RESEARCH ARTICLE

Can't see the wood for the trees? Canopy physiognomy influences the distribution of peninsular Indian Flying lizards

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Abstract

Aim: In the absence of topographic barriers to dispersal, spatial boundaries of species are largely governed by the environmental regimes they occupy. Flying lizards (Agamidae: *Draco*) from peninsular India have surmounted prominent geographic barriers, but their northern distribution abruptly ends at the 'Goa gap', a latitudinal boundary separating the wet and dry regions of the Western Ghats. Given their exclusively arboreal habits, we posit that canopy physiognomy determines *Draco* distribution in regions of climatic suitability.

Location: Peninsular India.

Taxa: *Draco dussumieri, Monilesaurus rouxii*.

Methods: We analysed occurrence data collated from multiple sources against a suite of climatic and canopy-specific predictors to model the occurrence of *Draco*. We used an information theoretic approach to binary logistic regression that incorporates presence/absence data, along with a maximum entropy-based algorithm that models ecological niches in space using presence-only data. Climatic data were obtained from CHELSA and WorldClim. We compared models for *Draco dussumieri* with the only other largely sympatric, arboreal agamid, *Monilesaurus rouxii*, which spans the Goa gap. Finally, we statistically tested how regions *Draco* inhabits differ in canopy physiognomy from the regions in the Western Ghats where it does not occur.

Results: Canopy height was the most influential predictor of *Draco* presence in regions of climatic suitability under both the logistic regression and maximum entropy models. While climatically suitable regions occur north of the Goa gap, these regions harbour significantly lower canopies with lesser coverage. Despite a narrower range of climatic suitability, *Monilesaurus* has spanned the Goa gap, presumably because it is less dependent on canopy traits.

Main conclusions: Lower canopies with lesser coverage act as a biogeographic barrier for the dispersal of *Draco* into regions of climatic suitability. In addition to being a climatic boundary, the Goa gap serves as a vegetational barrier that demarcates regions with significantly dissimilar canopy physiognomies. Our study highlights the importance of quantifying environmental regimes that organisms occupy to better understand distribution patterns. Our results implicitly predict the effects of deforestation on *Draco* distribution in the peninsula and therefore, influence its conservation strategy.
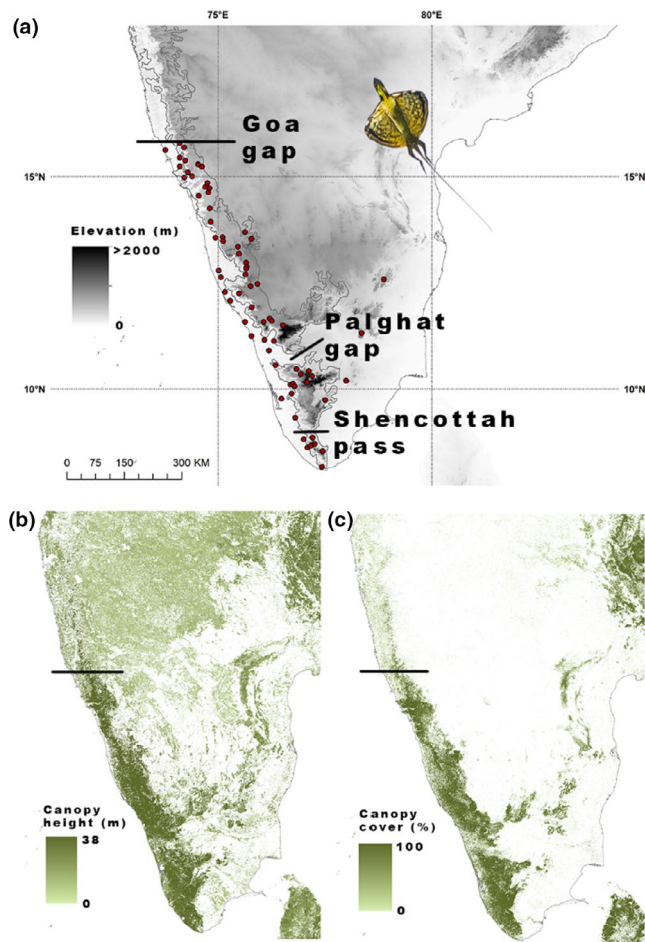
1 | INTRODUCTION

The Western Ghats mountain complex in peninsular India is characterized by three prominent biogeographic discontinuities—the Shencottah pass, the Palghat gap and the Goa gap (Figure 1) which act as either barriers or conduits of dispersal depending on the ecology of the organism (Bhimachar, 1945; Biswas & Karanth, 2021; Mani, 1974b). While these barriers to dispersal (and therefore to gene flow) have led to cladogenesis in several vertebrate groups (see the examples in Biswas & Karanth, 2021), the underlying biogeographic

FIGURE 1 Elevation map of peninsular India (a) showing the contours and major biogeographic barriers of the Western Ghats along with georeferenced occurrence records for *D. dussumieri* used in this study. Maps of peninsular India plotted against raster datasets of raw canopy height in metres (b) and canopy cover as percentages (c). The black line indicates the position of the Goa gap to help visualize the differences in canopy structure on either side of it. Maps are projected on the World Geodetic System 1984 (WGS84)

mechanisms at play have largely been different for the Palghat and Shencottah valleys vis-à-vis the Goa gap.

The Palghat and Shencottah gaps are deep valleys formed *ca.* 500 million years ago (mya) as a result of shearing and erosion (D' Cruz et al., 2000; Soman et al., 1990; Subramaninan & Muraleedharan, 1985). Time-calibrated phylogenies, of extant, wet-adapted small vertebrates such as *Nyctibatrachus* frogs (Bocxlaer et al., 2012), at least 10 species of montane birds (Robin et al., 2015), bush frogs of the genus *Raorchestes* (Vijayakumar et al., 2016), geckos of the genus *Dravidogecko* (Chaitanya et al., 2019) etc. suggest that cladogenesis in these groups coincide with the Late Miocene (*ca.* 11–5 mya) aridification of peninsular India. This aridification led to the formation of habitats unsuitable for organisms adapted to wetter climes in the intervening low-altitude regions, which prevented their dispersal across these valleys (Morley, 2000; Patnaik et al., 2012; Pound et al., 2012). Consequently, the Late Miocene aridification, in concomitance with deep valleys, led to climate-induced vicariance across the Palghat and Shencottah valleys. Subsequently, this resulted in clade endemism, leading to in situ radiations on either side of these biogeographic barriers, making these regions hotspots of biodiversity (Biju et al., 2014; Chaitanya et al., 2019; Vijayakumar et al., 2014).

