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Latitude and evolutionary history shape the global distribution of migratory butterflies

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16

17 **Abstract**

18 Hundreds of butterfly species migrate globally. Seasonal migration allows butterflies
19 track suitable environments across large distances, yet global distribution patterns and the
20 processes that shape them remain poorly understood. Here, using season-specific habitat
21 suitability maps for 426 migratory butterfly species, we assess how morphological traits,
22 environmental conditions and evolutionary history shape their distributions. Our analyses reveal
23 that migratory butterfly richness peaks at $\sim 12^\circ$ N, and the Nearctic and Palaearctic realms
24 together contain 64% of the global area of high-richness assemblages. Species concentrated in
25 tropical regions occupied smaller geographic ranges, whereas range size increased with
26 wingspan. The average wingspan declined with increasing latitude, but this association was not
27 significant after accounting for phylogeny. Bayesian phylogenetic models revealed significant
28 phylogenetic structure in geographic range size, suggesting that evolutionary history contributes
29 to contemporary range constraints. We show that while migratory butterflies can track seasonal
30 environments, environmental variation, morphology, and evolutionary history largely determine
31 their distributions. Our findings highlight tropical and subtropical regions as monitoring
32 priorities and the need to maintain seasonally suitable habitats across migratory ranges.

33

34 **Main**

35 Geographic range size often increases towards higher latitudes, although the patterns vary
36 substantially across taxa and regions¹⁻⁵. Such variation can arise from differences in climatic
37 variability, habitat availability and dispersal ability, all of which influence where species can
38 persist and how readily they can track suitable environments. Movement is a fundamental
39 component of species distributions, yet environmental conditions strongly structure even highly

mobile species^{6,7}. A key question is whether exceptional mobility weakens environmental variation's influence on range size and seasonal distributions.

Migratory species provide a particularly informative system for addressing this question because their distributions are dynamic, shifting seasonally as individuals or successive generations track favourable environments^{8,9}. Insects offer a distinctive example because long-distance migration can span multiple generations, requiring populations to occupy different environments at successive stages of the annual cycle^{10–14}. Butterflies are among the best-documented migratory insects, with around 3% (568 species) of the ~19,300 recognised species known to undertake seasonal migration^{15,16}. Their comparatively well-documented distributions, along with morphological and phylogenetic data, make butterflies a useful system for testing how mobility interacts with environmental variation and evolutionary history.

Migratory butterflies combine high mobility with dependence on suitable environments across multiple stages of the annual cycle. Traits and behaviours associated with migration, including reproductive diapause, specialised flight morphology, and the ability to select flight altitudes and headings that exploit favourable winds, facilitate movement over hundreds or thousands of kilometres^{17–21}. Variation in flight-related morphology may contribute to differences in geographic range size, with wingspan providing a measurable axis of this variation. Because migration often spans several generations, successive seasonal ranges must provide suitable climate, host plants and habitat structure throughout the annual cycle^{22–27}. The spatial extent of migration may reflect both the capacity for long-distance movement and the availability of seasonally suitable environments.

Geographic range size may reflect shared evolutionary history because closely related species often share ecological and morphological traits. These similarities can create

phylogenetic structure in range size even after accounting for contemporary environmental conditions^{28–31}. Importantly, migratory butterfly distribution patterns may differ from those described primarily for vertebrates. For example, bird migration is concentrated largely in temperate regions³², whereas butterfly diversity peaks in tropical and subtropical regions^{16,33}, where seasonal habitat switching among migratory butterflies is prominent³⁴. Whether migratory butterfly richness is similarly concentrated at low latitudes, and how climate, morphology and evolutionary history jointly shape variation among lineages, remain understudied.

To address these questions, we quantify the global distribution and seasonal dynamics of migration across 426 butterfly species by integrating season-specific habitat suitability maps with environmental, morphological and phylogenetic data. Specifically, we test whether migratory species richness and seasonal redistribution are concentrated at low latitudes; whether seasonal-switching richness is associated with climatic seasonality, land cover and human influence; whether geographic range size increases with wingspan, consistent with variation in flight-related morphology influencing spatial extent; whether this association varies across latitudes; and whether migratory distributions retain detectable phylogenetic structure after accounting for contemporary environmental predictors.

Results

Seasonal-switching richness peaks at low latitudes

Using global distribution maps for migratory butterflies (426 species) from Chowdhury et al.³⁵, we found that 418 species showed differences in predicted distribution among seasons, whereas 8 species had only one seasonal map. We defined seasonal-switching richness as the number of species predicted to occupy a grid cell in at least one, but not all, seasons, reflecting

seasonal species turnover³⁴ (see methods). This richness varied markedly worldwide (Fig. 1a), averaging 5.78 ± 6.55 species (mean $\pm$ s.d.) per 2.5-arc-minute grid cell (~ 21.6 km²) and reaching a maximum of 77 species. The broad spatial pattern held under an alternative continuous measure of seasonal occurrence, which correlated strongly with the binary richness metric (Spearman's $\rho = 0.98$) and identified 78% of the same cells in the upper 5% of both distributions (Fig. S1).

Seasonal-switching richness showed a pronounced latitudinal pattern, with mean richness peaking at approximately 12° N at 16.95 species per grid cell when averaged across occupied grid cells within each latitudinal band (Fig. 1b). The geographic distribution of high-richness areas (grid cells supporting ≥ 10 seasonal-switching species) differed among the 11 zoogeographic realms (Fig. S2). The Nearctic and Palaearctic contained 63.7% of the total global high-richness area. Within each realm's migratory land area, high-richness areas occupied 43% of the Nearctic, 34.6% of the Panamanian, and 22.6% of the Palaearctic, with lower proportions in the remaining realms (Fig. S2).

Seasonal changes in predicted richness were spatially asymmetric (Fig. 1c,d). During the S2–S1 transition, corresponding to Northern Hemisphere Spring, 55.2% of the migratory range showed a net gain in species, associated with a shift in predicted suitability towards higher northern latitudes. The pattern was opposite during the S4–S3 transition, corresponding to Northern Hemisphere autumn, when 55.7% of the migratory range showed a net loss in species, reflecting redistribution towards lower latitudes. Consequently, northern regions showed net losses in predicted richness, whereas subtropical regions gained species as distributions shifted toward lower latitudes.

109 **Range size increases with latitude and flight morphology**

110 Species with distributions concentrated in the tropics tended to occupy smaller seasonal
 111 ranges than those extending into temperate and higher-latitude regions (estimate = -0.48 , $P <$
 112 0.001 ; Fig. 2a). Seasonal range size also increased during Northern Hemisphere summer
 113 (estimate = 0.051 , $P = 0.002$), consistent with seasonal expansion of predicted suitability towards
 114 higher northern latitudes.

115 Across all species, both measures of wingspan declined weakly with increasing absolute
 116 latitude (Fig. 2b), and larger-winged species had a larger tropical range proportion. The negative
 117 association between wingspan and latitude was not evident within the phylogenetically matched
 118 subset or after accounting for shared ancestry (Table S1).

119 Geographic range size increased with wingspan (upper wingspan: estimate = 0.48 , $P <$
 120 0.001 ; lower wingspan: estimate = 0.29 , $P = 0.029$) and with absolute latitude (estimate = 0.018 ,
 121 $P < 0.001$). We found little evidence that the association between wingspan and range size varied
 122 with latitude (wingspan $\times$ absolute latitude interaction, $P = 0.33$). After accounting for shared
 123 ancestry, the positive association between wingspan and range size remained similar and positive
 124 in the integrated phylogenetic model. The association did not differ significantly between
 125 hemispheres (Table S2).

126

127 **Environmental correlates of seasonal-switching richness**

128 In the spatial generalised additive model, mean richness per grid cell was lower where
 129 temperature seasonality was high (estimate = -1.01 , 95% confidence interval = -1.13 to -0.89),
 130 and higher where the Human Influence Index was high (estimate = 0.12 , 95% confidence interval
 131 = 0.09 to 0.14). Precipitation seasonality (estimate = -0.07 , 95% confidence interval = -0.12 to

–0.02) and elevation (estimate = –0.06, 95% confidence interval = –0.09 to –0.04) showed weak negative associations. Relative to built-up areas, richness was significantly higher in forest (estimate = 0.16, 95% confidence interval = 0.01 to 0.31), whereas cropland, grassland, and shrubland did not differ clearly, and sensitivity analyses showed similar results (Fig. S5).

Geographic range size is phylogenetically structured

Bayesian phylogenetic mixed models revealed phylogenetic structure in geographic range size (Fig. 3). Among 207 species with complete predictor data and phylogenetic matches (803 seasonal observations), phylogenetic heritability was $H^2 = 0.28$ (Fig. S8), indicating that closely related species tended to have similar geographic range sizes after accounting for environmental covariates and non-phylogenetic species variation. Robustness analyses showed similar results (Tables S4 and S5).

An integrated phylogenetic model including environmental predictors, upper wingspan and phylogeny (231 species, 892 seasonal observations) showed that all three components contributed to variation in range size (Fig. S9; Table S6). Environmental predictors accounted for 19% of the variance, wingspan for 3% and phylogeny for 16%, with a further 45% attributable to non-phylogenetic differences among species. The estimated contributions of environmental predictors and phylogeny were comparable (difference = 3 percentage points).

Discussion

We show that migratory butterflies' broad-scale distribution has clear latitudinal and evolutionary structure. Seasonal-switching richness was concentrated at low latitudes, whereas geographic range size increased towards higher latitudes and was positively associated with

wingspan. Range size also showed moderate phylogenetic structure and a large species-level component, linking broad-scale spatial patterns with shared evolutionary history. When we considered environmental predictors, wingspan, and phylogeny together, environmental predictors and phylogeny contributed comparably to variation in range size, with a smaller contribution from wingspan.

The global distribution of migratory butterflies differs from the predominantly temperate pattern commonly described for vertebrate migration, particularly in birds¹⁰. Seasonal-switching richness peaked at low latitudes, broadly coinciding with regions of high butterfly diversity^{16,33,36,37}. However, the geographic distribution of high-richness areas showed a different pattern, with the Nearctic and Palearctic together accounting for 64% of the global area supporting at least 10 seasonal-switching species. These findings suggest that latitudinal peaks in seasonal-switching richness do not necessarily correspond to regions containing the largest areas of high richness.

The positive association between wingspan and range size suggests that flight morphology contributes to the spatial extent of migratory butterfly distributions^{17,20}. The association persisted after accounting for shared ancestry, but we found little evidence that its strength varied with latitude. Wingspan may reflect dispersal-related morphology, but it is unlikely to universally predict geographic extent, consistent with evidence that other traits also contribute to dispersal ability in butterflies³⁸.

The spatial model further indicated that seasonal-switching richness declined with temperature seasonality and increased with human influence. These associations reflect variation within the modelled distribution because climate shaped the underlying species distribution models. The positive association with human influence requires caution because occurrence

178 records are often concentrated in accessible, densely populated areas and can show strong spatial
179 biases across data sources³⁹. However, sensitivity analyses identified similar associations with
180 temperature seasonality and human influence.

