat associations, thus construct the Grinnellian niche based on abiotic habitat requirements [87,88] to map species distribution across broader spatial scales [14]. Our study mapped the island-wide geographic range of two bat species whose distribution is fundamentally governed by biophysical environmental conditions; thus, MaxEnt provides the most prudent approach. Bats are relatively vagile with high dispersal abilities, and thus less impeded by physical barriers to access suitable habitats. Therefore, abiotic features are a reliable proxy of their habitat occupancy [85,89]. Although biotic features (e.g., insect abundance, disease prevalence) are critical determinants of bat occupancy, physical habitat structure is a proxy for food availability and forage quality [90]. Therefore, modeling species distribution based on the Grinnellian-niche concept is both ecologically sound and computationally feasible.

The spatially weighted probability of species occurrence pictured in the ENM generated maps identify high quality habitats, which is useful for conservation planning [91,92]. Our models revealed that, despite the broader spatial distribution, the most optimal habitats for *K. picta* are restricted to parts of the southwestern lowlands. Neither the wide-ranging *K. picta* nor the narrow ranging *K. malpasi* showed tangible changes in the extent of their optimal habitats due to forecasted climate change. Yet, the spatial configuration of optimal habitats for both species showed remarkable shifts. Optimal habitats for *K. malpasi* became fragmented while those of *K. picta* became rather consolidated in the lowland wet zone. While fragmentation is less likely to impede bat navigation, fragmented habitats may deteriorate in quality and resource availability due to edge effects [93], become increasingly vulnerable to subsidized predation, and less resilient to disturbances as well as climate change [94–98]. Although conventional protected areas have static boundaries, our study revealed that the spatial configuration of and connectivity among habitats are likely to change in response to climate change. Therefore, future conservation planning (i.e., demarcation of protected areas and landscape-scale corridors) should consider the spatially and temporally dynamic nature of suitable habitats (i.e., distribution range shifts) [99,100]. The habitats with a high probability of occupancy in future scenarios should be considered climate refugia and protected as core habitats to ensure population persistence. The mod-

erately suitable habitats surrounding the highly suitable habitats should be managed as buffer zones.

In Sri Lanka, *K. picta* is found primarily across the low country and ranges up to the central hills (1372 m a.s.l) [3,37,45,48]. The species has been mainly documented in tropical dry-mixed and lowland wet evergreen forests [3,37,45], and our model predictions for the current range agrees with previous observations. The wide geographic range of *K. picta* predicted by our ENM is not surprising given its associations with a range of roosting sites (dried and dead leaves, flower clusters) located in different vegetation communities (primary and secondary forests, home gardens, forest plantations) [10,101,102]. Our model predictions on *K. malpasi* indicates its preference to higher altitudes (>2100 m a.s.l) characterized by low annual temperatures and high precipitation; these model predictions agree with the current consensus on its distribution range being limited to the central highlands [3,37,40]. *K. malpasi* has been reported in both natural and manmade ecosystems, such as dry-mixed evergreen forests, tropical montane forests, paddy fields, home gardens, and banana plantations [3,37,40]. Restricted distribution of *K. malpasi* to higher elevations is likely due to its lower physiological thermal tolerance.

Temperature seasonality (bio4) and precipitation seasonality (bio15) emerged as the most critical predictors of the current distribution of *K. picta* across all variable selection methods. Precipitation seasonality (bio15) and annual mean diurnal range (bio2) was the most important predictor to map the current distribution of *K. malpasi*, regardless of the variable selection method. The communality of precipitation seasonality (bio15) highlights the role of temporal variations in precipitation in defining the fundamental niche of both bat species. Between-species differences in the environmental drivers may suggest at least partial niche separation between species. Neither field observations nor ENM outputs suggest the presence of either bat species in the arid zone of Sri Lanka. Reduced access to water and other critical resources, increased risk of dehydration, and prolonged droughts can drastically limit these species in the arid zone.

The importance of bioclimatic variables as critical drivers governing the species distribution of bats and other mammals [103] have been well established. These bioclimatic predictors can override the effects of land-use and land-cover or topography. For instance, summer precipitation, maximum winter temperature, and annual precipitation had the greatest contribution in modeling distribution of the Great long-eared bat in the United Kingdom [104]. Minimum temperatures set the threshold for bat flight, foraging, navigation, and other metabolic activities [105,106]. Low air temperatures increase the metabolic costs of euthermic homeostasis and reduces aerial insect activities [107]. Precipitation dictates the insect abundance, which provides critical food resources for bats and has also been linked to reproductive success (i.e., gestation, late fledging of young) and postnatal care (i.e., lactation) of bats [108].

The future ENMs we developed suggested that the range-restricted species, *K. malpasi*, to be the most negatively impacted from climate change. The impact of climate change is disproportionately high in range-restricted, specialist species compared to wide-ranging generalists [32]. Geographic vulnerability assessments also identify tropical biomes rich in biodiversity and endemism to peril the most from climate change [109–112]. For instance, the extent of suitable habitats of 66 neotropical bat species are projected to decline by 2050 due to climate change [113]. Major declines in biodiversity due to range constrictions and extinctions have been projected even under optimistic climate-change scenarios for southeastern Asia [114].

Data availability on bat distribution in Sri Lanka through standard publications is scant. Lack of long-term island-wide monitoring further complicates this data deficiency. We strongly encourage field biologists as well as research and academic institutes to publish their biodiversity data via online open repositories (e.g., Global Biodiversity Information Facility) or citizen-science platforms (e.g., iNaturalist) with relevant metadata with proper curation of georeferenced points of bat distribution.