The Goa gap (~15.8°N), on the other hand, tracks the southern margins of the Deccan Traps—a large igneous region formed by a series of volcanic eruptions during the KT boundary (~66 mya) which had profound effects on biodiversity in the region and possibly led to successional vegetation cycles and regional extirpation events (Dzombak et al., 2020; Glasby & Kunzendorf, 1996; Knight et al., 2003). The Goa gap is not a topographic obstacle, but an invisible, yet effective barrier occurring at the cusp of a wet–dry gradient in the Western Ghats (Barboni et al., 2003; Biswas & Karanth, 2021; Ramachandran et al., 2017). Studies of the evergreen forests of the Western Ghats and their distributions indicate that the Goa gap also serves as a vegetational transition zone (Pascal, 1988; Qureshi, 1965; Reddy et al., 2016). Some lineages could traverse, colonize and diversify across the Goa gap while others could not overcome this environmental barrier. While the Palghat and Shencottah valleys have caused cladogenesis in organisms due to climate-induced vicariance, diversification across the Goa gap seems to have been governed by the ecological ability of certain lineages to disperse through and colonize it (Biswas & Karanth, 2021; Ramachandran et al., 2017).

Many vertebrate lineages such as frogs of the genera *Indirana*, *Nyctibatrachus*, *Raorchestes*, numerous birds and agamids of the genus *Monilesaurus* have colonized the regions north of the Goa gap (Van Bocxlaer et al., 2012; Dahanukar et al., 2016; Pal et al., 2018; Ramachandran et al., 2017). However, others with seemingly better dispersal abilities such as the King cobra, *Ophiophagus hannah* (Cantor, 1836) and the hump-nosed pit viper, *Hypnale hypnale* (Merrem, 1820) reach the gap from the south but are

conspicuously absent from north of it (Maduwage et al., 2009; Yadav & Yanakanchi, 2015). Noteworthy among the list of absentees is the peninsular Indian Flying lizard—*Draco dussumieri* (Duméril & Bibron, 1837), that inhabits both the wet and dry forests (Chandramouli & Ganesh, 2010; Pardeshi & Naik, 2017; Ganesh et al., 2018). These lizards are found commonly in high-canopy forests, or tall plantations that are proximate to such forests along the west coast, the Western Ghats and the Eastern Ghats in peninsular India. Interestingly, previous studies have suggested that *Draco* presence is negatively correlated with altitude in the Western Ghats (Ishwar et al., 2003; Sreekar et al., 2013; Venugopal, 2010).

Draco has successfully dispersed across the Palghat and Shencottah valleys and across the intervening arid plains into the Eastern Ghats, but has not traversed the Goa gap (Figure 1). We posit that canopy physiognomy is a crucial factor influencing the occurrence of the exclusively arboreal *Draco* (McGuire & Dudley, 2011). Thus, we hypothesize that lower canopies, with lesser coverage, will emerge as unsuitable for *Draco* even in regions of suitable climate such as the Western Ghats north of the Goa gap.

To test this hypothesis, we used ecological niche models (ENMs) built using maximum entropy and logit models based on binary logistic regression to ascertain environmental variables of significance that are associated with the presence of *Draco* in peninsular India. Along with a suite of bioclimatic variables, we tested canopy-specific parameters as predictors for the presence of *Draco*. Trees north of the Goa gap are purportedly shorter than in regions south of this gap (Qureshi, 1965; Subramanyam & Nayar, 1974), and here we test this by statistically comparing canopy profiles from these regions (Figure 1b,c) to assess habitat suitability. Further, we compare the ecological niches occupied by *D. dussumieri* with *Monilesaurus rouxii* (Duméril & Bibron, 1837), another endemic, arboreal agamid which unlike *Draco* has successfully traversed the Goa gap and colonized regions both north and south of it, but does not occur south of the Shencottah pass (Pal et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Occurrence records of *Draco dussumieri* and *Monilesaurus rouxii*

We collated 135 records for the presence of *D. dussumieri* from peninsular India as a result of fieldwork conducted between November 2019 and March 2020, and from unpublished occurrence data (S. R. Ganesh & S. Chinta, personal communication), research grade observation data from the Global Assessment of Reptile Distributions (GARD) database (Roll et al., 2017, http://www.gardinitiative.org/) and The Global Biodiversity Information Facility (http://www.gbif.org). Records for 187 occurrences of *M. rouxii* from the study area were obtained from Pal et al. (2018), the GARD database, The Global Biodiversity Information Facility (http://www.gbif.org) and unpublished occurrence data of the species (S. Pal, personal

communication). Repeated sites for the same species were excluded from the analyses as were multiple sites that were within a 1-km^2 area to ensure that each raster cell does not contain more than one presence record (see details on environmental layers below). Additionally, multiple georeferenced points for *Draco* occurrences were removed from further analyses to correct for spatial autocorrelation (see section on correcting for spatial autocorrelation below). The final datasets used for spatial and statistical analyses contained 73 and 85 unique occurrences of *D. dussumieri* and *M. rouxii*, respectively, that were not spatially autocorrelated. These data are available in the supplementary material (Appendix S1) and publicly accessible from the Open Science Framework repository (https://osf.io/nr6xd/?view_only=248cd1a0abb14c92a69f003a85805bf3).

2.2 | Environmental data

To examine the environmental factors that affect the occurrence of *D. dussumieri* and *M. rouxii*, data were obtained from two sources with differing mechanisms of spatially characterizing bioclimatic data. This approach was taken since single-source modelling approaches are known to bias spatial predictions derived from ecological niche models (Morales-Barbero & Vega-Álvarez, 2018). We used both WorldClim 2.1—the Global Climate Data (Fick & Hijmans, 2017) which provides interpolated data layers consisting of long-term monthly temperature and precipitation values based on weather station observations—and CHELSA (Karger et al., 2017), which combines statistic interpolation (like WorldClim) and quasi-mechanistic statistical downscaling of data.

We downloaded data on 10 bioclimatic variables (averaged between the years 1970 and 2000) that are biologically relevant to the study organisms (see below). Variables such as mean temperatures of the wettest and driest quarters (BIO8 and BIO9) and mean precipitation of the warmest and coldest quarters (BIO18 and BIO19) were not considered for analyses as they potentially leave spatial artefacts in the data as a consequence of their linking between precipitation and temperature (Campbell et al., 2015). Elevation data were downloaded from WorldClim. Values of the annual aridity index (AI) and potential evapotranspiration (PET) were downloaded from the CGIAR-CSI website (Zomer et al., 2008). The 10 bioclimatic layers, and the AI and PET datasets were at a spatial resolution of 1 km^2.