181 Closely related migratory butterflies tended to occupy ranges of similar extent, with a
182 phylogenetic heritability of 0.28 that was evident across alternative model specifications and
183 when analyses were restricted to exact phylogenetic matches. When we considered
184 environmental predictors and phylogeny together, both contributed comparably to variation in
185 range size, indicating that evolutionary history substantially shapes migratory range size. A large
186 additional species-specific component indicates that range size also reflects variation among
187 species that is not captured by shared ancestry. Range-size similarity between related species can
188 decline rapidly with time since divergence, which may make it difficult to attribute phylogenetic
189 structure to specific historical events⁴⁰. Such phylogenetic structure does not, by itself,
190 demonstrate phylogenetic niche conservatism, because similarity among relatives may arise from
191 shared climatic tolerances, host-plant associations, morphology, or biogeographic history^{28,41,42}.
192 Migration may nevertheless help maintain inherited ecological associations by allowing species
193 to track seasonally favourable environments across space. Comparable climatic tracking has been
194 proposed in migratory birds⁴³, and gene flow may further reduce local adaptation across
195 heterogeneous environments⁴⁴. Testing these possibilities will require assessing whether climatic
196 niches are more strongly phylogenetically conserved in migratory than in resident lineages
197 within a common phylogenetic framework.

198 This study has three potential limitations. First, species distribution models estimate
199 suitability rather than directly observed movement and partly inherit structure from their
200 environmental predictors. This limits inference about realised movement. However, the major

spatial patterns were consistent across alternative measures of seasonal occurrence and model evaluations. Second, wingspan captures only one component of dispersal-related morphology, yet it provides a consistently available comparative trait across hundreds of species. The positive association with range size suggests that wingspan captures biologically relevant morphological variation, although migratory capacity was not measured directly. Third, incomplete phylogenetic matching reduced taxonomic coverage, and species lacking wingspan data were, on average, more tropical and had smaller ranges than those retained (Table S7). Nevertheless, phylogenetic signal was evident when analyses were restricted to exact phylogenetic matches, and analyses of the full dataset recovered similar environmental associations.

Migratory butterflies depend on geographically separated habitats that remain suitable at different stages of the annual cycle, thereby environmental change in one part of the seasonal circuit can disrupt connectivity across the entire annual cycle^{45–48}. This dependence on spatially connected seasonal environments may become increasingly important as climate and land-use change alter the location and continuity of suitable habitats. The concentration of seasonal-switching richness at low latitudes highlights the importance of monitoring tropical and subtropical regions, particularly where occurrence data remain sparse, to better understand seasonal habitat use and identify potential bottlenecks. Conserving migratory butterflies will consequently require maintaining networks of seasonally suitable habitats across regions and political boundaries, and improving habitat connectivity as distributions shift under environmental change^{35,49}.

Methods

Data collation

We compiled a global list of 568 migratory butterfly species from Chowdhury et al.¹⁵ and cross-checked species classifications against Pinkert et al.³³. Season-specific habitat suitability maps for 426 species (at 2.5 arc min, 21.625 km²; 75% of the global list of migratory species) were obtained from Chowdhury et al.³⁵, which were generated following the seasonal modelling framework of Chowdhury et al.³⁴. We divided the entire world into 11 zoogeographic realms following Holt et al.⁵⁰: Afrotropical, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental, Palaearctic, Panamanian, Saharo-Arabian and Sino-Japanese.

We collated climatic variables and elevation raster from WorldClim (v.2.1)⁵¹ at 2.5-arc-minute resolution using the geodata R package (v.0.6-6)⁵². We obtained the land cover data from the Copernicus Global Land Service dataset (v.3.0.1, 100 m, 2019)⁵³ and human pressure, represented by the Human Influence Index (2022 release, 300 m), from the Wildlife Conservation Society⁵⁴. We obtained butterfly wingspan size (cm) from LepTraits (v.1.1.0)⁵⁵, from where we obtained upper wingspan data for 400 species and lower wingspan data for 363 species. We derived phylogenetic information for 231 species with wingspan data from the global butterfly phylogeny of Kawahara et al.⁵⁶. All statistical analyses were performed in R (v.4.5.3)⁵⁷ and Python (v.3.13)⁵⁸.

Spatial processing and derived variables

We transformed all spatial layers to WGS84 Robinson projection. We processed suitability maps using the terra R package (v.1.9-1)⁵⁹ and calculated species-level summaries with purrr (v.1.2.1)⁶⁰.

For each species and season, we calculated the geographic range area (km²), the absolute latitude of the range centroid, and the proportion of the predicted range area within the Tropics

of Cancer and Capricorn ($|\text{latitude}| \leq 23.44^\circ$). We further calculated the seasonal tropical range proportion and the mean tropical range proportion across seasons. These metrics allowed us to characterise each species' latitudinal distribution without relying solely on the geographic midpoint of its range.

We standardised species names before matching the LepTraits data to our migratory species list. We first matched species directly to the phylogeny, then used genus-level taxonomic information to resolve additional unmatched taxa. We assigned each species absent from the phylogeny to an unused tip of a congeneric species; within each genus, we paired unmatched species and available tips alphabetically, so the assignment was deterministic, and each tip was used once. This procedure matched 247 species to the phylogeny (150 exact matches and 97 congeneric tips).

We assessed potential bias from successive sample-size reductions by comparing retained and excluded species at each filtering stage across family composition, mean absolute latitude, tropical range proportion, and geographic range size (Cliff's δ calculated using the package *effsize* (v.0.8.1)⁶¹; Table S7). We then refitted the wingspan $\times$ latitude model of range size for each nested subset to determine whether changes in taxonomic coverage altered the estimated associations (Table S8).

264

265 **Mapping seasonal-switching richness**

Following Chowdhury et al.³⁴, we counted, for each species, the number of seasons in which conditions were predicted to be suitable. We classified cells as seasonal switching if the cell was suitable in at least one but not all seasons. This approach distinguished areas used seasonally from those predicted to remain suitable throughout a species' annual cycle⁶².

We summed the species-specific seasonal-switching maps to calculate seasonal-switching richness for each 2.5-arc-minute grid cell. For realm-level summaries, we resampled the species maps to a 0.5° grid using nearest-neighbour assignment. To account for variation in grid-cell area with latitude, we calculated each grid cell's true geodetic surface area (km²) based on its latitudinal position. For each realm, we quantified its contribution to the global high-richness area (km²) and the proportion of its migratory land area occupied by high-richness assemblages (Fig. S2).

To assess the sensitivity of the binary seasonal-switching criterion, we used a continuous metric. For each species and grid cell, we calculated occupancy as the ratio of the species' suitable seasons to the maximum number of existing seasons, then combined these values across species. We compared the resulting continuous surface with the binary richness map using Spearman's rank correlation and by assessing spatial overlap among the highest-ranked cells (top 5%; Fig. S1).

Finally, we quantified changes in predicted distributions by comparing binary suitability maps across consecutive seasons. For each 2.5-arc-minute grid cell, we calculated changes across four seasonal transitions: S2–S1 (Northern Hemisphere spring), S3–S2 (Northern Hemisphere summer), S4–S3 (Northern Hemisphere autumn) and S1–S4 (Northern Hemisphere winter). A species gain occurs when a species was absent from a cell in season (t) but present in season (t+1), and a species loss occurs when the reverse occurs. For each grid cell, we calculated net change as species gained minus species lost.

Geographic range and morphological analyses

We first examined geographic variation in seasonal range size using linear mixed-effects models of $\log_{10}$ -transformed seasonal range area, implemented in lme4 (v.2.0-1)⁶³, fitted by restricted maximum likelihood, with *P* values from Satterthwaite-approximated degrees of freedom by lmerTest (v.3.2-1)⁶⁴ (Table S1). We obtained model predictions for Fig. 2a–c using the packageggeffects (v.2.3.2)⁶⁵. We used the mean tropical range proportion as the primary geographic predictor and included season to account for seasonal variation in range area. For species with repeated seasonal observations, we included species identity as a random intercept. We then tested associations between wing morphology and range size using the 400 species with upper-wingspan data and 363 species with lower-wingspan data. We fitted separate models for upper- and lower-wingspan estimates, using absolute latitude as the predictor and family as a random effect to account for taxonomic non-independence. We further tested whether the association between morphology and geographic range varied with latitude by fitting an additional model in which $\log_{10}$ -transformed range area depended on wingspan, absolute latitude and their interaction.

Environmental correlates of seasonal-switching richness

We examined spatial associations between seasonal-switching richness and environmental conditions using equal-area grid cells as the unit of analysis and z-standardised all continuous predictors before fitting the model. Because temperature and precipitation seasonality contributed to the species distribution models used to derive seasonal suitability, we treated them as baseline covariates rather than interpreting their coefficients as independent environmental effects.

Our main model was a negative binomial generalised additive model with a log link and an estimated dispersion parameter, fitted with the bam function in mgcv (v.1.9-4)^{66,67} using fast restricted maximum likelihood. The response was seasonal-switching richness summed across the occupied 2.5-arc-minute cells within each equal-area cell, and we included the log number of occupied cells as an offset so the coefficients describe mean richness per 2.5-arc-minute cell. We entered temperature seasonality, precipitation seasonality, elevation, and human influence as linear terms, and land cover as a factor with built-up areas as the reference class. A two-dimensional thin-plate regression spline of projected cell coordinates (basis dimension $k = 800$) accounted for broad-scale spatial structure.

Bayesian phylogenetic models

We fitted Bayesian phylogenetic mixed models with a Gaussian likelihood and identity link using brms (v.2.23.0)⁶⁸ and a phylogenetic covariance matrix derived from Kawahara et al.⁵⁶. Our principal model analysed $\log_{10}$ -transformed geographic range area for 207 species with complete phylogenetic and predictor data, yielding 803 seasonal observations. We retained temperature and precipitation seasonality as baseline covariates because these variables informed the species distribution models from which we derived geographic ranges. We added elevation and seasonal deviation in tropical range proportion as predictors and included season as a fixed effect. We also fitted another Bayesian phylogenetic mixed model combining environmental predictors, wingspan, phylogeny, and range size to compare the effects of each aspect.

We modelled phylogenetic structure as a random effect with covariance proportional to the phylogenetic correlation matrix and included a non-phylogenetic species random intercept to account for repeated seasonal observations of the same species. We estimated phylogenetic

heritability (H^2) from posterior variance components as $\sigma^2_{\text{phylogeny}} / (\sigma^2_{\text{phylogeny}} + \sigma^2_{\text{species}} + \sigma^2_{\text{residual}})$.

We fitted each model using four Markov chains, with 6,000 iterations per chain and 2,000 warm-up iterations. We assessed convergence using $\hat{R}$, effective sample sizes and posterior diagnostics. All reported models achieved $\hat{R} \leq 1.01$. For Fig. 3, $\log_{10}$ mean range size was estimated at internal nodes by maximum-likelihood ancestral state reconstruction under Brownian motion using `phytools::fastAnc` (v.2.5-2)⁶⁹.

