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Distributions of mammals in Southeast Asia: The role of the legacy of climate and species body mass

Viktoriia Radchuk¹  | Stephanie Kramer-Schadt^{1,2}  | Joerns Fickel^{1,3}  |
Andreas Wilting¹ 

¹Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, Germany

²Department of Ecology, Technische Universität Berlin, Berlin, Germany

³Institute for Biochemistry and Biology, University of Potsdam, Potsdam-Golm, Germany

Correspondence

Viktoriia Radchuk, Leibniz Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17, 10315 Berlin, Germany. Email: radchuk@izw-berlin.de

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Abstract

Aim: Current species distributions are shaped by present and past biotic and abiotic factors. Here, we assessed whether abiotic factors (habitat availability) in combination with past connectivity and a biotic factor (body mass) can explain the unique distribution pattern of Southeast Asian mammals, which are separated by the enigmatic biogeographic transition zone, the Isthmus of Kra (IoK), for which no strong geophysical barrier exists.

Location: Southeast Asia.

Taxon: Mammals.

Methods: We projected habitat suitability for 125 mammal species using climate data for the present period and for two historic periods: mid-Holocene (6 ka) and last glacial maximum (LGM 21 ka). Next, we employed a phylogenetic linear model to assess how present species distributions were affected by the suitability of areas in these different periods, habitat connectivity during LGM and species body mass.

Results: Our results show that cooler climate during LGM provided suitable habitat south of IoK for species presently distributed north of IoK (in mainland Indochina). However, the potentially suitable habitat for these Indochinese species did not stretch very far southwards onto the exposed Sunda Shelf. Instead, we found that the emerged landmasses connecting Borneo and Sumatra provided suitable habitat for forest dependent Sundaic species. We show that for species whose current distribution ranges are mainly located in Indochina, the area of the distribution range that is located south of IoK is explained by the suitability of habitat in the past and present in combination with the species body mass.

Main conclusions: We demonstrate that a strong geophysical barrier may not be necessary for maintaining a biogeographic transition zone for mammals, but that instead a combination of abiotic and biotic factors may suffice.

KEYWORDS

habitat suitability, Isthmus of Kra, least-cost path, PanTHERIA, phylogenetic regression, species distribution model

1 | INTRODUCTION

It is widely accepted that species distributions and thus biodiversity patterns result from the interplay of both biotic and abiotic factors (Soberón, 2007), not only those currently active, but also those experienced in the past (Dullinger et al., 2012; Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015; Svenning & Skov, 2007a). However, the majority of biogeographic transition zones, i.e. zones separating the regions that encompass the distribution ranges of distinct groups of biota, are usually explained by the presence of a strong geological or geographic barrier to species movement (e.g. Isthmus of Panama; Bacon et al., 2015). One prominent biogeographic transition zone, however, cannot be explained by presence of such a geophysical barrier—the Isthmus of Kra (IoK) on the Malay Peninsula (Figure 1a), which separates mainland Indochina from Sundaland (Hughes, Satsook, Bates, Bumrungsri, & Jones, 2011; Woodruff & Turner, 2009). The IoK is located at 10°30' N and at its narrowest point is today only 44 km wide (Parnell, 2013). Depending on the taxa studied (i.e. bats: Hughes et al., 2011; birds: Hughes, Round, & Woodruff, 2003; butterflies: Corbet & Pendlebury, 1992; amphibians: Inger, 1999; mammals: Woodruff & Turner, 2009), the exact location of this zoogeographic transition zone was reported to be between 5 and 13° N. Understanding what factors shape species distributions around this biogeographic transition zone is especially important in a world facing a period of unprecedented environmental change. Indeed, such knowledge could shed light on possible future changes in species distributions and assist in formulating more efficient management plans.

To explain how IoK has become such a prominent biogeographic transition zone it has been suggested that rapid sea-level

risks during the last 5 Myr have submerged the narrow central and northern land stretches, causing local faunal extinctions and compressing species distributions to regions north and south of IoK (Woodruff & Turner, 2009). However, low sea levels during glacial periods in the last 2 Myr uncovered land bridges that connected Sundaic and Indochinese landmasses (Lohman et al., 2011). Such land bridges could allow for species movement across IoK only if they were covered by suitable habitat. Some studies that focused on the reconstruction of the vegetation cover in Southeast Asia during the last glacial maximum (LGM, ~21,000 years ago) suggest that central Sundaland was covered by humid tropical forest that connected the Sunda islands in west-east direction (Cannon, Morley, & Bush, 2009; Raes et al., 2014), whereas savanna-like conditions persisted on the emerged lands north of Sundaland. However, other studies provide support for a much larger spread of open savanna-like vegetation, which probably formed a transequatorial corridor that crossed Sundaland from north to south (Bird, Taylor, & Hunt, 2005; Gathorne-Hardy, Syaokani, Davies, Eggleton, & Jones, 2002; Meijaard, 2003). This would have restricted the tropical rain forests to smaller refugia mainly in Sumatra and Borneo. There is thus no consensus about what habitat prevailed on Sundaland during the LGM (Lohman et al., 2011).

Meijaard (2009) has suggested that even in the absence of a strong geophysical barrier, the distinction between the Sundaic and Indochinese biota could have been maintained by the ecology of the species in combination with availability of suitable habitat. More generally, a conceptual framework suggested by Soberón (2007) distinguishes three sets of factors that affect species distributions: abiotic factors (represented by habitat suitability, often inferred from climatic data), biotic factors (reflected by interactions with other species, often summarized by competitive ability of a species