Since *Draco* and *Monilesaurus* are exclusively arboreal (McGuire & Dudley, 2011; Pal et al., 2018), we downloaded data on canopy height (from Simard et al., 2011) and canopy coverage (from Hansen et al., 2013). Canopy coverage is defined as canopy closure for the year 2000 for all vegetation above 5 m in height and is encoded as a percentage of the area it occupies in a 1*1 arc-second (30 m^2) spatial grid. Canopy height data for 2005 are based on the spaceborne light detection and ranging (LiDAR) technique and were downloaded at a spatial resolution of 1 km^2. A limitation of the LiDAR technique is its inability to capture heights >40 m, especially emergent trees, in broadleaved, closed canopy tropical forests such as the Western Ghats. This limitation is mitigated by using the canopy height dataset

to quantify canopy heights accurately up to 40 m (Simard et al., 2011).

All layers were tested for collinearity by examining pairwise correlations between them. The Pearson's correlation coefficient between variable pairs was used to identify strongly correlated variables ($|r| > 0.75$) and six of the the 15 biologically relevant variables, that were weakly intercorrelated, were retained for further analyses. These variables take into account that these diurnal lizards are restricted to the tropics (BIO1—annual mean temperature, BIO4—temperature seasonality, BIO12—annual precipitation and BIO15—precipitation seasonality) and are chiefly arboreal (canopy heights, canopy cover).

All the georeferenced *D. dussumieri* and *M. rouxii* data along with the environmental layers were imported to ArcGis 10.2.2 (ESRI, 2011). The extents of all datasets were trimmed to accommodate the combined distributions of both species (7.94°N–22.63°N, 71.83E°–80.41°E) and the environmental data within these extents were extracted and exported for statistical analyses. To account for the difference in spatial resolution between canopy coverage and the other environmental layers, the canopy coverage layer was artificially resampled to 1-km^2 grids using bilinear interpolation implemented in the Spatial Analyst Tool in ArcGis 10.2.2.

2.3 | Statistical analyses of *Draco* presence/absence data

Owing to the lack of true absence data, we used 69 *Draco* pseudo-absence points that were collated from both sides of the Goa gap (15.8°N). Absence points were obtained from vegetational zones south of the Goa gap that are unsuitable *Draco* habitats such as the tropical montane forest–grassland mosaics or 'sky islands' and the arid scrub forests that intervene between the Western and the Eastern Ghats. Such regions, which are bereft of tall canopies, lie at the extremes of the temperature gradient prevalent in peninsular India. These biomes were identified using the vegetational classification of peninsular India by Renard et al. (2010) and Das et al. (2015). Further, occurrence data for *M. rouxii* that lie north of 15.8°N were used as pseudo-absence points for *Draco* since they further serve to identify regions with canopies that can support an arboreal agamid.

In order to identify the environmental variables that are significant for *Draco* occurrence and their effects, the predictors were subjected to binomial logistic regression to test their association with *Draco* presence/absence. Bioclimatic data from CHELSA and WorldClim were used for the analyses along with canopy-specific predictors to be able to ascertain model consistency between these dissimilar sources of data.

Given that we explicitly test the role of canopy physiognomy in shaping the distribution of *Draco,* we used an information theoretic approach. First, the best-subset regression using all six predictors was run to ascertain the model with the best fit out of all possible models. Best fit was evaluated using R^2-adj that accounts for the number of predictors in the model and Mallows' Cp (which compares the precision and bias of the full model with the best subset of predictors and must be a value close to the number of predictors used in the model). Once the best subset of predictors was ascertained, an a priori analysis containing this subset of predictors (H_0) was subjected to binary logistic regression analysis. Next, we eliminated the canopy variables (canopy height and canopy cover) from our best-subset model and estimated the new model (H_1) to ascertain whether the association of *Draco* can be attributed to climatic factors alone. A link logit function, with a confidence level of 95% for all intervals was used and model validation was done using the K-fold cross-validation method where $K = 5$ (instead of 10 to allow for more non-overlapping folds) with a pre-defined random number seed. Variance inflation factor was evaluated for each predictor. The models were evaluated using the AIC score, the Pearson's χ^2 and the Hosmer–Lemeshow χ^2 goodness-of-fit tests (Fagerland et al., 2008). All analyses were carried out using an online version of MINITAB (Arend, 1993).

2.4 | Ecological niche modelling

To ascertain the environmental variables that govern the presence of *D. dussumieri* and *M. rouxii*, a maximum entropy species distribution model was used as implemented in Maxent version 3.4.3 (Phillips et al., 2006). Maxent is a learning method that incorporates presence-only data and environmental variables to define and delimit the distribution of the maximum entropy and uses an algorithm that is less likely to be influenced by small sample sizes (Kumar & Stohlgren, 2009; Pearson et al., 2007). It uses a regularization parameter to control over-fitting and can handle both categorical and continuous variables (Phillips et al., 2006). Bioclimatic variables from CHELSA and WorldClim were used along with canopy-specific predictors to be able to compare the ecological niche models generated for *D. dussumieri* and *M. rouxii*. Further, in order to specifically test the role of canopy structure in shaping the distribution of *Draco*, we generated a Maxent model by excluding canopy variables from the analysis to test if regions north of the Goa gap are climatically suitable for the species.

The final raster format suitability models generated by Maxent using both datasets were analysed for spatial autocorrelation using the Spatial Analyst Toolkit implemented in ArcGis 10.2.2 (ESRI, 2011).