To assess the robustness of phylogenetic structure, we fitted two additional models to the larger set of 247 phylogenetically matched species: one included tropical range proportion and season as fixed effects, and the other included season alone. For both Bayesian phylogenetic mixed models, we tested a phylogenetic intercept-only model, a non-phylogenetic version of the principal model, and the principal model without the species random intercept to assess whether incorporating phylogenetic covariance improved predictive performance. Then compared models using leave-one-out cross-validation⁷⁰. Finally, we repeated the environmental analyses without phylogenetic structure, using the full available dataset, to determine whether the reduced phylogenetic sample altered the direction or magnitude of the principal associations.

Data availability

All data used are available at <https://doi.org/10.5281/zenodo.23306438>.

Code availability

Code is available via GitHub at <https://github.com/BEELHY/Latitude-and-evolutionary-history-shape-the-global-distribution-of-migratory-butterflies>.

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Author Contributions

H.L. and **S.C.** conceived and designed the study. **H.L.** and **Q.L.** performed the experiments and analysed the data. **H.L.** and **S.C.** developed the methodology. **S.C.** contributed data resources and materials. **R.H.C.** and **S.C.** supervised the research and secured funding. **H.L.**, **Q.L.**, and **S.C.** wrote the main manuscript text. All authors reviewed and edited the manuscript.

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Figures

Fig. 1 | Seasonal-switching richness of migratory butterflies. **a**, Global seasonal-switching richness: the number of species that use a grid cell in some seasons but not all (Robinson projection). **b**, Mean seasonal-switching richness per occupied cell, by latitude. **c**, **d**, Net seasonal change in predicted richness decomposed into net gain (**c**) and net loss (**d**) across the four transitions: S2–S1 (spring, N. Hemis.; cyan), S3–S2 (summer; magenta), S4–S3 (autumn; yellow) and S1–S4 (winter; blue). Values were converted by $\text{sign}(x) \cdot \ln(|x|+1)$; scale arrows show the maximum empirical values (38 for gain, 41 for loss).

Fig. 2 | Drivers of range size and richness. **a**, Range size against the proportion of each species' range in the tropics (426 species, 1,594 species–season observations). Points are coloured by temperature seasonality (grey, species not matched to the phylogeny). **b**, Upper and lower wingspan against absolute latitude (363–400 species). **c**, Predicted range size against wingspan at 0°, 20°, 40° and 60° absolute latitude (363 species); the wingspan $\times$ latitude interaction was not significant (phylogenetic model in Fig. S3). **d**, Environmental correlates of

544 seasonal-switching richness from a spatial generalised additive model (4,122 equal-area cells of
545 approximately 110×110 km); coefficients describe mean richness per 2.5-arc-minute cell on the
546 log scale. Land cover is shown relative to built-up areas. Filled symbols indicate 95% confidence
547 intervals that exclude zero. In **a–c**, lines are mixed-model fits; bands (a–c) and bars (d) show
548 95% confidence intervals. Range size is $\log_{10}$ km²; wingspan is $\log_{10}$ cm.

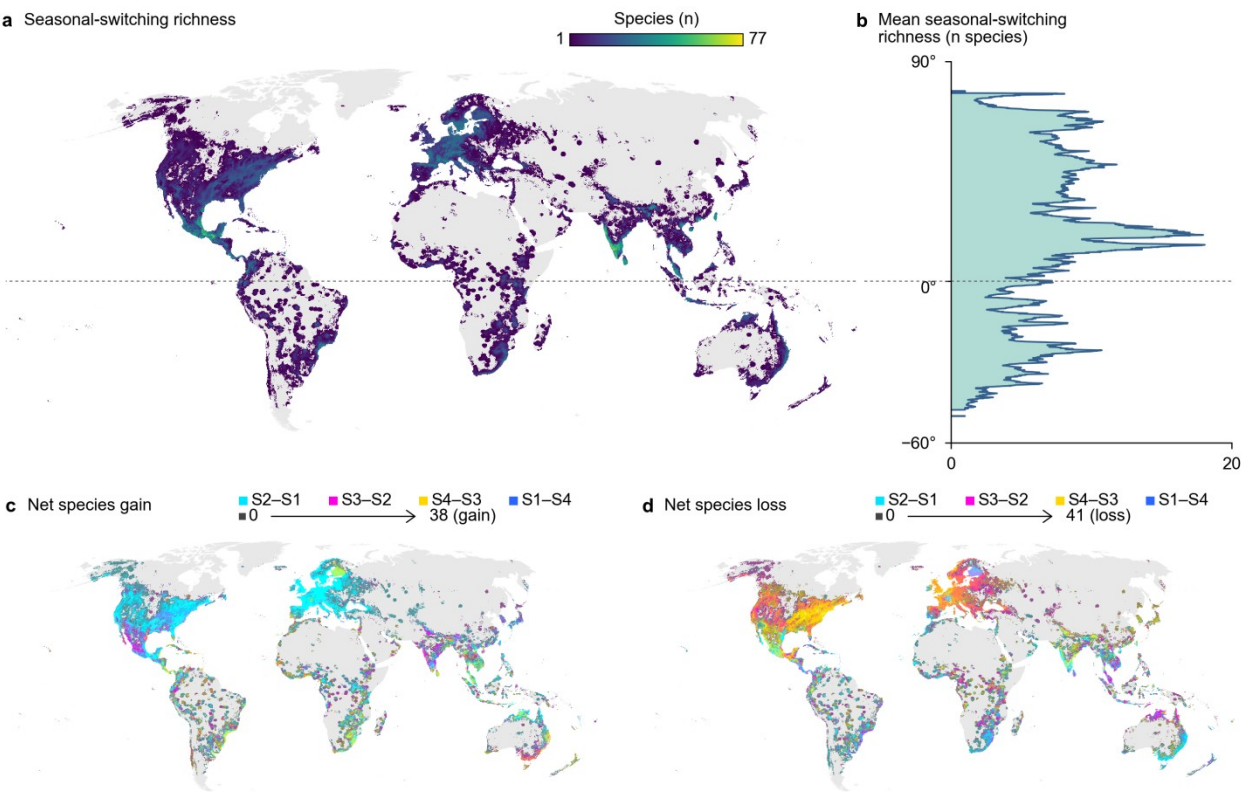
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550 **Fig. 3 | Phylogenetic structure of range size.** Phylogeny of 247 migratory butterfly
551 species. Branch colours show observed (tips) and reconstructed ancestral (internal nodes) $\log_{10}$
552 range size (km²). The inner ring shows species range size and the outer ring shows family. The
553 inset shows the distribution of species range size.

554

555

557 **Figures**



558

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560 switching richness: the number of species that use a grid cell in some seasons but not all
561 (Robinson projection). **b**, Mean seasonal-switching richness per occupied cell, by latitude. **c**, **d**,
562 Net seasonal change in predicted richness decomposed into net gain (**c**) and net loss (**d**) across
563 the four transitions: S2–S1 (spring, N. Hemis.; cyan), S3–S2 (summer; magenta), S4–S3
564 (autumn; yellow) and S1–S4 (winter; blue). Values were converted by $\text{sign}(x) \cdot \ln(|x|+1)$; scale
565 arrows show the maximum empirical values (38 for gain, 41 for loss).

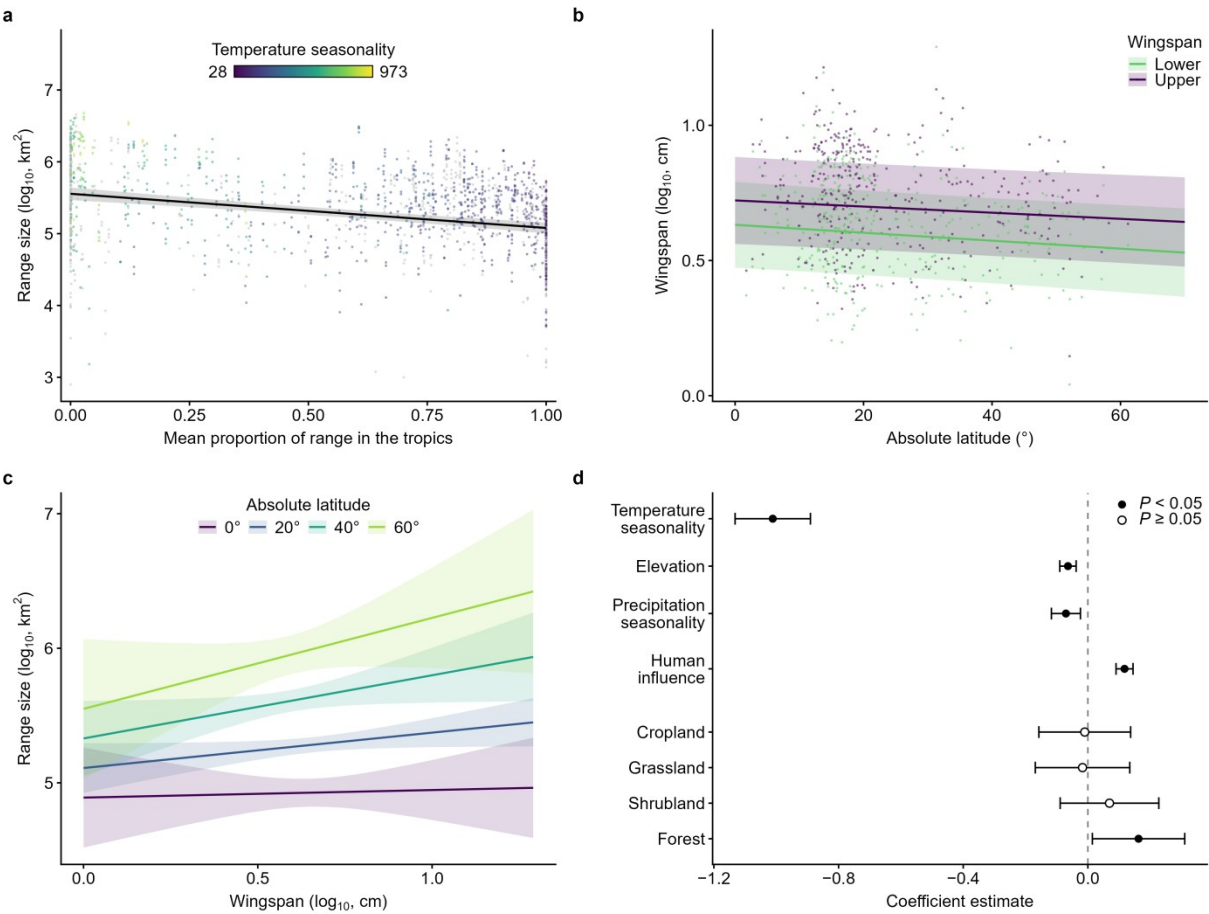


Fig. 2 | Drivers of range size and richness. a, Range size against the proportion of each

species' range in the tropics (426 species, 1,594 species–season observations). Points are

coloured by temperature seasonality (grey, species not matched to the phylogeny). **b,** Upper and

lower wingspan against absolute latitude (363–400 species). **c,** Predicted range size against

wingspan at 0°, 20°, 40° and 60° absolute latitude (363 species); the wingspan $\times$ latitude