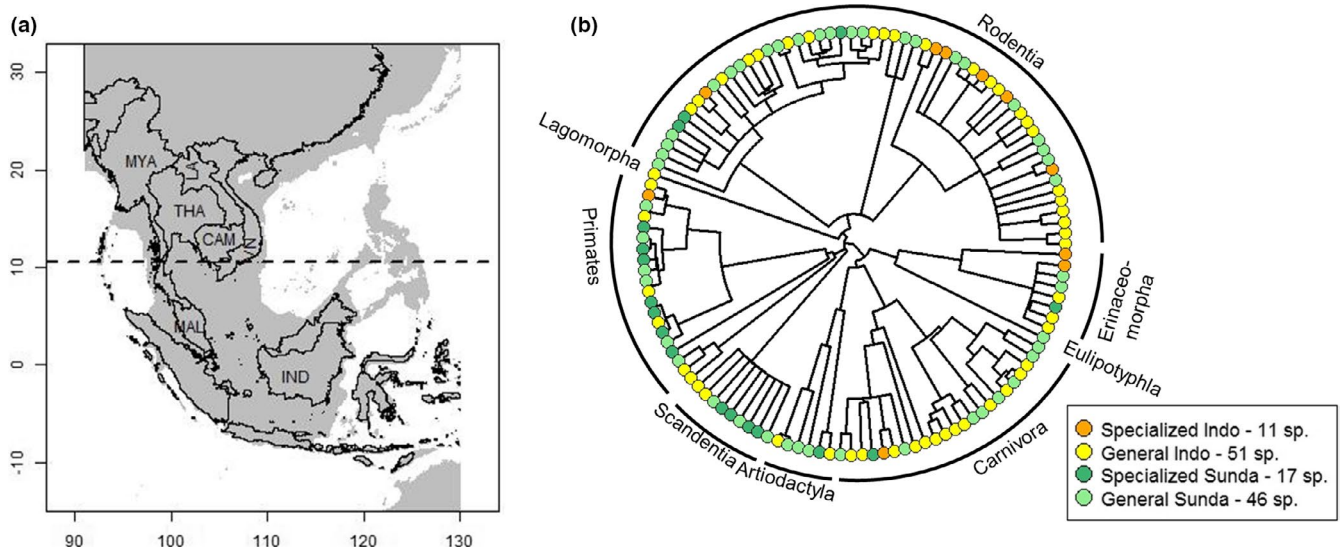


FIGURE 1 (a) Map of the study area showing the current landmasses with black solid line and landmasses during LGM in light grey. The abbreviations of the countries are as follows: VN—Vietnam, CAM—Cambodia, THA—Thailand, MYA—Myanmar, LA—Laos, MAL—Malaysia, IND—Indonesia. The horizontal dashed line indicates the latitude of the Isthmus of Kra (10°30' N); (b) The phylogeny of 125 non-volant mammal species used in our study, showing their distribution group (*specialized Indochinese*, *general Indochinese*, *specialized Sundaic*, *general Sundaic*), the number of species in each distribution group, and the taxonomic orders they belong to

in consideration) and connectivity (reflecting the accessibility of the suitable abiotic conditions). Thus, the current distribution ranges are shaped by these factors acting during consecutive periods from the past to the present (Svenning et al., 2015). Although the factors affecting species distributions presently received a fair share of attention, the “legacy” effects looking at the impacts of factors in previous periods have mainly been studied in plant species (Dullinger et al., 2012; Normand et al., 2011; Svenning & Skov, 2007a, 2007b).

We addressed the question of how abiotic and biotic factors as well as connectivity shape biogeographic transition zones over time in the absence of a geophysical barrier, by focusing on IoK. In particular, we assessed how the present distribution ranges of non-volant mammals inhabiting the areas around IoK are affected by (a) abiotic factors acting during the past (LGM, c. 21 ka and mid-Holocene, 6 ka) and present, (b) connectivity of available habitats during the LGM, and (c) biotic factors. Based on their present distributions, we classified 125 mammal species into two large distribution groups (Indochina and Sundaland), each with two subgroups, distinguishing the more specialized species (*specialized Indochinese*: ranges exclusively north of 12° N; *specialized Sundaic* species: ranges

exclusively south of 5° N) from the ones with more general requirements (*general Indochinese*: ranges predominantly in Indochina, but reaching into the transition zone from 5 to 12° N; *general Sundaic*: ranges mainly in Sundaland, but protruding into the transition zone). We note that the term “specialized” is used here to refer to general climatic (habitat) requirements of a species, and not to its diet.

To understand how IoK had become such a strong transition zone, we combined species distribution modelling (SDM), which allows hindcasting habitat suitability during the LGM and mid-Holocene, with comparative methods (phylogenetic linear model), which enable comparison of species-specific characteristics among related species, and tested the following two hypotheses (Figure 2):

H1—We hypothesized that the land emerged during LGM affected the habitat availability for predominantly *general Indochinese* and *general Sundaic* species, because they are less specialized and should be able to invade newly available habitats more readily. We derived two predictions based on H1: P1 (regarding the total habitat area in the past)—We predict that for *general Indochinese* species the total area of potentially suitable habitat was higher during the LGM

