

## Research



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### Author for correspondence:

João M. G. Capurcho  
e-mail: [jcapurcho@fieldmuseum.org](mailto:jcapurcho@fieldmuseum.org)

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# Dispersal ability correlates with range size in Amazonian habitat-restricted birds

João M. G. Capurcho<sup>1,2</sup>, Mary V. Ashley<sup>1</sup>, Brian R. Tsuru<sup>2</sup>, Jacob C. Cooper<sup>2,3</sup> and John M. Bates<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, University of Illinois at Chicago, 845 W. Taylor Street, Chicago, IL 60607, USA

<sup>2</sup>Life Sciences Section, Negaunee Integrative Research Center, The Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA

<sup>3</sup>Committee on Evolutionary Biology, The University of Chicago, 1025 E 57th Street, Chicago, IL 60637, USA

JMG, 0000-0002-0817-3243; JCC, 0000-0003-2182-3236

Understanding how species attain their geographical distributions and identifying traits correlated with range size are important objectives in biogeography, evolutionary biology and biodiversity conservation. Despite much effort, results have been varied and general trends have been slow to emerge. Studying species pools that occupy specific habitats, rather than clades or large groupings of species occupying diverse habitats, may better identify ranges size correlates and be more informative for conservation programmes in a rapidly changing world. We evaluated correlations between a set of organismal traits and range size in bird species from Amazonian white-sand ecosystems. We assessed if results are consistent when using different data sources for phylogenetic and range hypotheses. We found that dispersal ability, as measured by the hand-wing index, was correlated with range size in both white-sand birds and their non-white-sand sister taxa. White-sand birds had smaller ranges on average than their sister taxa. The results were similar and robust to the different data sources. Our results suggest that the patchiness of white-sand ecosystems limits species' ability to reach new habitat islands and establish new populations.

## 1. Introduction

The interplay between evolutionary processes, habitat characteristics and organisms' ecological, morphological and life-history attributes determine the geographical distribution of species [1]. For example, niche breadth, adaptive capabilities, population size and dispersal ability can all influence whether species will expand or contract their distributions through time [2]. Disentangling the factors that influence range size can improve our understanding of current and historical species distributions, and help predict distribution shifts under climate change scenarios [3–5], which may have important implications for conservation planning. Using a set of organismal traits that may influence whether and how fast species expand their distributions through time, we investigate their correlation with current range size in birds of Amazonian white-sand ecosystems.

Because most range size studies have examined clades encompassing species that occur in a wide variety of habitats, confounding factors are often an issue. For example, species adapted to more widespread habitats will tend to have larger ranges than species in more restricted habitats, irrespective of other species characteristics [6,7]. Also, circularity is often introduced into range size studies, exemplified by niche breadth proxies. Because niche data are commonly obtained from species records, inferred niche sizes of widespread species will be large, enforcing a positive correlation between niche breadth and range size [7,8]. Limiting analyses to species restricted to a single ecosystem provides a different perspective on how traits correlate with range size that could reduce circularity and issues related to confounding factors. We reduced dissimilarities in habitat distribution patterns, niche breadth and environmental history by focusing our analyses on bird species occurring in white-sand ecosystems.

Amazonian white-sand ecosystems occur patchily on nutrient-poor white-sand soils that were formed by different geological processes through time and space [9]. We selected species based on studies by Alonso *et al.* [10] and Borges *et al.* [11] that document avian taxa that are restricted to white-sand ecosystems. Our assumption is that all these species could occupy white-sand ecosystem patches across the Amazonian region, but how effectively they do so depends on their capability to expand their ranges.

The history of dynamic change across Amazonia is becoming increasingly well understood [12–14]. From the Late Pleistocene to the present, Amazonia has been affected by climatic changes associated with the glacial cycles that altered forest structure and habitat distribution, and, consequently, species distributions [13–16]. Phylogeographic analyses of three white-sand ecosystems birds show demographic expansion starting after the Last Glacial Maximum, probably a consequence of local extinction and subsequent recolonization of white-sand ecosystem patches [17,18]. In addition, analyses of community nestedness suggest regional patterns of extinction and recolonization of white-sand ecosystems patches [9,19]. Based on these previous results suggesting recent range expansion, we predict that the ranges of white-sand birds were reduced during the last glacial cycle and that current ranges were attained recently in evolutionary time. Therefore, current geographical ranges reflect recent dynamics, with specific organismal traits influencing how fast and how far species expanded to reach their current distributions.