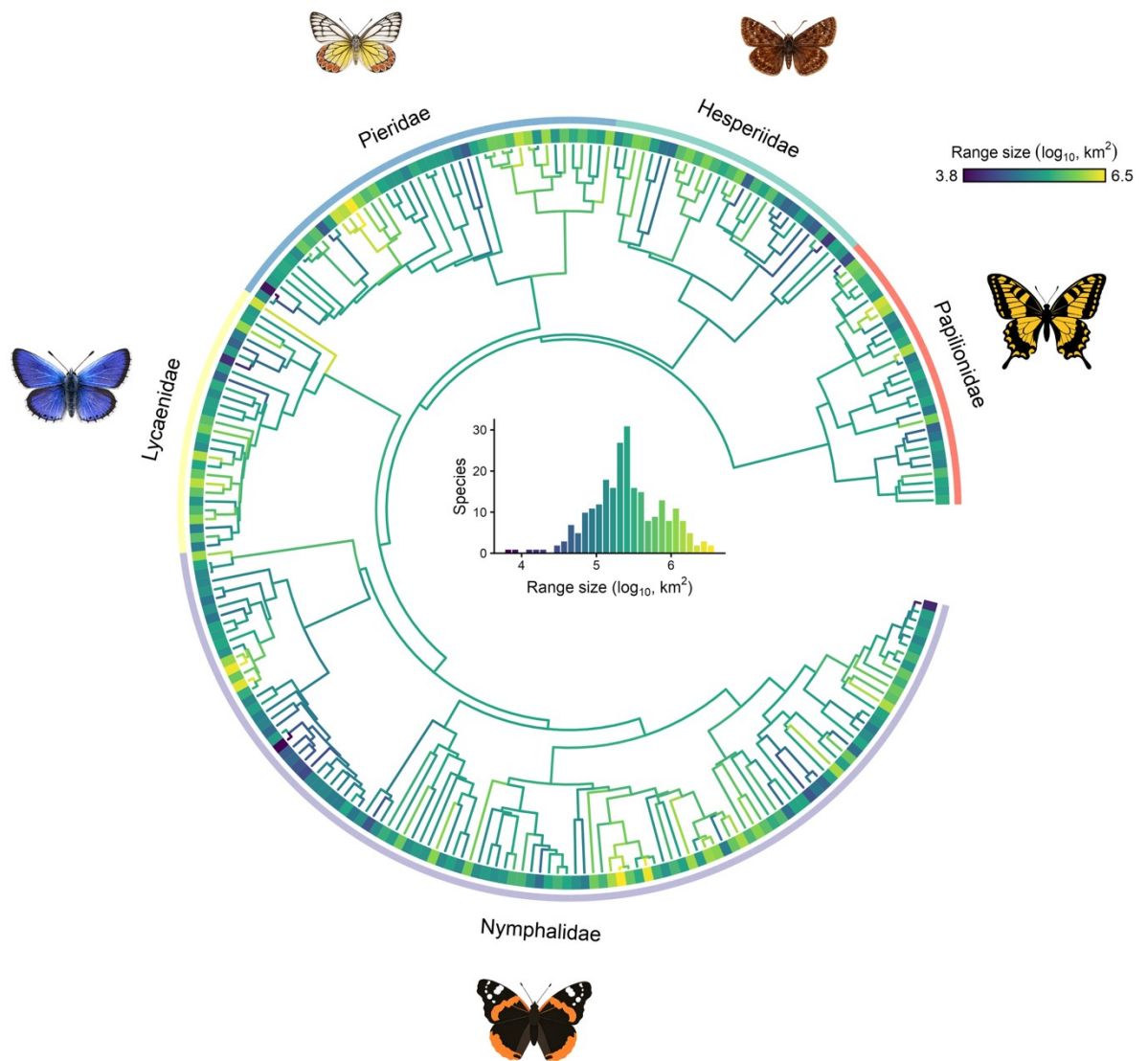
interaction was not significant (phylogenetic model in Fig. S3). **d,** Environmental correlates of

seasonal-switching richness from a spatial generalised additive model (4,122 equal-area cells of

approximately 110 $\times$ 110 km); coefficients describe mean richness per 2.5-arc-minute cell on the

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 582 inset shows the distribution of species range size.

583

584 Supplementary Information

585 Supplementary Results, Figures S1–S9 and Tables S1–S9 are provided in the Supplementary

586 Information.

Supplementary Information

Latitude and phylogeny shape the global distribution of migratory butterflies

Haiyu Li, Qiushuang Liang, Wei-Ping Chan, Zunyi Xie, Rohan Clarke, Shawan Chowdhury

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Table S9. Prior distributions of the Bayesian models

25 **Supplementary Results**

26 *Range size, latitude and wingspan*

27 Within species, seasons with a larger tropical proportion had smaller ranges (estimate = -0.30 , $P < 0.001$), and
 28 seasonal range size was larger during Northern Hemisphere spring and summer (S2: estimate = 0.12 ; S3:
 29 estimate = 0.10 ; both $P < 0.001$). Across all species, both measures of wingspan declined weakly with
 30 increasing absolute latitude (upper wingspan: estimate = -0.0011 , $P = 0.019$; lower wingspan: estimate =
 31 -0.0015 , $P = 0.006$), and larger-winged species had a larger tropical range proportion (upper wingspan:
 32 estimate = 0.44 , $P < 0.001$). The association between wingspan and range size did not differ significantly
 33 between hemispheres ($P \geq 0.20$; Table S2).

34 *Environmental correlates of seasonal-switching richness*

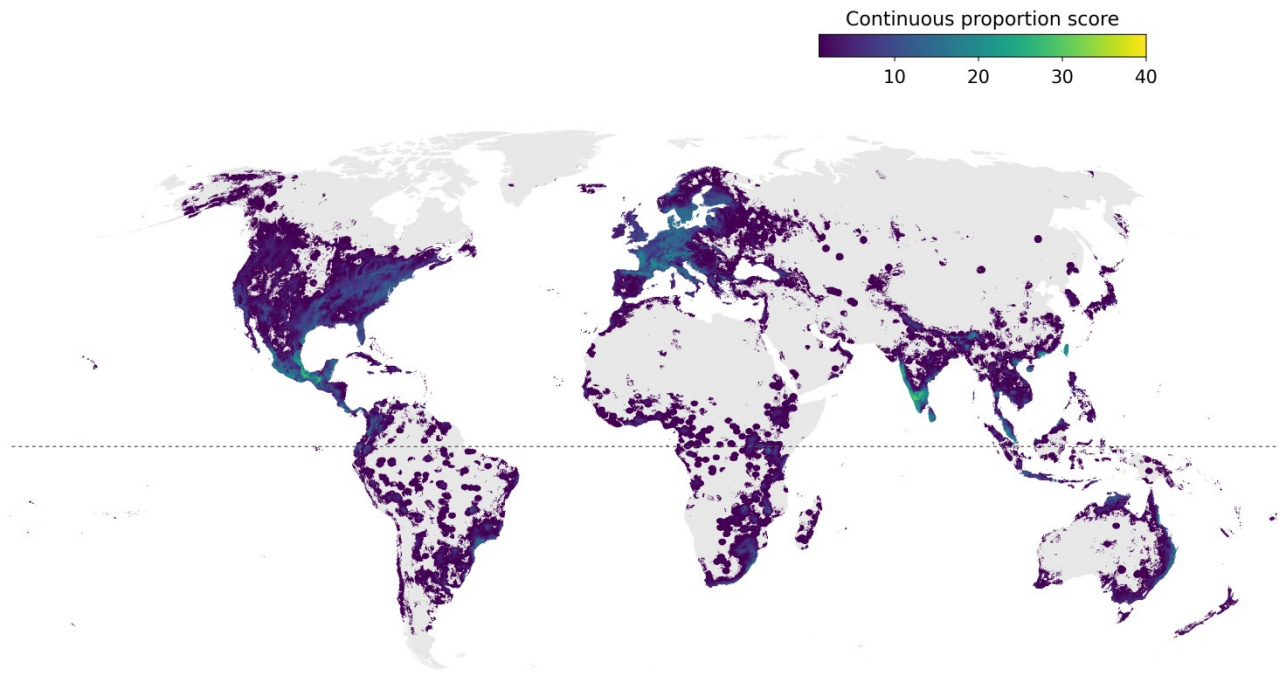
35 These associations were robust to alternative model structures, spatial resolutions and restriction to the
 36 phylogenetically matched subset (Table S3; Figs S4–S7). Higher richness in forest than in built-up areas was
 37 consistent across spatial models, whereas other land-cover contrasts varied among model formulations and are
 38 therefore interpreted cautiously. Residual spatial autocorrelation in the main model was low after accounting
 39 for broad-scale spatial structure (Moran's $I = 0.003$).

40 *Phylogenetic structure of range size*

41 Among the environmental predictors in the principal model, temperature seasonality (estimate = 0.23) and
 42 elevation (estimate = 0.07) were positively associated with range size, whereas precipitation seasonality
 43 (estimate = -0.03) and the seasonal variation in tropical range proportion (estimate = 0.01) were weakly
 44 associated with range size (Table S4). The phylogenetic signal did not depend on the environmental
 45 covariates. Models with tropical range proportion and season, season alone, or no fixed effects yielded $H^2 =$
 46 0.31 – 0.44 (Table S4), showing that phylogeny structured range size even when considered alone. Restricting
 47 the principal model to the 134 species with exact phylogenetic matches gave a similar estimate ($H^2 = 0.23$,
 48 95% credible interval = 0.03 – 0.50 ; Table S4), indicating that the use of congeneric surrogate tips did not
 49 substantially inflate phylogenetic signal. Incorporating phylogenetic covariance improved predictive
 50 performance relative to the equivalent non-phylogenetic model (Table S5).

51 *Integrated model*

52 In the integrated model, environmental predictors accounted for 19% (95% credible interval = 12–26%) of the
 53 variance, wingspan for 3% (0–9%) and phylogeny for 16% (2–36%), with a further 45% (31–58%)
 54 attributable to non-phylogenetic differences among species (Fig. S9; Table S6). Range size increased with
 55 temperature seasonality (estimate = 0.29 , 95% credible interval = 0.22 – 0.36) and wingspan (estimate = 0.09 ,
 56 95% credible interval = 0.01 – 0.17).



58

59 **Figure S1 | Sensitivity of seasonal-switching richness to the binary classification.** Continuous seasonal
 60 occurrence index, calculated for each grid cell as the sum across 426 species of the proportion of each species'
 61 suitable seasons in which the cell was suitable ($S/S_{\max}$). The index was strongly correlated with binary
 62 seasonal-switching richness (Spearman's $\rho = 0.98$), and 78% of cells in the upper 5% of the two distributions
 63 coincided.