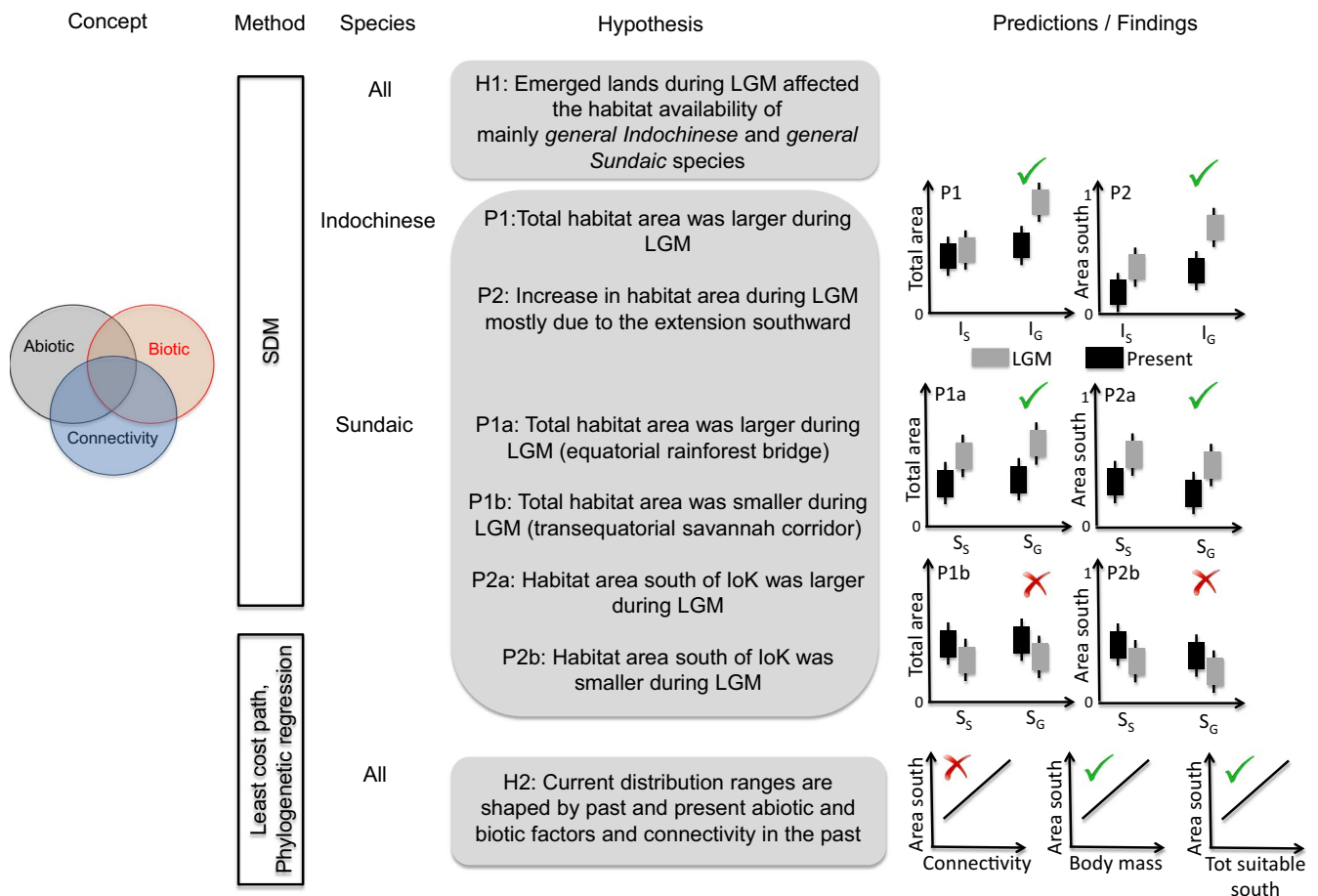


FIGURE 2 A schematic representation of the conceptual framework, hypotheses, respective predictions and findings (indicated as either support for or rejection of the hypotheses), and methods used to test specific hypotheses. The conceptual framework followed the one described in the text (Soberón, 2007). The numbering of hypotheses (i.e. H1, H2) and predictions (P1, P2) corresponds to the one used in the main text. For predictions the species distribution groups are abbreviated as follows: I_S—*specialized Indochinese*, I_G—*general Indochinese*, S_S—*specialized Sundaic*, and S_G—*general Sundaic* species. ‘Tot suitable south’ reflects the sum of predicted suitability values south of IoK



compared to present day conditions, because the emerged land provided additional habitat more similar to that of current Indochina, irrespective of whether a transequatorial savanna corridor was crossing Sundaland or the Sunda islands were connected by the tropical rain forest (in this case savannas would still cover emerged areas north of Sundaland). For *general Sundaic* species, however, we predict (a) an increase in the total habitat area during the LGM compared to nowadays if the emerged land connecting the Sunda islands was covered by tropical rain forests (P1a); and (b) a decrease in the habitat area if rain forest habitats were restricted to refugia (P1b).

Our second prediction (P2) derived from H1 states that the change in the available habitat was directional, i.e. newly available habitat was located mainly south of loK (as opposed to the newly available habitat located in mainland Indochina, north of loK). Thus, for *general Indochinese* species the area of the habitat south of loK would have been larger during the LGM compared to present day conditions (P2), because savanna-like conditions would be found at least on the emerged lands north of Sundaland (in case of a west-east rain forest bridge), and potentially, they would spread the whole way southwards to Java (in case of a trans-equatorial savanna corridor). For *general Sundaic* species, the area of the habitat south of loK is predicted to be higher during the LGM compared to nowadays (P2a) if tropical rain forests covered the emerged areas connecting Sundaic islands. However, if a trans-equatorial savanna corridor had crossed Sundaland in north-south direction, then the area of the habitat south of loK would have been smaller during LGM compared to present day (P2b), resulting in the confinement of *Sundaic* species to refugia (Figure 2).

H2 (factors affecting species distribution ranges)—We hypothesized that for *Indochinese* species, the area of the habitat presently located south of loK depends on (a) suitability of habitat south of loK now and in the past (abiotic factors), (b) connectivity between habitats north of loK and south of loK, and (c) competitive ability of species reflecting their ability to colonize the newly available habitats (biotic factor, as a proxy of which we used body mass).

Testing these hypotheses about how present and past factors have influenced mammal species distributions around loK provides an alternative explanation for the persistence of a biogeographic transition zone in the absence of a strong geophysical barrier.

2 | MATERIALS AND METHODS

2.1 | Study area and species selection

We constrained our species list to non-volant mammals that according to *The IUCN/SSC Red List of Threatened Species* (<http://www.iucnredlist.org/>) are distributed in Southeast Asia, defined as an area between 91° West, 130° East, −15° South and 33° North and whose distribution range overlapped with at least one of the following countries: Myanmar, Thailand, Cambodia, Laos, Vietnam, Singapore, Malaysia, Brunei and Indonesia. Additionally, because we aimed to reveal a general pattern across multiple species, we excluded the species with very small distribution ranges

(<130,000 km², roughly the size of Java) because they are likely to be confined to rather specific small-scale climatic conditions (e.g. top mountain endemics) that are not typical of the general regional pattern. These selection criteria resulted in a preliminary set of 189 mammalian non-volant species (henceforth referred to as mammal species), of which 64 had to be removed because (a) their distribution ranges were located mainly outside of the study area and overlapped <5% with the study area; or (b) their distribution ranges covered the whole study area, rendering assignment to one of the four distribution groups impossible; (c) they are being driven to extinction by humans (e.g. hunting) or are easily spread by humans, meaning their current distribution ranges are likely to be determined predominantly by anthropogenic rather than environmental factors. The remaining 125 species were assigned to one of the four distribution groups (see Introduction and Figure 1b; for more details on the selection criteria see Appendix S1 and for the resulting species list see Table S2.1).

2.2 | Palaeo-projections with SDMs

We fitted SDMs for all 125 species in the following way: for each species we obtained its current distribution range from the Red List (maps downloaded on May 12th 2017) by using selected IUCN categories of presence, origin and seasonality, as detailed in Appendix S1. We rasterized this distribution range shapefile with a resolution of 2.5 arc minutes, because this is the finest resolution at which the climatic data used for hindcasting were available (see below). Next, we randomly sampled 10% of raster cells as occurrences for model fitting. By sampling the presences from the complete distribution ranges for each species we thus made sure that we were capturing the present climatic niche of each species (Soberón, 2007). For the species with >90% of their distribution range located within the study area (in total 113 species), we used the extent of the study area as a background. For the remaining 12 species, we used as a background a square encompassing the whole distribution range. In both cases we excluded the Oceanian and Australian zoogeographic realms from our study area (Holt et al., 2013). We sampled the background points from the background area and set their number to 10,000 if the number of sampled presences was <35,000 (118 species), and to 100,000 otherwise (Table S2.1). We generated three sets of background samples to account for the randomness associated with their assignment. As environmental predictors for model fitting we used the bioclimatic variables provided by world clim.org/version1 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). To avoid multicollinearity, for each species we calculated Spearman correlation coefficients among the environmental predictors at the locations assigned as presences and background points (for this we lumped all three sets of background samples; van Proosdij, Sosef, Wieringa, & Raes, 2016). Only environmental predictors with $-0.7 < \rho < 0.7$ (Spearman correlation) were retained for model building, resulting in a different set of predictors for each species (Table S2.2). Models were fitted with the *biomod2* package in R (Thuiller, Georges, Engler, & Breiner, 2016) using MAXENT.