Dispersal ability would seem likely to be positively correlated with range size, but results have been mixed [2,20–23]. Birds are vagile animals, yet they vary widely in dispersal ability [24]. Several proxies of dispersal ability have been developed in birds [25]. The hand-wing index (HWI) is a morphological measurement that describes the shape of the wing and can be easily obtained from prepared specimens [25]. Higher values of HWI reflect more elongated wings, indicative of higher flight performance, while small values reflect shorter and more rounded wings associated with more limited flight performance. Previous studies have evidenced the usefulness of HWI as a proxy for dispersal ability [24,26,27] and here we evaluate the correlation between the HWI and range size.

Traits other than dispersal ability have shown correlations with range size in a variety of organisms [20,26,28,29]. However, these same traits may have positive, negative or no relationship to range size depending on the study (e.g. species age and body size [2,30–32]). Other traits have not yet been directly tested but indirect evidence suggests that they also could affect range patterns. The forest stratum occupied by Neotropical birds is a predictor of the genetic differentiation among populations [33,34], with species occupying higher strata having lower levels of genetic structure than understorey birds. This relationship appears to reflect species' ability or propensity to cross barriers [33], ultimately influencing range size. Diet is correlated with the way a species forages and uses the landscape, and has been related to home range size and migratory behaviour [35,36]. Other traits have been found to be indirectly correlated with range size. Beak depth is an example and is related to natal dispersal distances, possibly as a migratory behaviour correlate, although no direct causal relationship could be shown [37]. We explore a set of organismal traits to evaluate which are correlated with range size of white-sand species.

Studies using simulations have shown that range size can be phylogenetically constrained, generally justified based on niche conservatism and symmetrical split of ancestral species ranges [38–40]. The white-sand ecosystems' bird communities are phylogenetically overdispersed as species are distantly related [9]. Unlike some cases in which large parts of families diversified within Amazonian lowland *terra-firme* forests, such as *Thamnophilidae* and *Tyrannidae*, white-sand taxa are spread across the bird phylogeny generally with only a single representative from a given family [9]. Non-white-sand sister taxa occur in a wide variety of habitats, both within and outside of Amazonia [17,18,41,42]. To estimate the phylogenetic signal on range size and because of phylogenetic overdispersion in white-sand ecosystems communities, we included their sister taxa in our analyses. This approach reduces assumptions about trait evolution in the internal sections of the tree and among distantly related taxa [43].

Based on previous evidence and hypotheses, we selected and evaluated a set of morphological and ecological traits (hand-wing index, beak depth, body size, diet and habitat strata) that could influence species' ability to expand their ranges, in this case by colonizing white-sand ecosystems patches scattered across Amazonia. We evaluated whether these traits were correlated with current range size of white-sand birds and their sister taxa. Our goal was to understand how these organismal traits correlate with range size in a group of species restricted to the same ecosystem.

## 2. Material and methods

### (a) Study species and phylogenetic data

Using white-sand ecosystems species lists from Alonso *et al.* [10] and Borges *et al.* [11], we filtered taxa to include only those with available phylogenetic information (18 out of 35 [51%] species from Borges *et al.*'s [11] comprehensive analysis; electronic supplementary material, table S1). We only analysed species for which the sister taxon or clade was known, and which had available genetic sequence data for phylogenetic analyses. This allowed for estimation of phylogenetic signal on range size evolution.

We obtained three phylogenetic hypotheses that were used in the range size analyses. First, we downloaded 10 000 random subsampled trees from birdtree.org based on the Hackett *et al.* [44] backbone [45]. Using TreeAnnotator v. 1.8.4 [46], we built a Maximum Clade Credibility tree and the resulting phylogeny is hereafter referred to as 'JT'. Additionally, we downloaded available genetic data from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) for the following markers: CytB, ND2, ND3, COI, fib5, RAG-1 and RAG-2 (electronic supplementary material, table S1). We aligned all markers using GENEIOUS PRIME 2019.0.4 (<https://www.geneious.com>). Data partitioning and the best sequence evolution models were evaluated using PARTITION FINDER v. 2.1.1 [47] (best partition scheme can be found at electronic supplementary material, table S2). For a second phylogenetic hypothesis, we used a concatenated matrix and a GTR + G model to perform a maximum-likelihood analysis using RAxML v. 7.2.7 [48] in the CIPRES portal [49] and branch support was obtained based on 1000 bootstraps (the resulting tree being hereafter referred to as 'ML'). Lastly, we also performed a Bayesian Inference analysis (hereafter the 'BI' tree) on MrBAYES v. 3.2 [50] ran in the Field Museum of Natural History Grainger Bioinformatics Center computing cluster. The analysis was run for 10<sup>7</sup> steps sampling trees every 10<sup>4</sup> steps, with one cold and four heated chains.