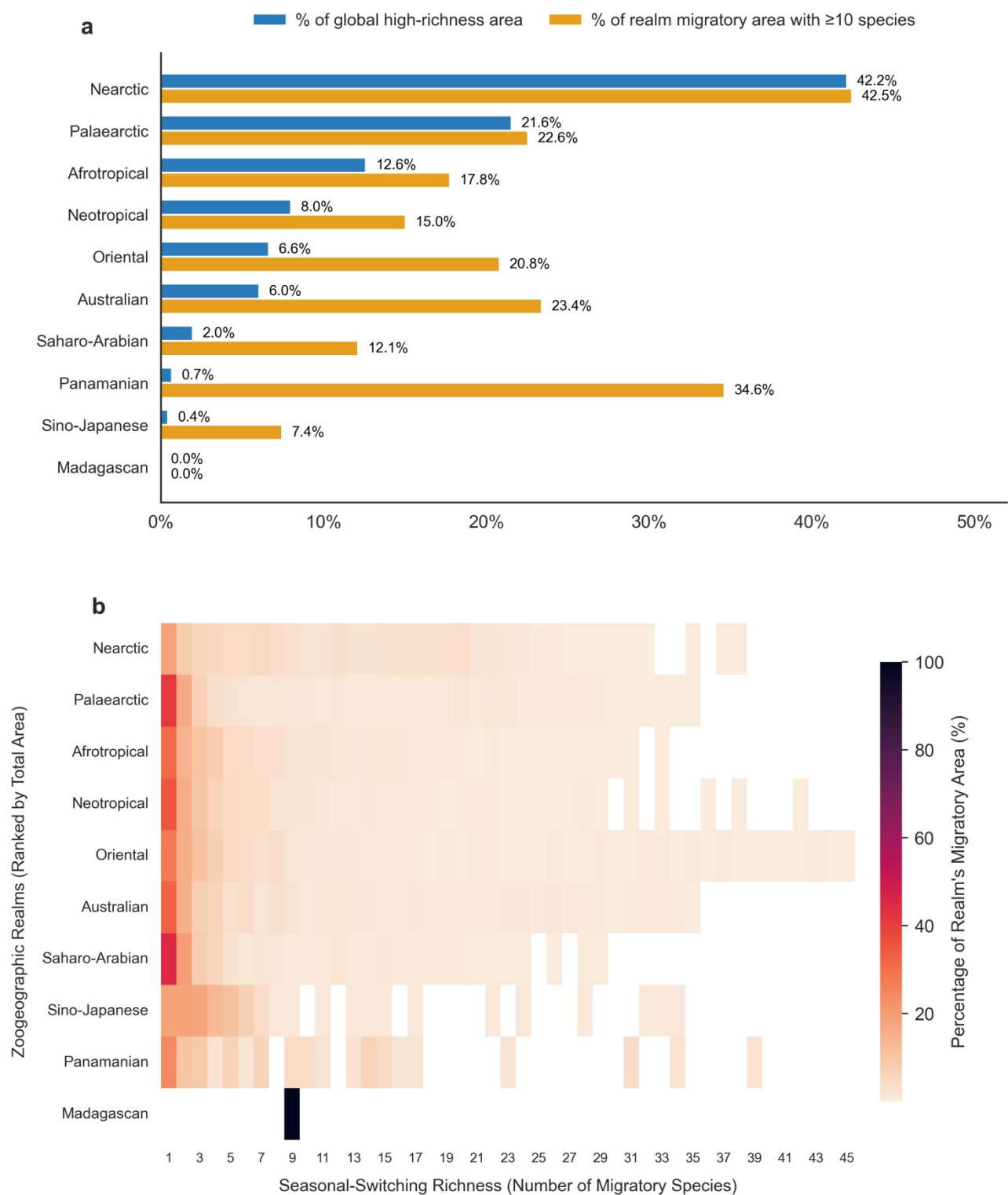
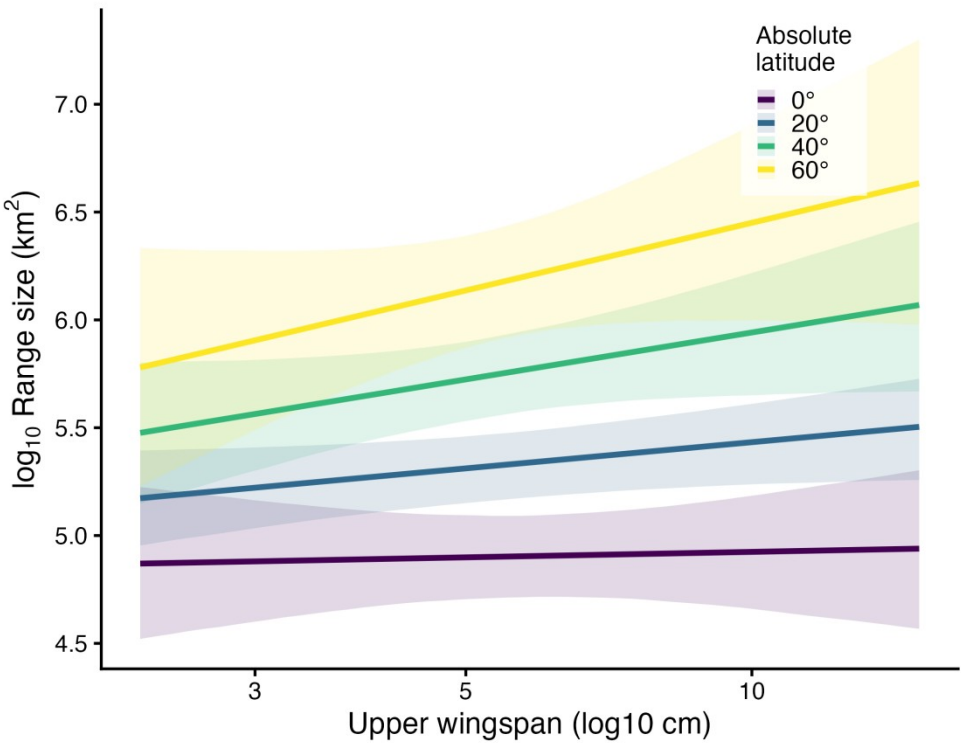


Figure S2 | High-richness area across zoogeographic realms. (a) For each zoogeographic realm (ref. 50 in the main text), the share of the global area supporting ≥ 10 seasonal-switching species (blue) and the percentage of the realm's own migratory land area supporting ≥ 10 species (orange). The Nearctic and Palaearctic together held 63.7% of the global high-richness area, whereas high-richness assemblages covered 42.5% of the Nearctic, 34.6% of the Panamanian, 23.4% of the Australian, 22.6% of the Palaearctic, 20.8% of

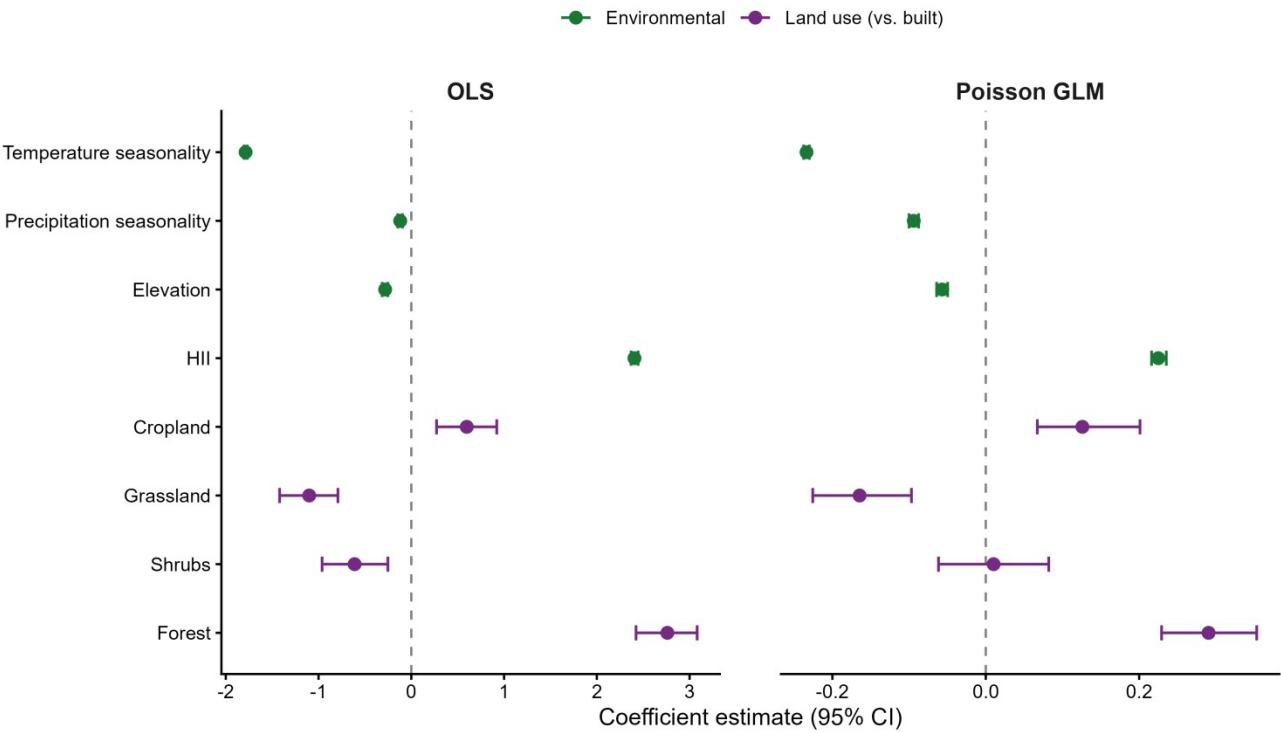
65

70 the Oriental, 17.8% of the Afrotropical, and 15.0% of the Neotropical realm. (b) Percentage of each realm's
71 migratory land area supporting a given number of seasonal-switching species; realms are ordered by total
72 migratory area. Areas were calculated from spherical cell areas on a 0.5° grid.