Georeferenced data for each species were randomly partitioned to allow 75% training data to fit the models and 25% for validation to evaluate model predictions for both species. We chose random partitioning over partitioning based on spatially stratified blocks to mitigate observation biases in the georeferenced data. For instance, certain broad regions where *Draco* and *Monilesaurus* occur tend to have more observation records in the data due to better access to these areas. Further, 30 replicates of each model were generated by bootstrapping to estimate variability, with the maximum number of background points set to 10,000. Bootstrapping was preferred over the cross-validation method due to a limited presence-only dataset. In order to choose the feature classes for our data, we selected both

linear and step functions (linear, quadratic, product and threshold) and allowed the Maxent 'auto features' option to automate the task of choosing the right feature types based on our sample sizes. Maxent uses regularization to limit model complexity in order to prevent over-fitting. Regularization is a penalty assigned to each term in the model in the form of a regularization parameter (β) specific to each feature class. We tested models calibrated with different values for β (0.25, 0.5,1.0, 2.0 and 5.0: 1.0 is the default) using the auto features option and used each model's discriminatory ability (AUC) and omission rates to choose the regularization multiplier that is best suited for our analyses. All models built using $\beta \leq 1.0$ resulted in models that were highly similar, with low omission rates and high discriminatory ability. We used $\beta = 1.0$ (default) as the regularization parameter for the rest of our analyses. The jackknife test in Maxent was used to estimate the contribution and significance of each variable to the final model when used in isolation as well as when omitted from the composite set of variables used to determine the model. Maxent generated response curves indicating change in suitability for both species were examined for each predictor variable. Finally, the mean (for 30 replicate runs) suitability maps generated by the logistic output format were obtained from the corresponding bootstrapped Maxent runs for each species, that depict an estimated probability of presence for the geographic extent used, with values ranging from 0 (unsuitable) to 1 (suitable).

2.5 | Evaluating ecological niche model performance

To evaluate the performance of the models generated, we used methods that were both dependent and independent of thresholds.

Area under the receiver operating characteristic curve (AUC), which calculates the ability of a model to discern areas where the focal species occurs and areas where it does not (1: perfect predictive ability, 0: no predictive ability), was used to evaluate model performance. It is a threshold-independent measure of the model's ability to separate presence from absence and is obtained by plotting sensitivity against 1–specificity. An AUC value of >0.9 was used to indicate high model performance.

However, the traditional evaluation based on AUC has been criticised, especially when using presence-only data, for being based on equal weighting of omission and commission errors (Lobo et al., 2008; Peterson et al., 2008). Therefore, we additionally used the partial area under the receiver operating curve (pROC) metric for ecological niche model evaluations following Peterson et al. (2008). This metric assesses the relationship between omission error for independent points and the relative area predicted as suitable for the species. In this metric, AUC ratios range from 0 to 2, where values of 1 represent random performance (Peterson et al., 2008). These analyses were carried out in the web-based application NicheToolbox (Osorio-Olvera et al., 2020) using 100 replicates with an omission proportion of 5%, 10% and 15%. Further, we used the true skill statistic (TSS) which is a threshold-dependent measure and accounts

for model omission and commission errors. The index ranges from –1 to +1, where +1 indicates perfect agreement with the model and 0 or less indicates performance no better than random. The TSS analysis was carried out in the NicheToolbox (Osorio-Olvera et al., 2020) and its own optimal threshold was used to evaluate model performance. Model performances were scored based on Araújo et al. (2005): excellent if $\kappa > 0.75$, good if $0.75 > \kappa > 0.4$ and poor if $\kappa < 0.4$. Models were considered useful if TSS ranged from 0.75 to 0.5.

The three measures of model performance (AUC, pROC and TSS) were evaluated for models generated using the CHELSA and WorldClim datasets, for both *Draco* and *Monilesaurus*.

2.6 | Correcting for spatial autocorrelation in Maxent models

We inspected the model residuals for evidence of spatial autocorrelation (Dormann et al., 2007). While there is an abundance of literature that discusses controls for spatial autocorrelation, little of it overlaps with models generated using Maxent (see Halvorsen et al., 2016; Phillips et al., 2017). For Maxent models that depict probability of habitat suitability, the residuals can be calculated using the probability of the observation (1) – probability of prediction (see Mateo-Tomás & Olea, 2010). With probability models as generated by Maxent, using either residuals (1 – predicted values), or the predicted values themselves to test spatial autocorrelation should yield the same result.

Once Maxent models for *D. dussumieri* and *M. rouxii* were generated (run 1), spatial autocorrelation was tested using the Spatial Statistics toolset in ArcGis. The Incremental Spatial Autocorrelation program implemented in ArcGis (Spatial Statistics toolset) was then used to find the minimum threshold distance between points within which spatial autocorrelation exists. The incremental spatial autocorrelation tool runs analyses for a series of increasing distances between points, measuring clustering in the data for each distance until the *z*-score for the Moran's Index peaks at a particular distance (ESRI, 2011). Once the threshold distance for spatial autocorrelation was determined, points within this distance were removed. Maxent models for the new dataset were then generated (run 2) and further tested for spatial autocorrelation.

2.7 | Zonal canopy statistics of regions from either side of the Goa Gap

Regions north and south of the Goa gap were examined to assess differences in canopy profiles, which might act as a potential barrier for an arboreal organism such as *D. dussumieri*. The region 'north of the Goa gap' was demarcated from slightly north of the northernmost distribution of *D. dussumieri* in the Western Ghats up to the northernmost distribution of *M. rouxii* (15.8°N–19.3°N). Despite the Western Ghats extending further up to 21°N, the northernmost distribution of *M. rouxii* was used as a proxy for the presence of canopies

that can support arboreal agamids. The distribution range of *D. dussumieri* in the Western Ghats (8.1°N–15.7°N) was aggregated from the north and south of the Palghat gap as the area 'south of Goa gap' for further analysis. Canopy cover and canopy height values for each 1-km^2 cell were obtained for the regions north and south of the gap and statistical analyses of their central tendencies were carried out for each of them to determine differences in canopy profiles. Extraction of raster data and zonal statistical analysis were carried out in ArcGis 10.2.2, implemented in the Spatial Analyst toolkit.

3 | RESULTS

3.1 | Spatial autocorrelation in the *D. dussumieri* and *M. rouxii* models

The occurrence data for *D. dussumieri* were found to be spatially clustered (Moran's *I*: 0.14, *z*-score: 4.667, *p*-value: <0.01) in run 1.

Consequently, points within a radius of <6.3 km were further removed, as suggested by the incremental spatial autocorrelation tool, leaving 73 occurrence records of *D. dussumieri* for further analyses. The corrected *D. dussumieri* dataset was spatially uncorrelated (run 2) and showed a more or less random clustering pattern (Moran's *I*: −0.02, *z*-score: −0.277, *p*-value: 0.78). The data for *M. rouxii* were not spatially autocorrelated (Moran's *I*: 0.0016, *z*-score: 0.879, *p*-value: 0.379) and therefore all 85 occurrence records were retained for spatial analyses.

While relative contributions of predictor variables to the Maxent models varied between run 1 and run 2 (the runs with and without spatial autocorrelation, respectively, for the *D. dussumieri* data), their relative significance did not change. Further, run 1 and run 2 returned similar AUC values indicating that spatial autocorrelation in the data had little influence on the Maxent models or their performance.