## (b) Range size estimates

We obtained range size estimates from two sources of data. First, we used the distribution maps downloaded from BirdLife (hereafter ‘BirdLife maps’; <http://datazone.birdlife.org/species/requestdis>; downloaded on 23 March 2018). Range sizes were calculated based on breeding ranges (of the studied taxa, only *Sporophila caerulea* is known to have migratory populations) using R v. 3.4.3 [51] and the package *letsR* v. 3.1 [52].

We also generated maps from species occurrence records using ecological niche models (ENMs). We downloaded occurrence records for all taxa from the Global Biodiversity Information Facility (GBIF; [gbif.org](http://gbif.org)) using a custom R script and the R package *rgbif* [53]. Initially, we restricted the download to specimen-based records, to decrease the likelihood of erroneous occurrences (such as species misidentifications) in the dataset. Additional occurrence records came from museum collections not available through GBIF (electronic supplementary material, table S3). For taxa still lacking occurrence data even after combing these sources, we used the full set of observation records available on GBIF to give the ENMs sufficient training data (electronic supplementary material, table S3). Specimen records from all data sources were manually verified to ensure accurate georeferencing, removing data points if they (1) were obviously misplaced over bodies of water; or (2) appeared outside of the known range of the taxon (e.g. across major rivers known as range-limiting barriers). Where sufficient sample sizes existed, the use of specimen-based occurrences helped mitigate the latter problem. In order to give the model an area to work within, we drew polygons in QGIS v. 3.0.1 [54] to constrain the training area of each distribution model (**M**, *sensu* [55]). These training areas were based on published ranges for each taxon [56], and included all post-rarefaction occurrence points. We drew boundaries of these model training areas in concordance with suspected or known biogeographic boundaries that constrain the movement and range of a given species, such as major rivers and the crests of mountain ranges.

We used global climate data available through WorldClim v. 2.0 [57] as climatic predictor variables for the ENMs and downloaded 19 Bioclimatic variables (BIOCLIM). We used the maximum entropy (MaxEnt v. 3.4.1) modelling approach [58] implemented with the R packages *dismo* [59] and *rJava* [60] to generate ENMs for each species in the study. To calculate the range size of each taxon from the ENMs, we set a threshold for each model to convert the probability distributions to binary presence–absence rasters. We examined the probabilities of occurrence for each species at each rarefied occurrence point and set a threshold for the presence–absence based on the top 90% of points with the highest probabilities of occurrence (after [61]). Points with the highest probabilities of occurrence are assumed to accurately reflect the presence of the species, and the remaining points were considered absences. For thresholding raw ENM outputs and calculate the range area, we used the R packages *raster* [62] and *letsR* v. 3.1. A detailed description of the methods to obtain the ENMs is available at electronic supplementary material, appendix S1.

## (c) Ecological and morphological data

Six traits were examined for a relationship to range size: (1) Hand-wing index (HWI) was used as a proxy of species’ dispersal capabilities [24,25]. The HWI is obtained by measuring the wing length (WL; from the carpal joint to the tip of longest primary feather) and the secondary length (SL; from the carpal joint to the tip of the first secondary feather) [25] and defined as:  $HWI = ((WL - SL) / WL) \times 100$ . (2) Beak depth was measured from the proximate end of the nostrils. All measurements were taken by JMGC in the bird collections of the following institutions: Field Museum of Natural History, American Museum of Natural History, Smithsonian Museum of Natural History, Louisiana

Museum of Natural History, Instituto Nacional de Pesquisas da Amazônia and Museu Paraense Emílio Goeldi. Whenever possible, measurements were taken from at least four males and four females, and the average per species was used in the models (see electronic supplementary material, table S1 for sample sizes). Also, when two or more subspecies have been described, we obtained measurements for all taxa and they were lumped to calculate the average. (3) Body weight was included in the analyses as a measure of body size and taken from the *Handbook of the Birds of the World Alive* [56]. We expect that, as previously hypothesized [2], species with higher weight (body size) would have larger ranges. (4) Percentage of fruits and/or seeds in diet. Frugivores are expected to move longer distances to forage due to the seasonality and distribution patterns of their plant resources [63]. We hypothesize that bird species with a higher proportion of fruits or seeds in their diet will have larger ranges than insectivorous or omnivorous species. (5) Foraging stratum defined as the percentage of foraging activities on the ground or understorey—which is correlated with higher genetic structure in Amazonian forest birds [33,34]. We predict that species occupying mid to high canopy levels will have a higher dispersal propensity and larger ranges. Information for the previous two traits was obtained from EltonTraits v. 1.0 [64]. We opted for transforming the available data because our statistical analyses (see below) only accept dummy categorical variables (e.g. the presence versus the absence), preventing the use of variables with more than two categories. Transforming the data into several dummy categorical variables would greatly increase the variables-to-samples ratio, therefore reducing the power to evaluate the different models [65]. Finally, (6) habitat association divided into white-sand species and non-white-sand species (sister taxa) was evaluated as a factor affecting range size.