To evaluate the quality of the fitted models we used the approach suggested by Raes and Ter Steege (2007) for SDMs based on presence-only data. This approach is based on a comparison of the area under the curve (AUC) for the actually fitted model against a null distribution of expected AUC values. This null distribution is obtained by calculating AUC values for 999 models fitted to 999 sets of randomly drawn presence sets (and respectively generated background samples). We then compared the AUC value obtained with the model with the one-sided 95% confidence interval (CI) produced under the null distribution to determine whether the fitted model performed significantly better than expected by chance. Next, we took the mean of the probabilities predicted with the models that were significantly better than expected by chance (all three models for each species, see Table S2.1) to obtain a single model for each species (Table S2.1). We found high consistency among the models based on the three sets of background samples for each species (results not shown), justifying averaging over these three models.

Next, we used the fitted habitat suitability model for each species to hindcast its habitat suitability to two past time periods using climatic data for the mid-Holocene (c. 6 ka) and the LGM (c. 21 ka), which were obtained with the following global climate models: CCSM4, MIROC-ESM and MPI-ESM-P (<http://www.worldclim.org/paleo-climate1>). These global climate models are commonly used for projecting the past habitat suitability with SDMs (Barker, Rodríguez-Robles, & Cook, 2015; Raes et al., 2014; Wilting et al., 2016). Finally, we built one model for each of the two past time periods by averaging the predicted probabilities obtained across the three climate models to account for uncertainty in climate model predictions (see Appendix S1 for details about the choices and assumptions made for SDM).

To test the sensitivity of our findings to the choice of the algorithm, we also fitted the models with boosted regression trees (BRT), and as the results obtained with the two algorithms were consistent (Appendix S2, Figures S2.1–S2.5), we here report the results based on MAXENT only. Additionally, we assessed the sensitivity of our findings (see Appendix S1) to (a) the grid cell size used (by running the analyses with grid cells of 0.5°) because previous research found that predictions of SDMs based on fine-resolution environmental data may be biased (Hurlbert & Jetz, 2007); and (b) the proportion of the raster cells used as presences (in addition to the 10% reported in the main text we also used 1% and 20%). Our sensitivity analyses (see Appendix S2, Figure S2.6–S2.10) indicated that the results were not sensitive to the choice of the grid cell size and the proportion of cells used as presences. Therefore, our results validate our choices of using (a) the grid cell size of 2.5 arc minutes and (b) 10% of distribution range as presences.

2.3 | Impact of abiotic factors on species distributions

To assess how the habitat area of species inhabiting Southeast Asia changed across periods (H1), we converted the predicted habitat

suitability values into presence/absence maps using as a threshold the value with maximum sum of sensitivity and specificity (i.e. max-SSS, Liu, Berry, Dawson, & Pearson, 2005; Liu, Newell, & White, 2016). To test prediction P1 we then used a linear model (Gaussian error distribution) with the total habitat area as response and period, species distribution group and their interaction as predictor variables. This model allowed us to assess how the total habitat area changed across the three periods for species in the four different distribution groups. Because the interaction of the period with distribution group was not significant, we excluded it from the model used to predict the total habitat area of each distribution group in each period.

To test prediction P2 we used the area of the habitat south of IoK as a response variable and fitted a linear model (Gaussian error distribution) with period, species distribution group, and their interaction as predictor variables. This model allowed us to assess how the area of the habitat south of IoK changed across the three periods for species in the four different distribution groups.

To account for the fact that the total landmass area changed in the LGM compared to the mid-Holocene and the current period, we fitted the two above-mentioned models by including another “period”, which corresponded to the hindcasted LGM suitability map clipped to the current landmass. Furthermore, because the biogeographic transitions around IoK are reported to cover the latitudinal range from 5° N to 12° N, depending on the taxon considered (Hughes et al., 2011, 2003; Woodruff & Turner, 2009), we checked the robustness of our results by using both the southern (5° N) and the northern (12° N) boundaries of the zoogeographic transition zone to recalculate the area of the habitat south of these boundaries.

2.4 | Impact of a suite of factors on species distributions

Since we have shown that during the LGM potentially suitable areas existed for *Indochinese* species south of IoK (see Results), we here focused on *Indochinese* species only. We tested the hypothesis that for *Indochinese* species, the area of the habitat that is currently available south of IoK depends on abiotic factors, a biotic factor and connectivity. As abiotic factors we used, for each species, the sum of predicted suitability values in raster grids south of IoK (10°30'N) during the LGM, mid-Holocene and present. The connectivity between the suitable areas located north and south of IoK in the LGM was calculated for each species using the least-cost path (LCP) analysis. We first assigned as the start and end points the grid cells with the maximum suitability value north and south of IoK (using the hindcasted LGM suitability map). The LCP algorithm then uses as costs the sum of resistance values (=inverse suitability values, i.e. 1/ suitability value) of each grid cell on the potential routes between the start and end points and selects a single path characterized by the least cost. Next, for each species, we converted the least-cost distance (a sum of resistance values along the LCP) into connectivity (inverse of the least-cost distance value). For 14 species the least cost distance was estimated as infinity, a case when the resistance values of some of



the grid cells on the identified path between the start and end points equal infinity because their suitability values are approaching 0. In such cases no LCP could be identified and we, therefore, assigned the least-cost distance to the maximum least cost distance identified across all species. We recognize that the LCP analysis provides only a proxy of connectivity while omitting the details of the movement path (e.g. inability to cross barriers such as rivers), but this method offered the best compromise between the detailed depiction of the movement (data-demanding) and discerning the pattern across multiple species within a large spatial extent.

As biotic factors we initially aimed to use several life history traits, such as adult body mass, age at first reproduction, inter-birth interval, litter size, number of litters per year, and age at sexual maturity, all available from the PanTHERIA database (Jones et al., 2009). But because most data were missing for many species (cf. González-Suárez & Revilla, 2013) we had to restrict our analysis to a single trait, body mass, which we used as a proxy of competitive ability of species, in particular reflecting the species' ability to colonize newly available habitats. Indeed, in mammals, adult body mass correlates strongly (Pearson correlation coefficient = 0.97) with adult forearm length (González-Suárez & Revilla, 2013), which is a known proxy for mammal mobility. Furthermore, larger body mass is associated with wider diet breadth, meaning that larger predators can feed on a wider range of prey species (Gilljam et al., 2011). And, generally, for predators, the larger their size, the larger their prey, meaning that they would out-compete smaller-sized predators (Brose et al., 2006).

We then used a phylogenetic linear model to assess how body mass, connectivity during the LGM, and availability of suitable area

south of IoK during all three periods affected the area of the habitat currently located south of IoK for *Indochinese* species (Figure 2), H2. We standardized (mean = 0 and SD = 1) all predictors prior to model fitting. The model was fitted using the function 'pgls()' from 'caper' package in R (Orme et al., 2013). Prior to model fitting, we tested for correlation among explanatory variables to avoid multicollinearity. Because the sum of suitability values correlated strongly among three periods ($r > 0.7$) and because the sum of suitability values in the LGM correlated with connectivity (Figure S2.11), we only retained the sum of suitability values estimated for the current period as an explanatory variable and excluded the suitability sums for the other two periods. For phylogeny we relied on the updated mammalian supertree (Fritz, Bininda-Emonds, & Purvis, 2009) and resolved polytomies randomly. To test how sensitive our results were to the assignment of the maximum least-cost distance for species for which the least-cost distance was estimated to infinity, we also re-run the model on the subset of data without these 14 species.