3.2 | Significant environmental predictors and their effects on the distribution of *D. dussumieri*

The best-subset model comprised of the predictors BIO1, BIO4, BIO12, canopy height and canopy cover (R^2-adj = 52.2, Mallows' Cp = 5.0; see Appendix S2.1 for evaluations of all other models). Tests for the best-subset binary logistic regression (H_0) produced similar models with low AIC scores (87.3) and good fits for both the CHELSA

(The Hosmer–Lemeshow test failed to reject the null hypothesis of a good fit; $\chi^2 = 5.84$, *df* = 8, *p* = 0.67) and WorldClim ($\chi^2 = 4.77$, *df* = 8, *p* = 0.78) datasets. Both models (CHELSA/WorldClim) indicate positive associations of *Draco* presence with canopy height (odds ratio: 1.62/1.59), BIO1—mean annual temperature (1.04/1.49) and canopy cover (1.02/1.03), whereas other variables had marginally negative effects (Table 1; Appendices S2.2 and S2.3).

However, the model generated after the elimination of canopy effects (H_1) returned a much higher AIC score (153.04) and the goodness-of-fit tests rejected the null hypothesis ($\chi^2 = 13.94$, *df* = 8, *p* = 0.01; Appendix S2.4). These results suggest that, while climatic predictors when used in isolation fail to predict *Draco* presence, canopy structure has the most influence on their occurrence in regions of climatic suitability.

3.3 | Ecological niche models of *D. dussumieri* and *M. rouxii*

Maxent analyses on *D. dussumieri* occurrence data generated using both the CHELSA and WorldClim datasets resulted in model predictions that were strongly correlated (Pearson's *r* = 0.99) and accurate under all criteria used for model evaluation (Table 2, Appendices S3.1 and S3.2). The predictors influencing *Draco* presence in both models were similar with slightly varying contributions (Table 3). The Maxent models for *M. rouxii* using the CHELSA and WorldClim datasets were also strongly correlated (Pearson's *r* = 0.95) and returned accurate predictions under all criteria used for evaluation (Table 2, Appendices S3.3 and S3.4).

However, the relative significance and contributions of predictors influencing *M. rouxii* occurrence varied marginally between the WorldClim and CHELSA datasets (Table 3).

The environmental variables that had the greatest influence on *D. dussumieri* presence were canopy height, canopy cover and BIO4, accounting for a cumulative contribution of ~94% (using the CHELSA dataset) to the fit of the model. The jackknife test indicated that canopy height both improved the fit of the model the most when considered in isolation and reduced the fit of the model the most when omitted from the multivariate analyses (see Appendices S3.1 and S3.2). Suitable habitat range for the species (suitability >0.60) was disjunct, with a cumulative area of 32,920 km^2, mostly occurring in the Western Ghats and a few isolated hills in the Eastern Ghats (Figure 2a).

TABLE 1 Coefficients and odds ratios for the best-subset binary logistical regression model (H_0) with the CHELSA dataset (see Appendix S2.3 for the WorldClim model)

Term	Coefficient	SE coefficient	Z-value	p-value	VIF	Odds ratio	95% CI
Constant	−12.61	5.13	−2.46	0.014			
Canopy height	0.483	0.127	3.8	<0.001	2.06	1.6217	(1.2640, 2.0806)
BIO1	0.045	0.0147	3.05	0.002	1.21	1.046	(1.0162, 1.0766)
Canopy cover	0.0243	0.0118	2.07	0.038	1.34	1.0246	(1.0013, 1.0485)
BIO4	−0.0037	0.00129	−2.86	0.004	1,21	0.9963	(0.9938, 0.9988)
BIO12	−0.000914	0.000342	−2.67	0.008	1.78	0.9991	(0.9984, 0.9998)

TABLE 2 Evaluation metrics for the four niche models using mean area under the curve (AUC; 30 replicates), partial receiver operator characteristics ratio according to three omission proportions (pROC ratio 5%, 10% and 15%; 100 replicates) and true skill statistic (TSS)

Model	AUC	pROC ratio			TSS
		5%	10%	15%	
Draco/WorldClim	0.951±0.007	1.876	1.873	1.874	0.686
Draco/CHELSA	0.951±0.004	1.876	1.879	1.876	0.694
Monilesaurus/ WorldClim	0.967±0.005	1.930	1.937	1.937	0.735
Monilesaurus/ CHELSA	0.967±0.005	1.930	1.930	1.930	0.721

TABLE 3 Estimates of relative (%) contributions of predictor variables to the Maxent models using WorldClim and CHELSA bioclimatic datasets
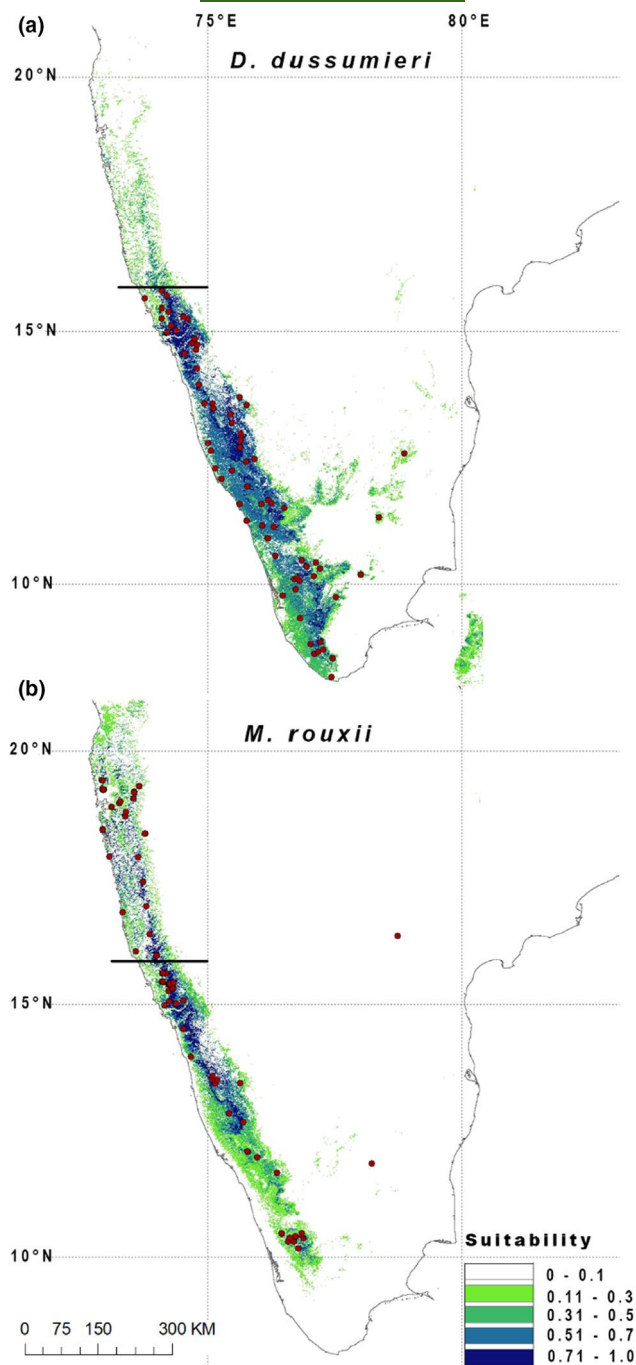
Variable	*D. dussumieri*		*M. rouxii*	
	WorldClim	CHELSA	WorldClim	CHELSA
Canopy heights	**54.3**	**57.1**	5.6	5.9
Canopy cover	**22.5**	**16.4**	**10**	**11.5**
BIO4	**13.6**	**20.4**	7.8	**12.2**
BIO12	7.2	3.2	**62.1**	**58.1**
BIO15	1.2	2.1	**8.3**	8.3
BIO1	1.2	0.9	6.3	4.1