73

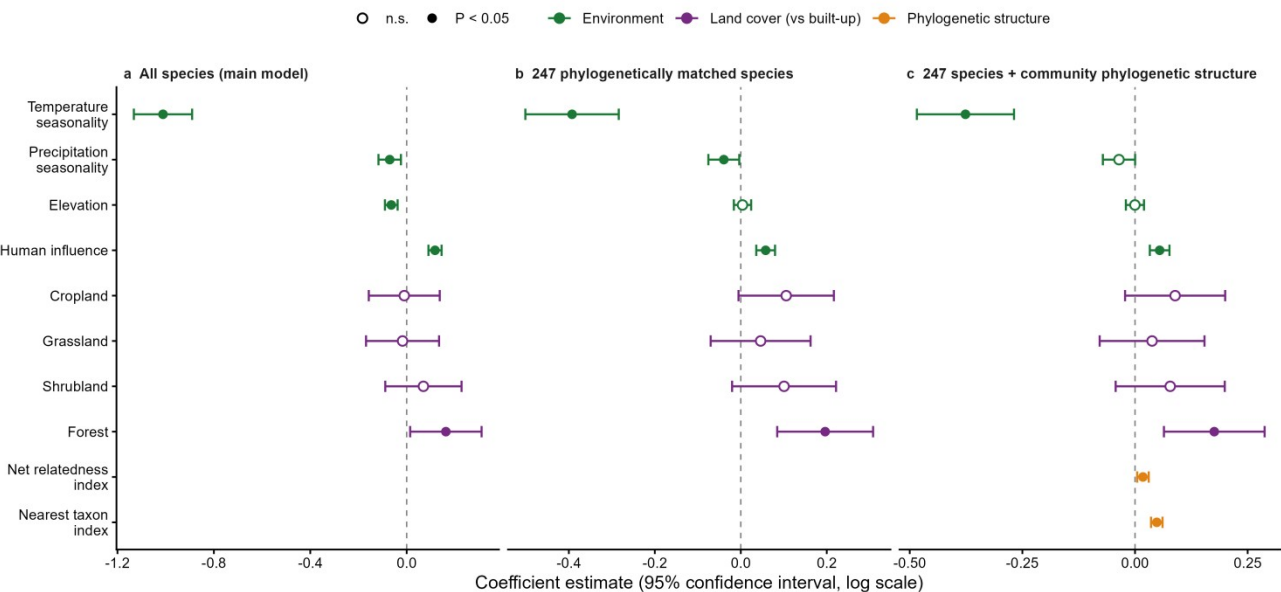
74 **Figure S3 | Range size–wingspan association across latitudes in the phylogenetic model.** Posterior mean
75 predictions (lines) and 95% credible intervals (bands) of log₁₀ seasonal range size against upper wingspan at
76 0°, 20°, 40° and 60° absolute latitude from the Bayesian phylogenetic mixed model (231 species, 892 seasonal
77 observations; Table S1), with the seasonal deviation in tropical proportion at its mean and season at the
78 reference level. As in the non-phylogenetic model (Fig. 2c), range size increased with wingspan and the
79 wingspan × latitude interaction was not significant (estimate = 0.03, 95% credible interval = −0.03 to 0.09).



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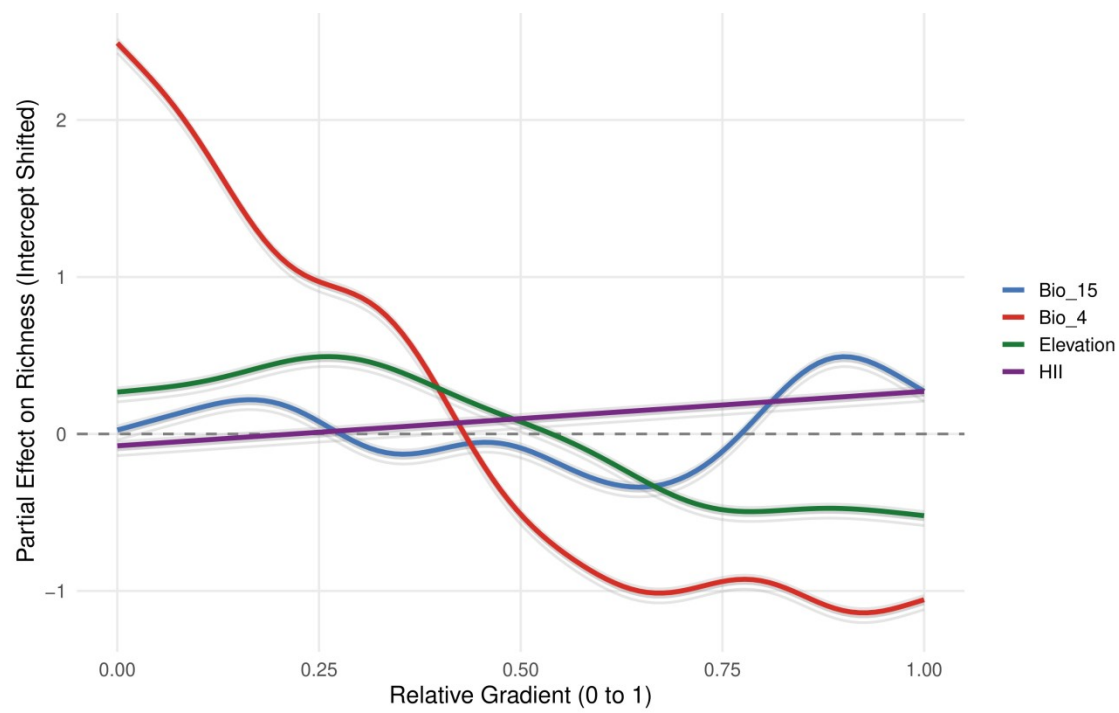
81 **Figure S4 | Environmental correlates of richness in ordinary least squares and Poisson models.**

82 Coefficients (95% confidence intervals) from models without spatial terms: ordinary least squares (OLS;
83 response scale, stability assessed across 100 resampling iterations) and a Poisson generalised linear model
84 (GLM; log scale) fitted after thinning the grid to a minimum separation of 50 km. Continuous predictors are z-
85 standardised and land cover is expressed relative to built-up areas. Residual spatial autocorrelation remained
86 high (Moran's I = 0.880 and 0.703), so these models were treated as sensitivity analyses; coefficients are
87 listed in Table S3.

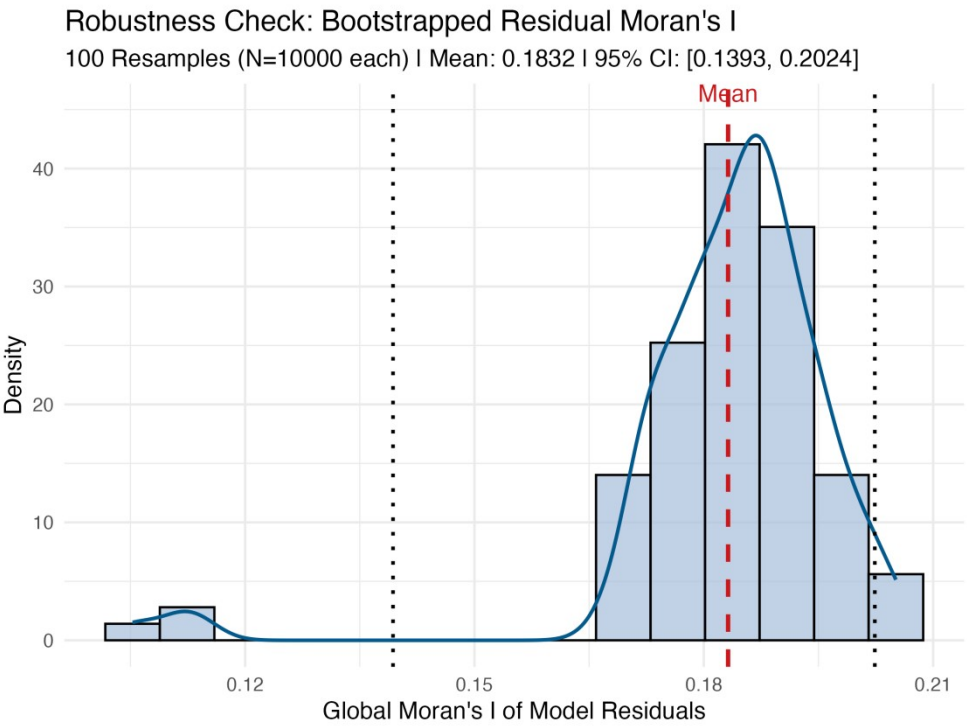


88

89 **Figure S5 | Sensitivity of richness correlates to species pool and community phylogenetic structure.**
90 Coefficients (95% confidence intervals, log scale) from negative binomial generalised additive models with a
91 two-dimensional spatial smooth fitted to 4,122 equal-area cells (approximately 110 × 110 km): (a) the main
92 model for all species (Fig. 2d); (b) richness of the 247 phylogenetically matched species; (c) as (b) with the
93 net relatedness index (NRI) and nearest taxon index (NTI) as covariates. Continuous predictors are z-
94 standardised, land cover is expressed relative to built-up areas, and open symbols indicate $P \geq 0.05$.
95 Temperature seasonality (negative), human influence and forest (positive) were consistent across models; NRI
96 and NTI were positively associated with richness but did not alter the environmental associations (residual
97 Moran's I = 0.003, 0.018 and 0.018).



98
99 **Figure S6 | Partial effects of the 2.5-arc-minute sensitivity model of richness.** Negative binomial
100 generalised additive model fitted to 1,324,697 grid cells, with smooth terms for temperature seasonality,
101 precipitation seasonality and elevation, linear terms for the Human Influence Index and land cover, and a
102 Duchon spline of longitude and latitude ($k = 1,500$). Predictors are rescaled to 0–1. Coloured curves are
103 shown for built-up areas and grey curves for other land-cover classes, shifted by their intercepts. Deviance
104 explained = 77.7%.

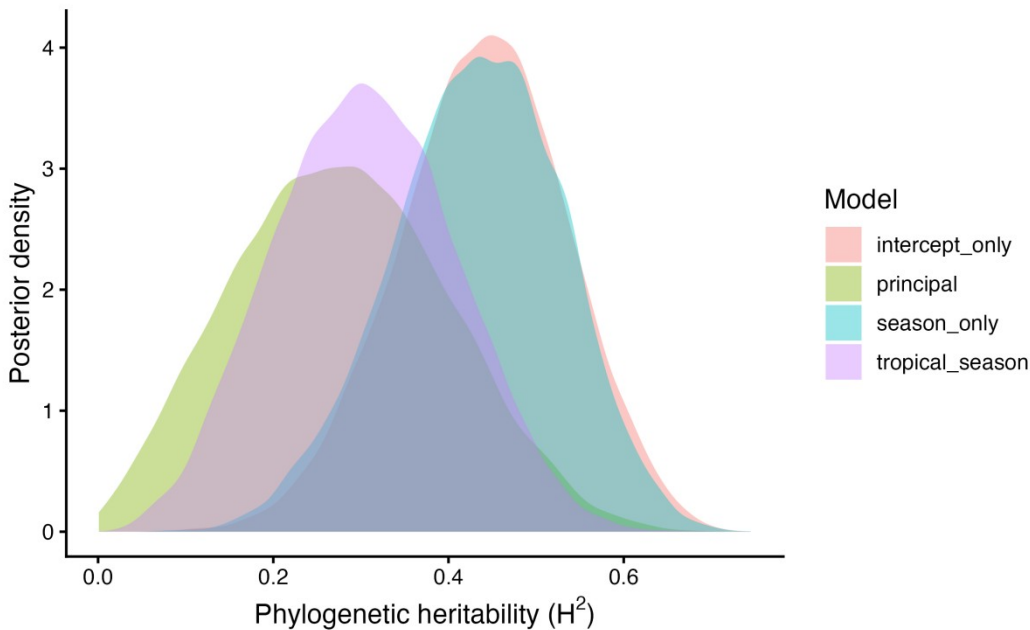


105

106 **Figure S7 | Residual spatial autocorrelation of the 2.5-arc-minute sensitivity model.** Distribution of global

107 Moran's I of Pearson residuals across 100 random subsamples of 10,000 cells, with neighbours defined as the

108 12 nearest cells (mean = 0.18, 95% interval = 0.14–0.20).