For model diagnostics of all the fitted models we checked the normality of model residuals (with a quantile-quantile plot), and plotted the residuals versus the response variable and each of the predictors. The model diagnostics were satisfactory for the phylogenetic linear model (testing H2). However, the distributions of residuals of the models fitted to test the predictions P1 (about the total habitat area) and P2 (about the habitat area south of IoK) deviated strongly from normal. After log-transforming the area, the model diagnostics improved in both cases. All analyses were conducted with R 3.4.1 software (R, 2018); the R package 'gdistance' (van Etten, 2015) was used for LCP analysis.

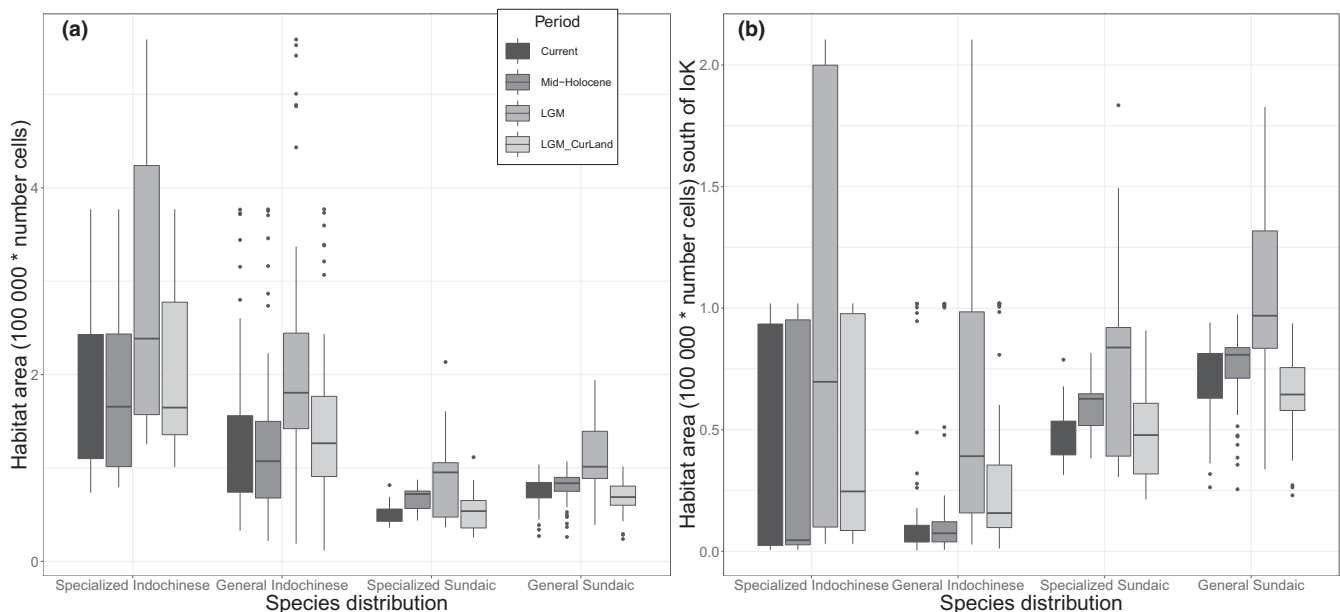


FIGURE 3 (a) Total predicted habitat area for species in the four distribution groups in each period (LGM, mid-Holocene and current) and (b) the area of the predicted habitat located south of the Isthmus of Kra for the species in the four distribution groups, per period. LGM_CurLand denotes the habitat area in the LGM calculated when considering current landmasses (to account for the differences in emerged landmasses between periods with different sea levels)



TABLE 1 Results of linear models assessing the effects of predictors on a log-transformed (a) total habitat area (P1) and (b) habitat area south of IoK (P2) across the species in four distribution groups. As a baseline we used the distribution group *specialized Indochinese* species and the “current” period. Period corresponds to one of the studied time periods: current, mid-Holocene, LGM, and LGM corrected for the current landmasses (see Methods)

Response	Parameter	Modality	Estimate	SE
Log-transformed total habitat area	Intercept		12.038	0.087
	Distribution group	General Indochinese	−0.358	0.086
		Specialized Sundaic	−1.135	0.099
		General Sundaic	−0.873	0.086
	Period	Mid-Holocene	0.013	0.063
		LGM	0.418	0.063
		LGM (current landmasses)	0.002	0.063
Log-transformed area of habitat located south of IoK	Intercept		9.135	0.296
	Distribution group	General Indochinese	−0.221	0.323
		Specialized Sundaic	1.644	0.373
		General Sundaic	2.005	0.326
	Period	Mid-Holocene	0.146	0.418
		LGM	1.467	0.418
		LGM (current landmasses)	0.934	0.418
	Distribution group:Period	General Indochinese:Mid-Holocene	−0.078	0.457
		Specialized Sundaic:Mid-Holocene	0.038	0.527
		General Sundaic:Mid-Holocene	−0.104	0.461
		General Indochinese:LGM	0.142	0.457
		Specialized Sundaic:LGM	−1.075	0.527
		General Sundaic:LGM	−1.102	0.461
		General Indochinese:LGM (current landmasses)	−0.054	0.457
		Specialized Sundaic:LGM (current landmasses)	−0.984	0.527
		General Sundaic:LGM (current landmasses)	−1.040	0.461

3 | RESULTS

3.1 | Impact of abiotic factors on species distributions

As predicted (P1), we found that for *general Indochinese* species the area of suitable habitat had been larger during the LGM compared to the current period (Figure 3a, Table 1). The same was found for *general Sundaic* species (Figure 3a, Table 1), providing support for the prediction that species dependent on evergreen rain forests found suitable habitat on the exposed Sunda Shelf (P1a). We did not find a stronger increase in the habitat area during the LGM for some distribution groups compared with others, as indicated by non-significant interaction between period and distribution group ($F = 0.919$, $d.f. = 9$, $p = .5082$). Importantly, if the hindcasted suitability maps for LGM were clipped to current landmasses we found that for all species there was a non-significant slight increase in the habitat area in the LGM compared to the current period

(Table 1), indicating that additional suitable areas during the LGM were mainly located outside of the present landmasses.