Values are averaged across 30 bootstrap replicates and the three most influential predictors for each model are highlighted.

The model (see Appendices S3.1 and S3.2) suggests that *D. dussumieri* inhabit (suitability >0.60) regions with low temperature seasonality (BIO4: 100–150 standard deviation * 100) and a mean annual temperature (BIO1) in the range of 15°C–25°C. Overall, regions with an annual average rainfall of >2000 mm are suitable for *D. dussumieri*. The factor that influences the *D. dussumieri* suitability model the most is canopy heights. Habitat suitability increases to >0.60 in regions where the canopy is ~17 m or higher, and peaks (>0.90 suitability) in regions where canopies heights >35 m. Further, suitability for *Draco* increases with 40% canopy cover and peaks at about 80% after which it decreases marginally.

Further, the Maxent model for *Draco* generated without canopy-specific variables increases the area of high suitability (>0.70) in regions north of the Goa gap when compared with the model generated using both canopy and climatic variables. This further supports our hypothesis that *Draco* could not span the Goa gap due to a lack of suitable canopies, rather than differences in climate. The suitability maps for ecological niche models with and without canopy variables are provided in Appendix S3.5 for comparison.

For *M. rouxii*, (see Appendices S3.3 and S3.4) annual precipitation (BIO12), temperature seasonality (BIO4) and canopy cover accounted for ~82% of the overall contribution towards the Maxent model. Jackknifing indicated that annual precipitation was the

FIGURE 2 Suitability maps of peninsular India generated using climatic (CHELSA dataset) and canopy variables, averaged over 30 bootstrap replicates for (a) *Draco dussumieri* and (b) *Monilesaurus rouxii*. Occurrence data for the species are marked with red dots and the dark lines indicate the position of the Goa gap. Maps are projected on the World Geodetic System 1984 (WGS84)

variable influencing model-fit the most when considered in isolation while temperature seasonality reduced the fit of the model the most when omitted. The models suggest that mean annual temperature preferences of *M. rouxii* are higher than *D. dussumieri* but largely overlap in range (BIO1: 16°C–26°C). They exhibit a similar tolerance

to temperature seasonality but prefer wetter habitats with a mean annual precipitation >2500 mm. Despite being arboreal, *M. rouxii* can cope with canopy coverage as low as 10% where trees are 17–35 m tall. However, the presence probability of *M. rouxii* declines in regions where tree heights are >30 m unlike *D. dussumieri* that seems to prefer taller canopies (Figure 2b, Appendix S3).

Response curves of the significant environmental variables to the *D. dussumieri* and *M. rouxii* Maxent models using CHELSA and WorldClim datasets are provided in Appendix S3.

## 3.4 | Differences in canopy structure across the Goa gap

The analysis of the canopy cover raster data reveals that north of Goa gap constitutes >73% area where trees are less than 5 m tall (raster value 0%). Contrastingly, in the south of Goa gap, only ~30% of the area consists of regions with trees that are less than 5 m. As a result, canopy cover north of Goa gap is significantly lesser (median 0%) than the regions south of it (median 52%; Kruskal–Wallis H test: $\chi^2 = 9.88$, $H_c = 1.07$, $p < 0.0001$), indicating much higher habitat suitability for *D. dussumieri* south of the Goa gap. Similarly, canopy heights are lower north of the gap (median 13 m), where *Draco* is not observed as opposed to the south of it (median 22 m; Kruskal–Wallis H test: $\chi^2 = 7.62$, $H_c = 7.64$, $p < 0.0001$). The numerical differences and central tendencies in canopy variables between these regions are listed in Appendix S4.1 and illustrated in Figure 3a–c.

4 | DISCUSSION

4.1 | Interpreting responses to climatic and canopy predictors

Across the Western Ghats, overall suitable habitats (presence probability >0.60) are larger for *D. dussumieri* than for *M. rouxii* (Figure 2, Appendix S3). According to the maximum entropy models, these two species respond similar to most climatic variables, although *M. rouxii* is more dependent on higher mean annual precipitation (BIO12). This ties-in with the ecology of *M. rouxii* that are wet-habitat specialists (Pal et al., 2018) while *D. dussumieri* inhabit both the wet and dry deciduous forests in the Western Ghats (Chandramouli & Ganesh, 2010; Pardeshi & Naik, 2017; Ganesh et al., 2018). This lesser dependence on the amount and seasonality of rainfall probably explains why habitable areas for *Draco* are significantly larger in the Western Ghats despite being restricted to the south of the Goa gap (Figure 2a,b).