Given the absence of evidence for population stability or reliable population assessments, on-going anthropogenic threats (e.g., pesticide applications) and uncertain protection outside conservation lands, plus our estimations on their ENM-generated AOO and EOO calculations, the IUCN conservation status for both *K. picta* and *K. malpasi* in Sri Lanka should remain “Near Threatened” and “Critically Endangered”, respectively [34,39]. Geographically restricted distribution evident in our ENM maps, and the likelihood of fragmentation of highly suitable habitats with climate change, justify the retention of the highest possible conservation status for *K. malpasi*. Forecasted fragmentation of most suitable habitats can further be compounded by changes in natural land-cover in the central highlands of Sri Lanka. The Global IUCN Red List of *K. malpasi* is yet to be assessed [3,34]. Since this species is a Sri Lankan endemic, we recommend applying “Critically Endangered” as the conservation status to the Global IUCN Red List as well. When assessing bat conservation status, we propose that conservation authorities calculate both the AOO or EOO for areas with high probability of species presence (e.g., >60%) based on ENMs in place of the overall AOO and EOO.

### 5. Limitations of ENM and Future Work

Future range predictions via MaxEnt ENMs assume no changes in the Grinnellian niche (i.e., abiotic habitat preferences remain the same over time) [85,115], although counter evidence to niche conservatism has frequently appeared in the published literature [116,117]. Hence, these future predictions should be used with caution. Accurate distribution modelling warrants the inclusion of non-climatic environmental variables, such as species dispersal ability and distance constrained variables (e.g., distance to built-up environments and farmlands, proximity to water sources), which can alter the distribution of bats [118–120]. Covering multiple threats, especially anthropogenic disturbances and fine-scale land-use modifications will help harness the maximum predictive power from ENMs since species responses to changing environments can either emerge from or become modified by interactions between threats [121,122].

As an oceanic island, the impacts of sea-level rise on future species distributions are non-trivial. While the negative impacts of sea-level rise on Sri Lanka is well documented, most such adversities impact shorelines and nearshore coastal zones [123]. As environments most vulnerable to sea-level rise in Sri Lanka fall outside the distribution range of both focal species [124–126], thus we opted not to include sea-level rise as a predictor. The environmental variables we used in our ENMs were of coarse resolution (~1 km), which is sufficient for broad-scale ENMs. Species responses to environmental conditions, conservation planning, and habitat management actions operate at variable spatial scales, including both fine and broad scales [126]. For instance, foraging-site selection and nocturnal activities of bats are only evident at fine scales, while ecoregion-wide distribution can be reliably determined at coarse scales. Therefore, a multiscale approach that combines both fine- and broad-scale environmental drivers produces the most reliable ENMs [104]. However, developing such complex models require individual-specific behavioral data from radio-telemetry studies, as well as high-resolution geospatial data on local-scale habitat features. Lack of such fine-scale, open-access geospatial data in Sri Lanka precluded us from developing such intricate models.

Low extent of predicted suitability areas and range restrictions of *K. malpasi* could be due to spatial bias resulting from lack of observations [85]. Given small sample size, the fundamental niche of *K. malpasi* could not be fully characterized in our modeling approach. Therefore, despite the model validation metrics, our results on *K. malpasi* must be interpreted with caution when making conservation decisions. The ENM frameworks based on abiotic factors and presence-only data are frequently used for ENMs. Nonetheless, these approaches do not account for biological drivers of species distribution (e.g., competitors, predators, diseases, symbionts), thus cannot correctly represent species occupancy because the resultant models may not approximate the realized niches.

## 6. Conclusions

Our study mapped the distribution and applied ENMs for current and future distribution (the latter based on climate-change scenarios) for two bat species of the genus *Kerivoula* for Sri Lanka. According to our ENMs, highly suitable areas for *K. malpasi* lie in the central highlands, whereas the lowland wet zone provide optimal habitats for *K. picta*. We underscore the need to validate the current distribution we predicted, which necessitates either active field surveys or the deployment of automated ultrasonic recording devices. Given logistic and financial constraints in field surveys, we propose that these efforts be concentrated in regions of high habitat suitability.

Although neither of our study species showed dramatic changes in their optimal habitat extent due to climate change, these species should not be treated as resilient to climate change without additional observations and more comprehensive modeling on their realized niche. Our study provides a blueprint to utilize ENMs for predicting the current and future distribution of bat species. We encourage conservation authorities to follow our ENM approach to map distribution ranges for bat species, particularly when field data is insufficient to establish long-term monitoring focusing on specific sites with a high probability of occurrence. Such mapping efforts, together with subsequent monitoring, will help effectively target and prioritize conservation efforts.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14070506/s1>, Table S1. AUC values of MaxEnt models under the current and future (2050) scenarios based on GFDL-CM3 and NorESM1-M data sets; Figure S1. Relative predictive power of different environmental variables based on the Jackknife of regularized training gain in MaxEnt model for *K. picta* (a) current (b) for the predicted scenario in the year 2050 based on GFDL-CM3 (c) for the predicted scenario in the year 2050 based on NorESM1-M; Figure S2. Relative predictive power of different environmental variables based on the Jackknife of regularized training gain in MaxEnt model for *K. malpasi* (a) current (b) for the predicted scenario in the year 2050 based on GFDL-CM3 (c) for the predicted scenario in the year 2050 based on NorESM1-M; Table S2. Predicted suitable areas for *Kerivoula picta* and *Kerivoula malpasi* under current and future (Year 2050) scenarios based on GFDL-CM3 and NorESM1-M (km<sup>2</sup>) Unsuitable 0–0.2, less suitable 0.2–0.4, moderately suitable 0.4–0.6, and highly suitable 0.6–1.0.

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