## (d) Data analyses

We estimated phylogenetic signal on range size and on the species traits by calculating Pagel’s  $\lambda$  [66] and Blomberg’s  $K$  [67]. These analyses evaluate if, due to common ancestry, sister taxa are more similar to (or different from) each other than expected under a Brownian motion model of evolution, therefore characterizing trait conservatism within lineages [66–68]. The analyses were implemented in R v. 3.4.3 using the packages *phytools* v. 0.6-44 [69] and *geiger* v. 2.0.6 [70] and significance levels were estimated based on 1000 permutations. To test if results for range size would change depending on the sample size, we repeated this procedure based on an extended dataset consisting of 68 white-sand species and sister taxa using the BirdLife maps and a phylogeny estimated using the same method as the JT.

We implemented the phylogenetic generalized least-squares method (PGLS) [68,71] to evaluate which traits are good predictors of range size. We generated a set of models based on prior knowledge and hypothesis regarding the explanatory variables and performed model selection using the Akaike’s information criterion corrected for small sample sizes (AICc) [72]. The models were generated for every combination of tree topology—with their specific branch lengths (JT, ML, and BI trees)—and map source (BirdLife and ENM maps). We estimated the phylogenetic signal in range size by calculating  $\lambda$  in all models using maximum likelihood. Data manipulation and analyses were performed in R v. 3.4.3 using the packages *ape* v. 5.0 [73], *phytools* v. 0.6-44, *geiger* v. 2.0.6 and *caper* v. 0.5.2 [74]. We also used PGLS to evaluate if HWI is different between white-sand species and their sister taxa. Our expectation was that white-sand species had higher dispersal ability as an adaptation to the fragmented nature of white-sand ecosystems. Because results were consistent and robust among dataset combinations, we present the results for the ML tree and ENM range size. The results from the remainder of the dataset combinations can be found in the electronic supplementary material.



**Table 1.** Number of species included in each phylogenetic hypothesis dataset.

phylogenetic tree	white-sand species	sister taxa	total
JT	19	24	43
ML	19	23	42
BI	19	21	40
total	21	24	45

### 3. Results

#### (a) Phylogenetic trees and map sources

The phylogenetic trees had very similar topologies and variations were mostly related to differences in species sets between JT and both the ML and BI trees (table 1; electronic supplementary material, table S1). The JT tree had more inconsistencies with published phylogenies probably due to incorporation of species with missing genetic data [45]. Branch support for species relationships was high as expected due to the overdispersed nature of white-sand ecosystems avifauna resulting in low taxonomic sampling within each clade (white-sand species + sister taxon/clade) and high genetic distance among clades (electronic supplementary material, figures S1–S6).

The ENM maps resulted in range sizes similar to BirdLife maps, although the two methods often produced different range maps (electronic supplementary material, figures S7–S52). The map sources are based on occurrence records and represent hypotheses about the true distribution of the species, and there were instances in which the BirdLife maps or the ENMs failed to cover known species records (electronic supplementary material, figures S7–S52). The median percentage of difference in range size between BirdLife and ENM maps was 3.23% (s.d. = 44.72; min. = −7.69; max. = 285.3). A linear regression of these data shows a negative correlation between range size and percentage of difference ( $F_{1,43} = 42.02$ ;  $p < 0.001$ ; adjusted  $R^2 = 0.48$ ) indicating that species with small ranges had greater differences between BirdLife and ENM range sizes, with larger ranges estimated by ENMs (electronic supplementary material, figure S53).

#### (b) Range size evolution

HWI was phylogenetically constrained in all three phylogenetic datasets ( $\lambda$  ranging from 0.89 to 0.93; electronic supplementary material, table S5), showing that sister species had more similar wing shapes. There was not a significant difference between the HWI of white-sand birds and their sister taxa (JT dataset,  $F_{1,41} = 0.059$ ;  $p = 0.8$ ; electronic supplementary material, figure S54; the overall variation in HWI is shown in electronic supplementary material, figure S55) based on all phylogenetic hypotheses (electronic supplementary material, table S10).