The binary regression models suggest that mean annual temperature (BIO1) is the second strongest variable influencing *Draco* presence, unlike what the maximum entropy models reveal. The difference is likely due to the dissimilar approaches these methods employ in model building. Maximum entropy algorithms as implemented

(a)

(b) **Canopy Cover**
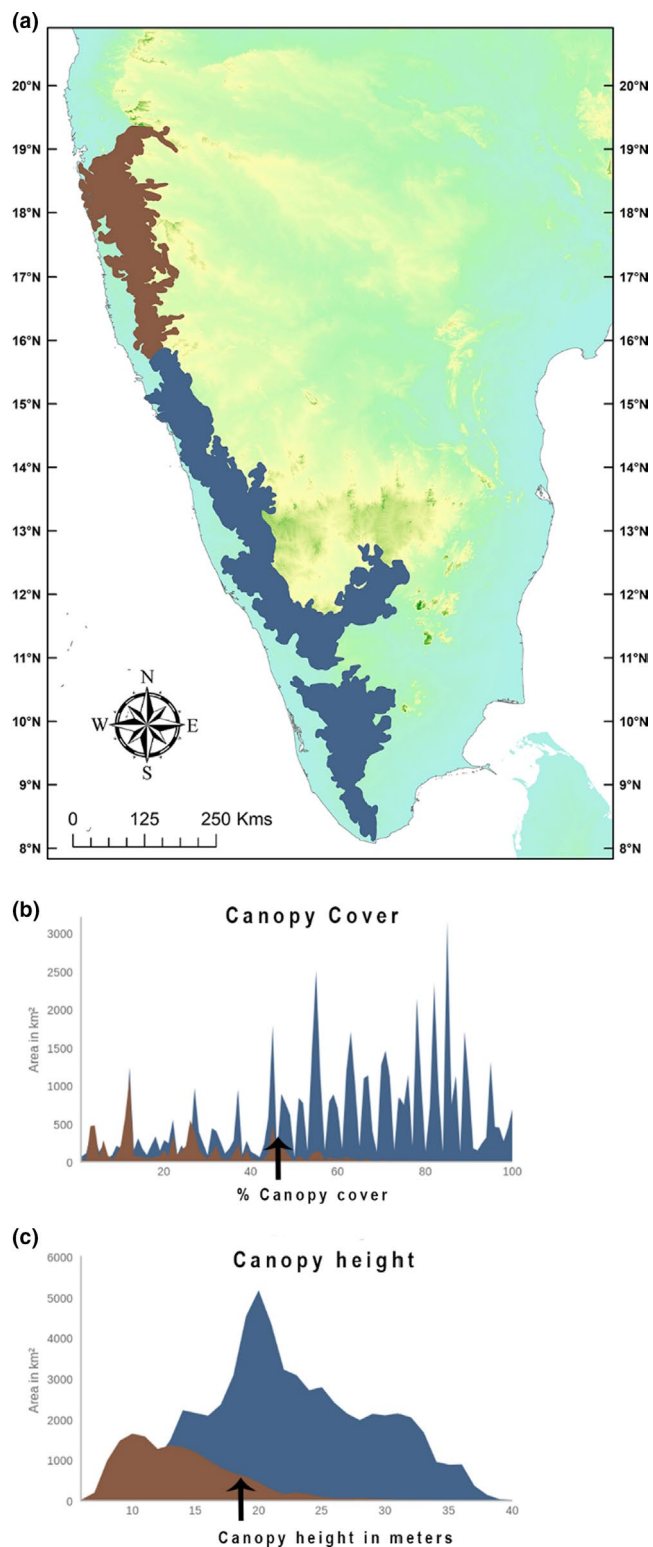
(c) **Canopy height**

FIGURE 3 Map of peninsular India (a) showing the regions of the Western Ghats demarcated as south of Goa gap (blue) and north of Goa gap (brown). Area graphs depicting differences in (b) canopy cover and (c) canopy height between the two regions (grids with 0% canopy cover are omitted from the graph to improve visualization). The arrows indicate points after which *Draco* habitat suitability increases (presence probability >0.60) according to the maximum entropy models. Maps are projected on the World Geodetic System 1984 (WGS84)

in Maxent use presence-only data to infer bioclimatic ranges an organism cannot tolerate. Contrastingly, the binary regression analysis uses both presence and absence data while building the model and are therefore able to categorically implicate temperature (and other bioclimatic predictors) ranges that *Draco* does not survive in. Consequently, the regression models are able to better recognize the strong association of *Draco* presence with a specific temperature range, explaining why BIO1 is a significant predictor for *Draco* occurrence. Nevertheless, both the logistic regression models and the maximum entropy models generated in this study, using the CHELSA and WorldClim datasets, indicate that canopy height is the most important environmental predictor for the presence of *Draco* in peninsular India.

Despite their arboreal habits and extensive sympatry across the Western Ghats, *D. dussumieri* and *M. rouxii* significantly differ in their choice of tree niches. During fieldwork, RC observed that *Draco* usually inhabit the high canopies, and venture down the trunk to bask, forage or to attract mates during the breeding season. Their response to threat is usually by fleeing to the higher reaches of the canopy or gliding to an adjacent tree. They have therefore eliminated the need to descend to the ground except for when the females have to lay their eggs. The ecology of *D. dussumieri* suggests an affiliation to tall trees (>18 m), and so it is unsurprising that in regions of suitable climate, the ecological niche models implicate canopy height and coverage as the crucial predictors of *Draco* presence. On the other hand, RC's field observations suggest that *M. rouxii* prefer to occupy the mid to lower regions of the tree trunk and are seen on the ground foraging or moving to an adjacent tree. Juveniles are often seen on low shrubs during the day and sleeping on them at night. While *M. rouxii* requires regions with reasonable canopy cover, our observations and analytical results suggest that they are not as dependent on the height of the canopy as *D. dussumieri* are.

The canopy height dataset (Simard et al., 2011) is limited in its ability to discern heights above 40 m in broadleaved evergreen closed canopy forests. Our study indicates that *Draco* suitability increases where canopies are at least 18 m tall but does not evaluate the upper limits because of this limitation. Nevertheless, the canopy height dataset provides sufficient statistical signal of the association between *Draco* presence and tree height. Further, the canopy height and coverage datasets do not discriminate between forests and human-modified landscapes such as plantations. Our results thus indicate that habitat suitability for *Draco* increases in regions with tall canopies and reasonable cover which includes high-canopy plantations such as Areca and Coconut.