The area of the habitat south of IoK depended on time period, species distribution group and the interaction between them (Table 1). As predicted (P2), we found that for *general* and *specialized Indochinese* species the area of the habitat south of IoK during the LGM was higher compared to the current period, even if the landmasses in the LGM were clipped to match the current period (Figure 3b, Table 1). Similarly, for *Sundaic* species, the area of the habitat south of IoK was higher in the LGM compared to the current period, but only if we used the LGM landmasses. By clipping the LGM landmasses to match the current period, we found a slight decrease in the area of the habitat south of IoK for *Sundaic* species (compared to the current period), suggesting that the habitat available to *Sundaic* species in the LGM was mainly present on the emerged landmasses. The results were qualitatively unaffected by use of either the southern or northern boundaries (5° N and 12° N) of the biogeographic transition zone to calculate the proportion of the habitat south of IoK (Table S2.3 and Figure S2.12).

TABLE 2 Results of the phylogenetic model testing how the area of the habitat south of IoK during the current period was affected by connectivity during the LGM, body mass, and sum of suitability values for the current period. Significant variables are highlighted in bold. The predictors were standardized (mean = 0 and SD = 1) prior to the analysis. The estimated phylogenetic signal alpha is 0 (bootstrap CI: NA, 0.269)

Parameter	Estimate	SE
Intercept	21,401.3	2,847.0
Body mass	7,883.8	2,888.4
Current total suitability South of IoK	23,722.7	3,149.4
Connectivity	-565.5	3,132.7

3.2 | Impact of a suite of factors on species distributions

We found partial support for H2 according to the phylogenetic model (Table 2). The area of the habitat that is currently located south of IoK for *Indochinese* species was affected by the abiotic factor (i.e. sum of suitability values south of IoK; $F = 56.73$, $d.f. = 1$, $p = 4.6E-10$) and the biotic factor (i.e. species body mass; $F = 7.45$, $d.f. = 1$, $p = .009$), but we found no significant effect of connectivity ($F = 0.03$, $d.f. = 1$, $p = .86$). The larger the sum of suitability values south of IoK and the

larger the species body mass, the larger was the habitat area south of IoK within the current species distribution range. The phylogenetic signal was negligible, as evidenced by $\lambda = 0$ (CI: NA, 0.269). Our results were qualitatively the same when excluding the species for which the least-cost distance was estimated to infinity (Table S2.4).

4 | DISCUSSION

We showed that both present and historical abiotic factors in combination with body mass, as one proxy for biotic characteristics of the species, affect the current distribution ranges of mammals in Southeast Asia. Our findings suggest that a strong geophysical barrier may not be necessary to maintain a biogeographic transition zone. Climatic conditions during the LGM provided suitable habitat (presumably drier and more open habitats, similar to current habitats in many areas of Indochina) for *Indochinese* species south of IoK, allowing them to increase their distribution ranges (Figure 4). Despite this southwards range expansion we found only limited support that these suitable climatic conditions stretched all the way southwards to Java, as would be expected in the presence of a transequatorial savanna corridor (Bird et al., 2005; Gathorne-Hardy et al., 2002; Meijaard, 2003). We found that large parts of the exposed shelf around the equator between Borneo and Sumatra were not predicted to contain suitable habitat for *Indochinese* species (Figure 5).

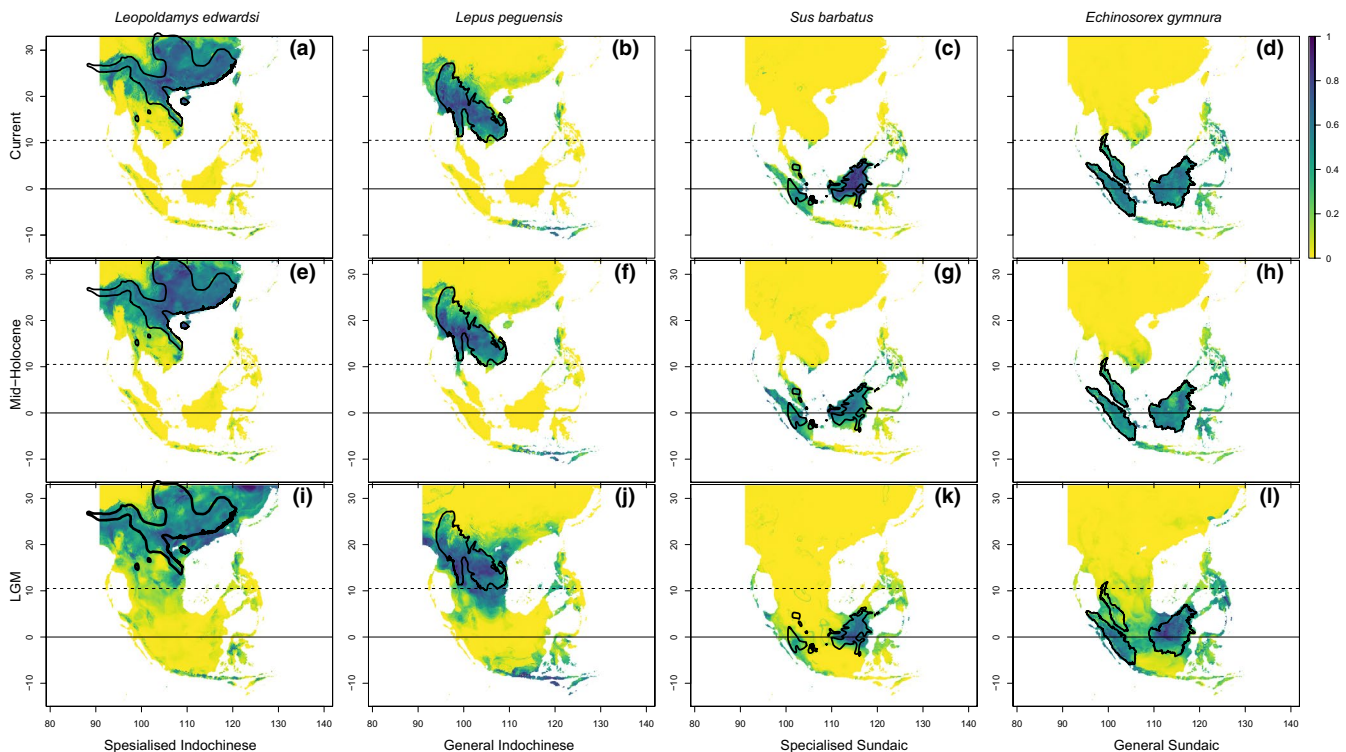


FIGURE 4 Predicted habitat suitability for four species, representative of the *specialized Indochinese* distribution group: *Leopoldamys edwardsi* (a, e, i), the *general Indochinese* distribution group: *Lepus penguensis* (b, f, j), the *specialized Sundaic* distribution group: *Sus barbatus* (c, g, k), and the *general Sundaic* distribution group: *Echinorex gymnura* (d, h, l). The predictions are shown for three periods: current (a, b, c, d); mid-Holocene (e, f, g, h); and LGM (i, j, k, l). The outline of the present species distribution range is shown with the thick solid black line, the equator with the thin horizontal line, and the latitude of the Isthmus of Kra with the dashed horizontal line