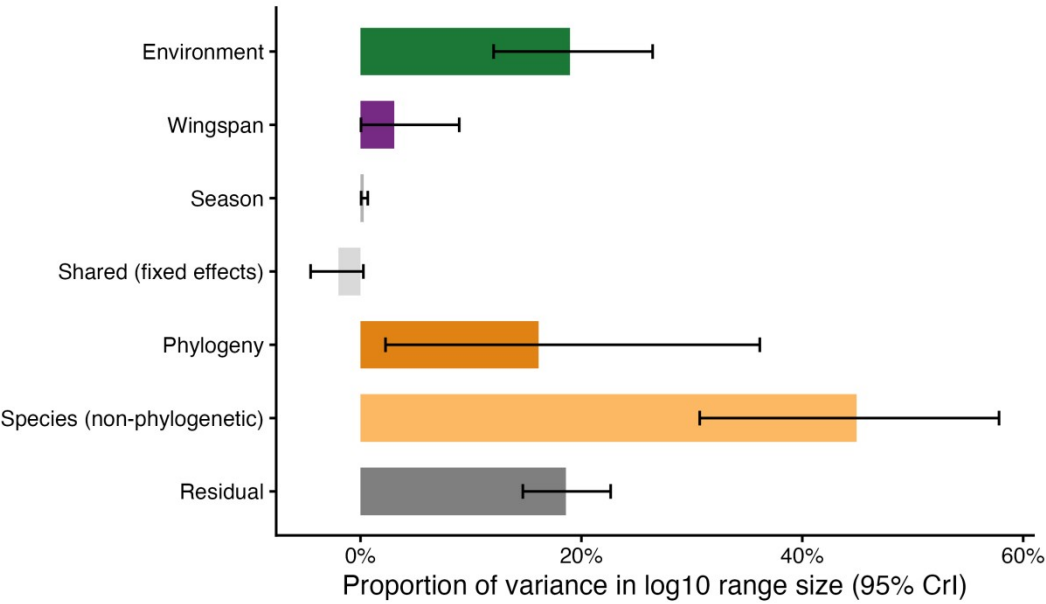
109

110 **Figure S8 | Posterior distributions of phylogenetic heritability.** Phylogenetic heritability (H^2 , phylogenetic

111 variance as a proportion of total variance, from models with phylogenetic and species random effects) in the

112 principal Bayesian phylogenetic mixed model (207 species, 803 seasonal observations) and in three

113 alternative models fitted to 247 phylogenetically matched species (943 observations): tropical range
114 proportion and season, season only, and intercept only.



115
116 **Figure S9 | Variance partitioning of range size in the integrated model.** Proportion of variance in $\log_{10}$
117 seasonal range size explained by environment, migratory capacity (upper wingspan), season, variance shared
118 among fixed effects, phylogeny, non-phylogenetic species differences and residual within-species variation
119 (posterior means and 95% credible intervals; 231 species, 892 seasonal observations; Table S6).

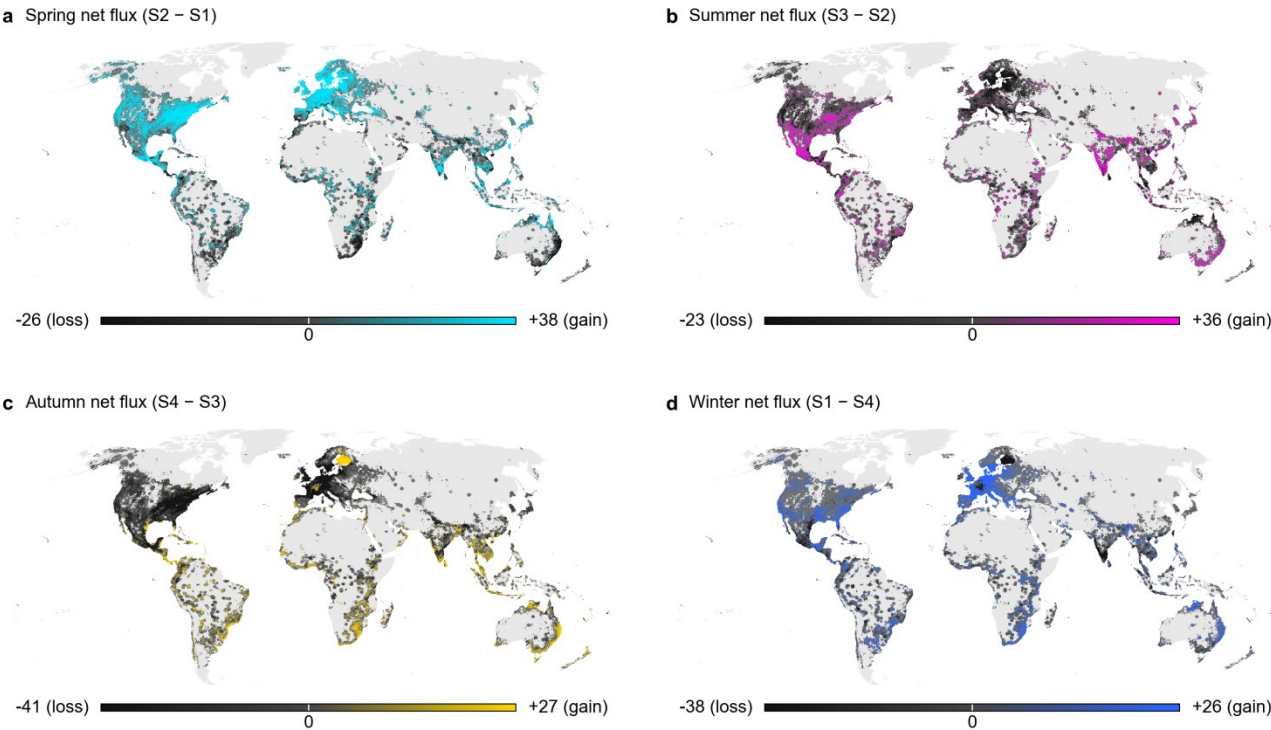


Figure S10 | Seasonal switching patterns a–d, Net seasonal change for each of the four transitions (Robinson projection): S2–S1 (spring, N. Hemis.) (a), S3–S2 (summer) (b), S4–S3 (autumn) (c) and S1–S4 (winter) (d). Values were converted by $\text{sign}(x) \cdot \ln(|x|+1)$; diverging colour bars indicate empirical endpoints for net loss (dark tones) and net gain (seasonal colours).

Table S1 | Wingspan models with and without phylogeny. Range size models (400 species, 1,510 observations; phylogeny-matched: 231 species, 892 observations): response is $\log_{10}$ seasonal range size and continuous predictors are z-standardised. Linear mixed models include a species random intercept (estimate (SE) and Satterthwaite P); the Bayesian phylogenetic mixed model (BPMM) includes phylogenetic and non-phylogenetic species random effects (posterior mean [95% credible interval]; max $\hat{R} = 1.004$). Range size increased with wingspan and latitude, and the wingspan $\times$ latitude interaction was not supported in any model. Species-level models: the latitudinal decline in wingspan was significant across all species but not within the phylogenetically matched subset or after accounting for phylogeny; larger-winged species had a larger tropical range proportion.

Term	LMM, all species	LMM, phylogeny-matched species	BPMM with phylogeny
Range size models (seasonal observations)			
Absolute latitude	0.231 (0.023); $P < 0.001$	0.226 (0.027); $P < 0.001$	0.220 [0.164, 0.277]
$\log_{10}$ upper wingspan	0.088 (0.023); $P < 0.001$	0.076 (0.027); $P = 0.006$	0.076 [–0.002, 0.149]
Wingspan $\times$ absolute latitude	0.025 (0.025); $P = 0.330$	0.029 (0.030); $P = 0.331$	0.030 [–0.029, 0.089]
Seasonal deviation in tropical proportion	–0.029 (0.007); $P < 0.001$	–0.037 (0.008); $P < 0.001$	–0.037 [–0.053, –0.021]
Season S2	0.123 (0.021); $P < 0.001$	0.071 (0.024); $P = 0.003$	0.071 [0.025, 0.117]
Season S3	0.105 (0.021); $P < 0.001$	0.093 (0.024); $P < 0.001$	0.093 [0.047, 0.139]
Season S4	–0.028 (0.021); $P = 0.186$	–0.019 (0.024); $P = 0.419$	–0.020 [–0.067, 0.027]
Species-level models (family random intercept in LMMs)			
Upper wingspan $\sim$ absolute latitude	–0.0011; $P = 0.019$ (400 sp.)	–0.0006; $P = 0.448$ (231 sp.)	0.0002 [–0.0012, 0.0015]
Lower wingspan $\sim$ absolute latitude	–0.0015; $P = 0.006$ (363 sp.)	–0.0009; $P = 0.283$ (207 sp.)	–0.0004 [–0.0020, 0.0012]
Tropical proportion $\sim \log_{10}$ upper wingspan	0.439; $P < 0.001$ (400 sp.)	0.442; $P = 0.004$ (231 sp.)	0.314 [–0.063, 0.672]
Tropical proportion $\sim \log_{10}$ lower wingspan	0.467; $P < 0.001$ (363 sp.)	0.437; $P < 0.001$ (207 sp.)	0.400 [0.028, 0.771]

Table S2 | Hemisphere sensitivity of the wingspan–range size association. Species-level models of $\log_{10}$ mean range size (363 species: 265 with northern and 98 with southern range centroids) comparing a pooled model (wingspan $\times$ absolute latitude) with a model in which all terms interact with hemisphere. Allowing terms to differ between hemispheres did not improve the model, and the three-way interaction was not significant.

Wingspan measure	ΔAIC (hemisphere – pooled)	LRT χ^2 (df = 4)	LRT P	Wingspan $\times$ latitude $\times$ hemisphere: estimate (SE)	P
Upper wingspan	+2.2	5.83	0.212	–0.004 (0.044)	0.920
Lower wingspan	+2.0	5.97	0.201	–0.026 (0.036)	0.482

141 **Table S3 | Environmental correlates of seasonal-switching richness across model formulations.**

142 Coefficients (95% confidence intervals) on the log scale for negative binomial generalised additive models
 143 (GAMs) and Poisson generalised linear model (GLM), and on the response scale for ordinary least squares
 144 (OLS); continuous predictors are z-standardised and land cover is expressed relative to built-up areas. The
 145 main model (Fig. 2d) uses all species with an offset for the number of occupied 2.5-arc-minute cells per equal-
 146 area cell (approximately 110×110 km, Behrmann projection); the 247-species models use richness of
 147 phylogenetically matched species, with and without community phylogenetic structure (NRI, NTI). All GAMs
 148 include a two-dimensional spatial smooth.