4.2 | The curious distribution of *Draco* in peninsular India

Draco occur across deep valleys, such as the Palghat gap and Shencottah pass, and in certain isolated hills in the southern Eastern Ghats, a disjointed mountain range that runs parallel to the eastern coast of peninsular India (Ganesh et al., 2018). In the Western Ghats, *Draco* does not occur in the high-elevation shola forests that consist of stunted short-boled evergreen trees (Meher-Homji, 1967). That said, anecdotal evidence suggests their presence in the eastern escarpments abutting shola forests where tall trees are present (S. R. Ganesh, personal communication). The Eastern and Western Ghats mountain complexes are separated by arid plains bereft of tall trees (Mani, 1974a) that are inhospitable for forest dwelling, arboreal lizards, such as *Draco*. In the Western Ghats, the northern distribution limit of *Draco* is reached abruptly at the Goa gap, which is not a physical barrier but a climatic boundary demarcating the wet and dry regions in the Western Ghats (Ramachandran et al., 2017). While *Draco dussumieri* inhabit both wet and dry forests of the Western Ghats (Chandramouli & Ganesh, 2010; Ganesh et al., 2018; Pardeshi & Naik, 2017), *M. rouxii* are restricted to the wet regions (Pal et al., 2018). This ecological dissimilarity is further corroborated by our Maxent models that show that *M. rouxii* are more dependent on mean annual precipitation (BIO12) than *Draco* are. Further, the Maxent model for *Draco* constructed only with climatic variables shows a significant increase in suitable habitats north of the Goa gap. Therefore, the drier climatic regime prevalent north of the Goa gap is unlikely to have acted as a barrier to the dispersal of *Draco* into these regions. So why have *Draco* succeeded in dispersing across deep valleys and arid plains, also bereft of tall canopies, but have curiously failed to cross the Goa gap despite climatic suitability in this region?

Tall canopies of tropical evergreen broadleaved forests persisted across peninsular India between the mid-Miocene climatic optimum (17–15 mya) until the beginning of the Tortonian (11.6 mya) (Pound et al., 2012; Prasad et al., 2009). Subsequently, alternating cooling and warming events, including severe aridification during the Late Miocene (*ca.* 11–5 mya), resulted in the fragmentation of these forests and the spread of drier biomes (Morley, 2000; Patnaik et al., 2012; Pound et al., 2012). While such forest fragmentation resulted in climate-induced vicariance of many faunal groups (Biswas & Karanth, 2021), there is sufficient evidence to suggest continued dispersal in some of these organisms well into the Pliocene (5.33–2.58 mya) and into the Quaternary (<2.58 mya) (Vijayakumar et al., 2014). Therefore, many biogeographers argue that the valleys in the Western Ghats, and the intervening arid plains that separate the Western and Eastern Ghats, retained permeable causeways until very recently (Chaitanya et al., 2019; Hegde et al., 2020; Vijayakumar et al., 2014). Since *Draco* can subsist in drier vegetation with tall trees such as the dry deciduous forest types in the Western Ghats, we posit that they would have been able to use these Pliocene–Quaternary vegetation corridors to traverse these disjunct habitats. Moreover, Pleistocene relict forests still persist in the isolated hills of the southern Eastern Ghats, with evergreen elements typical of the Western Ghats at the higher reaches, and tall deciduous trees with high canopies in the escarpments that are suitable habitats for *Draco* (Mani, 1974a).

On the contrary, the regions north of the Goa gap seem to be a distinct phytogeographic realm. Subramanyam and Nayar (1974) classified the vegetation of the Western Ghats where they demarcate the region from the Tapti River up to Goa as a distinct zone. Qureshi (1965)

notes that the regions north of the Goa gap (state of Maharashtra) harbour atypical evergreen forests that are characteristically 'dwarfish' and classifies them as montane subtropical evergreen forests to distinguish them from the evergreen forests in the rest of the Western Ghats. Our statistical analyses of these regions also reveal canopies with distinctly shorter tree heights and lesser canopy coverage when compared with the rest of the Western Ghats (Figure 3b,c).

Draco in peninsular India inhabits a vegetation gradient ranging from dry deciduous to wet evergreen forests. Their ability to occupy these different biomes seems to allow them to disperse more readily than organisms that are adapted to a specific habitat. However, they are not found in regions that are bereft of contiguous tall canopies. Consequently, despite being restricted in area, the Eastern Ghats harbour canopies that are conducive to the subsistence of *Draco* while shorter trees and constricted canopy cover seem to impede their dispersal into the regions north of the Goa gap.

4.3 | Future work

The Goa gap is a climatic and vegetational barrier to the dispersal of organisms. For example, certain ubiquitous snake species such as the King cobra and the hump-nosed pit viper are also precluded in their range at the Goa gap (Maduwage et al., 2009; Yadav & Yanakanchi, 2015). However, given their predominantly terrestrial habits, the variables that govern their biogeography are bound to be quite different from *Draco* and are worth investigating. The Goa gap also demarcates the southern boundary of the Deccan Trap lava flows that occurred during the KT boundary, which implies that geology and soil composition also differentiate lands to the north of it from the rest of the Western Ghats. All these differences may serve as important barriers to organisms such as the above-mentioned snakes and are worthy of investigation.

The absence of *Draco* in Sri Lanka is intriguing. India and Sri Lanka have been connected by land bridges throughout their geological history and have only been separated by the narrow and shallow Palk Strait as recently as 6000 years ago (McLoughlin, 2001). Consequently, these landmasses share numerous faunal lineages such as bush frogs (Meegaskumbara et al., 2019), toads (Van Bocxlaer et al., 2009), night frogs (Vijayakumar et al., 2019) and agamids (e.g. *Calotes*; Pal et al., 2018). Moreover, our ecological niche models reveal large, contiguous regions in Sri Lanka that are suitable habitats for *Draco*. The absence of *Draco* in Sri Lanka therefore warrants a study that investigates the factors that may have prevented dispersal, or made existing populations there go extinct.

The remarkable radiation of *Draco* in Southeast Asia (39 species; Uetz et al., 2021) implores investigations on the distribution patterns of species in the region. Klabacka et al. (2020) demonstrated that the major rivers in the Indochinese region have impeded gene flow in the *D. maculatus* species complex causing phylogenetic breaks that spatially coincide with these riverine barriers. Further, the lesser Sunda Shelf is peppered with numerous islands of varying sizes and harbours a great diversity of *Draco* species. Reilly et al. (2021) suggest

that geological and oceanographic conditions have influenced *Draco* dispersal pathways, leading to speciation in these islands. However, Southeast Asia harbours a wide diversity of forest types, ranging from the tropical rain forests comprising tall trees in the Sunda shelf to tropical savannas and the temperate forests of Indochina (Stibig et al., 2007; Heinicke et al., 2012). Since *Draco* cannot thrive in the absence of tall trees, studies that examine how forest types affect the distributions of *Draco* species in Southeast Asia will contribute immensely to our understanding of their biogeography.

CONFLICT OF INTEREST
The authors declare that there exists no conflict of interest.

DATA AVAILABILITY STATEMENT
All georeferenced location data used in this study are made available in the supplementary material (Appendix S1) and are publicly accessible from the Open Science Framework repository (https://osf.io/nr6xd/?view_only=248cd1a0abb14c92a69f003a85805bf3).

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