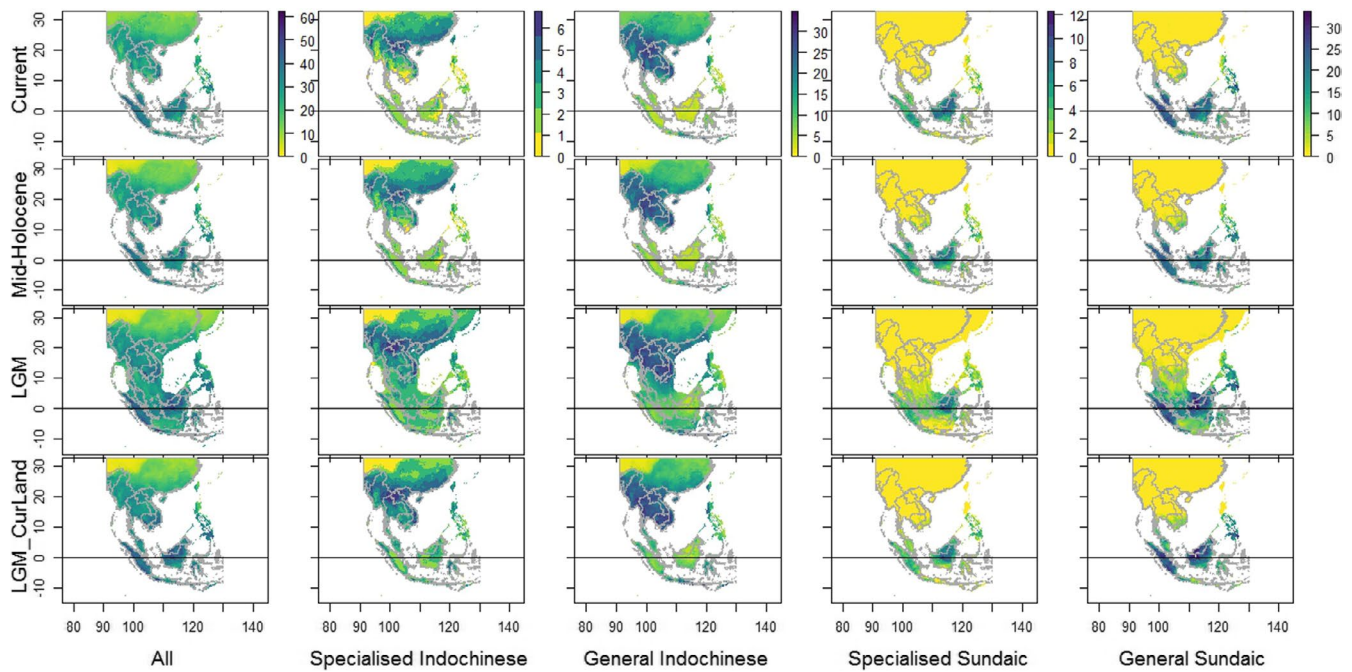


FIGURE 5 Maps of projected species richness in SE Asia (Y-axis: latitude, X-axis: Eastern longitude). Columns from left to right depict projected species richness for: (1) all species, (2) *specialized Indochinese* species, (3) *general Indochinese* species, (4) *specialized Sundaic* species, and (5) *general Sundaic* species in the current period (top row), mid-Holocene (second row), LGM (third row), and LGM corrected for the current landmass (bottom row). Coloured bars to the right of the maps in the top row indicate number of species for the respective column. Species richness was obtained using a max-SSS threshold to convert habitat suitability to presence/absence (see Methods) and by summing these predicted presences across all species. The equator is indicated by the horizontal solid black line

In contrast, this equatorial area was predicted to be suitable for many *Sundaic* species (both *general* and *specialized*), supporting the suggestion that rain forest-like habitats connected the emergent lands between Borneo and Sumatra (support for P1a, Figures 4 and 5). This finding is in line with the hindcasts of the likely persistence of rain forest dipterocarp habitats throughout the LGM between Sumatra and Borneo (Raes et al., 2014). Indeed, of 46 *general Sundaic* species on our list, around 15–20 could have existed on the emergent landmasses between Sumatra and Borneo during the LGM (Figure 5). It is conceivable that such larger evergreen rain forest-like habitats prevented a stronger imprinting of the Indochinese fauna onto Sundaland during the LGM.

Although our results suggest the existence of rain forest habitats on the equatorial masses connecting Borneo and Sumatra in east-west direction, the extent of such habitats is unclear and we do not know whether they formed a continuous stretch or rather fragmented patches (Mason, Helgen, & Murphy, 2018). Thus, it looks like the savanna corridor running from north to south was either interrupted by a continuous rain forest corridor or, perhaps more likely (cf. Mason et al., 2018), was interspersed by patchy rain forest habitat around the equator. Moreover, our findings point out that habitats further to the south of such rain forest habitats were likely drier and colder, resembling the conditions of a savanna corridor. Indeed, for *Indochinese* species our models predicted high habitat suitability during the LGM on Java and the Lesser Sunda islands (cf. Figures 4 and 5). These findings are in line with previous pollen records (van

der Kaars, Kershaw, Tapper, Moss, & Turney, 2001) and speleothem evidence (Westaway et al., 2007), suggesting drier and colder conditions on Java around the LGM.

Ideally, fossil records could be used to validate the hindcasts made here (e.g. Metcalf et al., 2014). Unfortunately, the Quaternary fossil record in Southeast Asia is of poor temporal and spatial resolution (Louys, Curnoe, & Tong, 2007), limiting our ability to compare fossil data with our projections for each species for the two past periods with any accuracy. Another issue with the fossil record concerns poor knowledge about the history and formation of fossil sites, which means that the absence of a species from the fossils recovered at a particular site cannot be interpreted with 100% confidence as the absence of that species from the study area during a particular historical period. Nevertheless, we tested our hindcast projections by matching them with the fossil data (cf. Davis, McGuire, & Orcutt, 2014; Martínez-Meyer, Peterson, & Hargrove, 2004) that are contemporaneous with our chosen palaeo-periods and come from the areas north and south of IoK. Relevant fossils with ages close to the LGM are only available from four caves (one on Borneo, one on Java, one in Vietnam and one in Thailand) for 19 of 125 species used in this study. The limited fossil data available for Southeast Asia support our SDM projections for the LGM: three of the four species that overlapped between our species list and the fossils recovered in northern Vietnam (Ma U'O'i cave, 20°37'22" N, 105°16'40" E, fossil age 49 ka: Bacon et al., 2006) had high habitat suitability (>max-SSS for each respective species) in that region



during the LGM. Furthermore, five of the eight species that overlapped between our species list and the fossils from northern Thailand (The Cave of the Monk, 19°24'36" N, 98°48'58" E, fossil age 19–32 ka: Zeitoun et al., 2010) had high habitat suitability in this region during the LGM. Similarly, 11 of the species found in Niah cave (northern Borneo, Sarawak, 3°49'09" N, 113°46'42" E, fossil age 35–44 ka: Barker et al., 2007; Louys, 2012) that were also included in our species list, had high habitat suitability during the LGM at the Niah cave locality (Table S2.5). And one of three species that overlapped between our species list and the fossils from Java (Wajak Cave, 8°37'59" S, 116°9' E, fossil age 30–40 ka: Storm et al., 2013) had high habitat suitability in that region according to the hindcasts to the LGM. Although these few records cannot ascertain the accuracy of our model projections for all species, they provide some credibility for the overall patterns found in our study.