Predictor	Main GAM (all species)	GAM, 247 species	GAM, 247 species + NRI/NTI	Non-linear GAM (2.5')	OLS	Poisson GLM
Temperature seasonality	-1.011 [-1.132, -0.890]	-0.393 [-0.501, -0.284]	-0.376 [-0.484, -0.269]	smooth (edf 8.9)	-1.787 [-1.803, -1.769]	-0.234 [-0.237, -0.230]
Precipitation seasonality	-0.070 [-0.117, -0.024]	-0.039 [-0.075, -0.004]	-0.036 [-0.071, 0.000]	smooth (edf 9.0)	-0.119 [-0.146, -0.096]	-0.094 [-0.100, -0.088]
Elevation	-0.064 [-0.090, -0.038]	0.004 [-0.016, 0.024]	-0.000 [-0.020, 0.020]	smooth (edf 8.2)	-0.282 [-0.314, -0.253]	-0.057 [-0.064, -0.050]
Human Influence Index	0.118 [0.090, 0.145]	0.058 [0.036, 0.080]	0.055 [0.033, 0.076]	0.057 [0.056, 0.058]	2.406 [2.369, 2.446]	0.225 [0.216, 0.235]
Cropland (vs built-up)	-0.010 [-0.157, 0.137]	0.106 [-0.005, 0.217]	0.089 [-0.022, 0.200]	-0.026 [-0.032, -0.020]	0.598 [0.272, 0.921]	0.126 [0.067, 0.201]
Grassland (vs built-up)	-0.017 [-0.169, 0.134]	0.046 [-0.070, 0.162]	0.038 [-0.078, 0.154]	-0.025 [-0.031, -0.018]	-1.100 [-1.420, -0.791]	-0.165 [-0.226, -0.097]
Shrubland (vs built-up)	0.069 [-0.089, 0.228]	0.101 [-0.020, 0.222]	0.078 [-0.043, 0.199]	-0.063 [-0.070, -0.056]	-0.611 [-0.962, -0.253]	0.010 [-0.062, 0.082]
Forest (vs built-up)	0.163 [0.015, 0.311]	0.196 [0.085, 0.308]	0.176 [0.064, 0.288]	0.026 [0.021, 0.032]	2.761 [2.422, 3.081]	0.291 [0.229, 0.353]
NRI	—	—	0.018 [0.005, 0.030]	—	—	—
NTI	—	—	0.048 [0.036, 0.061]	—	—	—
Residual Moran's I	0.003	0.018	0.018	0.18 [0.14, 0.20]	0.880	0.703
Deviance explained	85.40%	89.90%	90.10%	77.70%	—	—
Grid cells	4,122 (equal-area)	4,122 (equal-area)	4,122 (equal-area)	1,324,697 (2.5')	100 resamples (300/grid)	thinned to ≥ 50 km

149

150

151 **Table S4 | Bayesian phylogenetic mixed models of geographic range size.** Posterior means [95% credible
 152 intervals]; response is $\log_{10}$ seasonal range size and continuous predictors are z-standardised. All models
 153 include a phylogenetic random effect (correlation-scaled phylogenetic covariance) and a non-phylogenetic
 154 species random intercept; $H^2 = \sigma^2_{\text{phylogeny}} / (\sigma^2_{\text{phylogeny}} + \sigma^2_{\text{species}} + \sigma^2_{\text{residual}})$ and $\lambda = \sigma^2_{\text{phylogeny}} /$
 155 $(\sigma^2_{\text{phylogeny}} + \sigma^2_{\text{species}})$. The last row refits the principal model with the phylogenetic effect only. The
 156 exact-match model repeats the principal model using only species matched exactly to a phylogeny tip. Four
 157 chains of 6,000 iterations (2,000 warm-up); seed = 1.

Term	Principal model	Tropical proportion + season	Season only	Intercept only	Principal, exact matches only
Species / observations	207 / 803	247 / 943	247 / 943	247 / 943	134 / 522
H^2	0.277 [0.055, 0.520]	0.305 [0.114, 0.505]	0.432 [0.231, 0.610]	0.438 [0.244, 0.619]	0.227 [0.035, 0.501]
λ (phylogenetic / species-level variance)	0.353 [0.073, 0.631]	0.389 [0.152, 0.616]	0.524 [0.293, 0.713]	0.538 [0.313, 0.727]	—
Temperature	0.231 [0.177, 0.285]	—	—	—	0.260 [0.195, 0.325]

seasonality					
Precipitation seasonality	-0.031 [-0.072, 0.010]	—	—	—	-0.017 [-0.070, 0.035]
Elevation	0.071 [0.028, 0.113]	—	—	—	0.070 [0.025, 0.116]
Mean tropical range proportion	—	-0.511 [-0.679, -0.345]	—	—	—
Seasonal deviation in tropical proportion	0.009 [-0.010, 0.028]	-0.036 [-0.052, -0.020]	—	—	0.017 [-0.008, 0.041]
Season S2	0.051 [0.005, 0.098]	0.066 [0.021, 0.112]	0.059 [0.013, 0.106]	—	0.060 [0.003, 0.117]
Season S3	0.060 [0.013, 0.108]	0.091 [0.045, 0.136]	0.091 [0.045, 0.138]	—	0.059 [0.001, 0.117]
Season S4	-0.023 [-0.070, 0.023]	-0.030 [-0.077, 0.016]	-0.039 [-0.087, 0.007]	—	-0.042 [-0.100, 0.015]
Maximum $\hat{R}$	1.004	1.001	1.001	1.002	<1.01
H ² without species random effect	0.925 [0.899, 0.946]	—	—	—	—

158

159 **Table S5 | Non-phylogenetic models and leave-one-out comparison.** Bayesian Gaussian models of $\log_{10}$
160 seasonal range size without phylogenetic structure, fitted to the principal phylogenetic subset (z-standardised
161 predictors) and to the full dataset (unstandardised predictors). Leave-one-out cross-validation strongly
162 favoured the phylogenetic model (difference in expected log predictive density, ΔELPD).

Term	Phylogenetic subset	Full dataset
Temperature seasonality	0.193 [0.156, 0.230]	0.0008 [0.0007, 0.0010]
Precipitation seasonality	-0.051 [-0.087, -0.017]	-0.0013 [-0.0026, -0.0001]
Elevation	-0.002 [-0.037, 0.032]	-0.0001 [-0.0002, -0.0001]
Seasonal deviation in tropical proportion	0.007 [-0.023, 0.038]	0.0651 [-0.1999, 0.3302]
Observations	803	1,594
LOO ΔELPD vs principal BPMM (SE)	-405.7 (24.2)	—

163

164 **Table S6 | Integrated model and variance partitioning of range size.** Bayesian phylogenetic mixed model
165 of $\log_{10}$ seasonal range size (231 species, 892 seasonal observations) including environmental predictors,
166 upper wingspan, season, and phylogenetic and non-phylogenetic species random effects. Percentages of total
167 variance (posterior mean [95% credible interval]) were obtained for each posterior draw from the variance of
168 each group of linear predictors, their covariance, and the random-effect and residual variances (ref. 71 in the
169 main text).

Component	% of variance / estimate
Environment (temperature and precipitation seasonality, elevation, tropical proportion)	19.0 [12.1, 26.5]
Migratory capacity ($\log_{10}$ upper wingspan)	3.0 [0.0, 8.9]
Season	0.3 [0.1, 0.7]
Shared among fixed effects	-2.0 [-4.5, 0.3]
Phylogeny	16.1 [2.3, 36.2]
Species (non-phylogenetic)	44.9 [30.7, 57.8]
Residual (within species)	18.6 [14.7, 22.7]
Environment – phylogeny (difference)	2.8 [-21.9, 21.0]
Fixed effects (standardised)	
Temperature seasonality	0.285 [0.215, 0.356]
Precipitation seasonality	-0.036 [-0.078, 0.006]
Elevation	0.073 [0.035, 0.110]
Mean tropical range proportion	0.074 [-0.012, 0.161]
Seasonal deviation in tropical proportion	0.021 [-0.001, 0.044]
$\log_{10}$ upper wingspan	0.086 [0.007, 0.167]

170

171 **Table S7 | Sample attrition across filtering steps.** Retained versus excluded species at each step: medians
 172 (retained vs excluded) of absolute latitude, mean tropical range proportion and log₁₀ range size, with Cliff's δ
 173 and Wilcoxon P; family composition compared with a χ^2 test (simulated P where expected counts were small;
 174 seed = 1).

Filtering step	Retained	Excluded	Latitude	Tropical proportion	log ₁₀ range size	Family composition P
568 migratory species → 426 with suitability maps	426	142	not assessable	not assessable	not assessable	—
426 → 400 with wingspan data	400	26	18.6 vs 10.3 ($\delta = +0.46$, $P = 0.000$)	0.705 vs 1 ($\delta = -0.54$, $P = 0.000$)	5.4 vs 4.87 ($\delta = +0.61$, $P = 0.000$)	0.009 (simulated)
400 → 231 with wingspan data and phylogenetically matched	231	169	17.9 vs 20.7 ($\delta = -0.22$, $P = 0.000$)	0.746 vs 0.559 ($\delta = +0.25$, $P = 0.000$)	5.4 vs 5.42 ($\delta = +0.03$, $P = 0.616$)	0.003

175

176 **Table S8 | Nested-subset re-estimation of the wingspan × latitude model.** Linear mixed model of log₁₀
 177 range size with absolute latitude × log₁₀ upper wingspan, seasonal deviation in tropical proportion, season and
 178 a species random intercept, refitted to each nested subset (estimates [95% confidence interval]). The
 179 interaction was not significant in either subset.

Species subset	n species (n obs.)	Wingspan at equator	Wingspan × latitude
Wingspan data	400 (1510)	0.242 [−0.306, 0.789]	0.011 [−0.011, 0.032]
Wingspan data, phylogeny-matched	231 (892)	0.093 [−0.613, 0.799]	0.016 [−0.016, 0.047]

180

181 **Table S9 | Prior distributions of the Bayesian models.** All Bayesian models used weakly informative priors.

Parameter	Principal, wingspan and exact-match models	Alternative and interaction models
Population-level (fixed) effects and intercept	Normal(0, 1)	Normal(0, 1)
Phylogenetic and species standard deviations	Exponential(1)	Half-Student-t(3, 0, 1)
Residual standard deviation	Exponential(1)	Half-Student-t(3, 0, 1)

182 Alternative models: tropical proportion + season, season only and intercept only (Table S4); interaction model: Table S1; integrated
 183 model: Table S6.

184 **Table S10 | Role of each variable in this study, seasonal habitat suitability was modelled from**
 185 **bioclimatic variables alone (ref. 34 in the main text). Variables already used in fitting those models are**
 186 **retained here as baseline controls and their coefficients are not interpreted as effects.**

187

Variable	Role	Note
Seasonal suitability map	Response variable	Range size and migratory richness from SDM
Temperature seasonality	Baseline control	Already informed in SDM for the suitability

Precipitation seasonality	Baseline control	As above
Elevation	Test variable	
Land cover	Test variable	Class only
Human influence index	Test variable	Not independent of recording effort
Tropical range proportion	Test variable	
Absolute centroid latitude	Test variable	
Wingspan (upper, lower)	Test variable	
Phylogeny	Random-effect	