In addition to abiotic factors (suitable climatic conditions), a biotic factor, body mass, also affected the current distributions of *Indochinese* species. Larger bodied *Indochinese* species had larger predicted distribution ranges south of the IoK compared to smaller bodied *Indochinese* species. This might have provided these *Indochinese* species a competitive advantage over *Sundaic* species and increased their chances of expanding their range to the south. However, additional studies would be needed because body mass is a trait correlated with many other species characteristics (Gonzalez-Suarez, Gomez, & Revilla, 2013; González-Suárez & Revilla, 2013).

While for numerous plant species, proximity to LGM refugia shaped their present distributions (Dullinger et al., 2012; Normand et al., 2011; Svenning & Skov, 2007a), distribution ranges of *Indochinese* mammal species were not affected by the measure of connectivity. This may simply reflect the difference in the importance of mobility for plant and animal distributions, suggesting that this factor is not as influential for mammals due to their high dispersal ability. Alternatively, the different findings may stem from different approaches to quantifying connectivity. Whereas plant and forest studies (Normand et al., 2011; Svenning & Skov, 2007a) have used accessibility measures (based on the sum of inverse distances from each focal grid to likely LGM refugia), we applied a LCP analysis to measure species-specific connectivity between suitable habitats north and south of IoK in the LGM. We could not use accessibility measure in our case as we did not know where the refugia were, and rather wanted to have a proxy for the costs incurred by species when moving between two most distant potentially suitable areas located north and south of IoK.

To answer a macroecological question across dozens of species we here used species distribution models that rely on several assumptions. One such assumption is niche conservatism, according to which the ecological niche of a species is assumed to be constant through time. Indeed, by using a snapshot of the current species distribution and assuming that the ecological requirements of the species were similar in the past, we hindcasted the habitat suitability of this species to the past periods. Although the niche conservatism assumption is highly debated (Davis et al., 2014; Martínez-Meyer et al., 2004; McGuire & Davis, 2013) no better

alternative is yet available for projecting the habitat suitability of hundreds of species on a large spatial extent. To fit our SDMs we used species distribution maps available from the IUCN Red List, which despite of the lack of accuracy for some of the mammal species in our analysis, provide the best available data source for mammals. Similarly, PanTHERIA (Jones et al., 2009) remains the largest database for mammalian life history traits, even though data coverage for some traits is low for many species. Although animal databases detailing life history traits are in the process of being compiled (e.g. Kissling et al., 2014; Salguero-Gómez et al., 2016), these are still much poorer than the global plant databases (e.g. TRY database: Kattge et al., 2011). Furthermore, predicted suitabilities in our SDMs are based on climatic variables only, because no habitat reconstructions at the spatial resolution we used in this study are available for the mid-Holocene and the LGM. The climate projections of global climate models, although surrounded by uncertainty, are commonly used in studies projecting habitat suitability for different species into both past and future periods (e.g. Barker et al., 2015; Cooper et al., 2016; Fitzpatrick et al., 2011; Mathai et al., 2019; Patel et al., 2016; Raes et al., 2014; Wilting et al., 2016). Indeed, for our study region, the global climate models provide the best available climate projections in terms of spatial resolution. Furthermore, our analyses were conducted at a spatial resolution of <1°, which may be prone to commission errors (Hurlbert & Jetz, 2007), although our sensitivity results based on 0.5 degree resolution were consistent with the results reported in the main text. Taken together, we would like to highlight that SDMs used here have a number of uncertainties, and cannot reflect the true distributions of species in the past. Despite imperfect data and simplifying assumptions, however, we think that the clear patterns detected across more than hundred species provide a useful approximation of the past distributions of mammal species in Southeast Asia.

Our findings have important implications for the conservation of species in the biodiversity hotspots of Indochina and the Sunda Shelf. On the one hand, our data reinforce that habitat suitability in the past and today are important drivers of current species distributions. The ongoing habitat loss and degradation in Southeast Asia therefore not only restricts the current distributions of species, but the often fragmented remaining populations also lose their ability to respond to further environmental changes, for example climate change. In addition, our data highlighted that species characteristics were important in determining species distribution ranges, meaning that conservation efforts should account for species traits (González-Suárez & Revilla, 2013). For example, small-bodied species are often sensitive to habitat loss and degradation, whereas large-bodied animals with small litter sizes are often more threatened by direct effects on their survival (Gonzalez-Suarez et al., 2013). Moreover, given the high habitat fragmentation in our study region, special attention should be devoted to the species with lower mobility, particular as it has been predicted that suitable ecological conditions for 23%–46% of Bornean mammals will shift upslope under forecasts of land cover and climate change (Struebig et al., 2015).

Similarly to studies on plants (Normand et al., 2011; Svenning & Skov, 2007b), amphibians and reptiles (Araújo et al., 2008), we demonstrated that the legacy of previous climatic conditions and current climate have also affected mammal species distributions. We showed that, at least during the LGM, savanna-like habitats apparently did not stretch all the way southwards to Java. We further showed that the transition at the IoK between the distinct Indochinese and Sundaic biota was maintained through different climatic periods during the Late Pleistocene, even though the biota were directly connected during long periods of the Late Pleistocene by the exposure of the Sunda Shelf. This finding provides the first evidence that biogeographic transition zones may be explained by climatic factors and their legacy, and that a strong geophysical barrier, such as the Isthmus of Panama is not needed to maintain the separation of biota.

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DATA AVAILABILITY STATEMENT

The data supporting the results are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qp44619>.

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ORCID

Viktorii Radchuk  <https://orcid.org/0000-0003-3072-0095>

Stephanie Kramer-Schadt  <https://orcid.org/0000-0002-9269-4446>

Joerns Fickel  <https://orcid.org/0000-0002-0593-5820>

Andreas Wilting  <https://orcid.org/0000-0001-5073-9186>

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BIOSKETCH

The researchers involved in this analysis differ in their backgrounds (geneticists, biogeographers and ecological modellers) but share a common broad interest in understanding the factors shaping biodiversity patterns on ecological and evolutionary scales. This paper is a part of the research project focussing on understanding such patterns for Southeast Asian mammals.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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