Range size was not phylogenetically constrained as both  $\lambda$  and  $K$  were not significantly different from zero in the estimates with all three phylogenetic hypotheses (JT, ML, BI; table 2). The same result was obtained with the expanded dataset (table 2). As expected from a phylogenetically

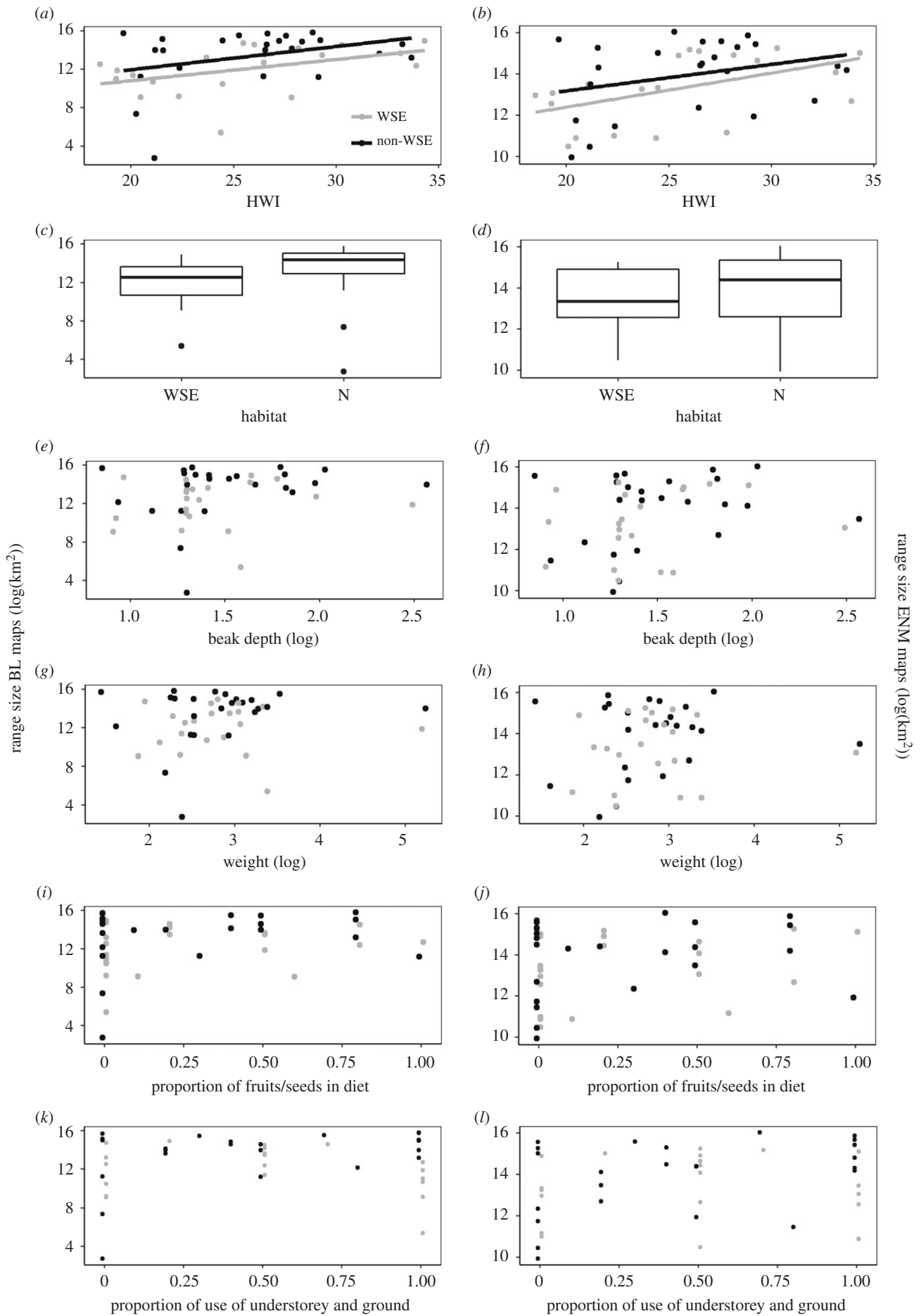
**Table 2.** Blomberg's  $K$  and Pagel's  $\lambda$  values for range size. Significance values ( $p$ ) were assessed based on 1000 permutations to evaluate if significantly different from 0 (zero).

dataset	$K$	$p$	$\lambda$	$p$
JT tree/BirdLife maps	0.039	0.8	0.199	0.107
JT tree/ENM maps	0.115	0.07	0.214	0.113
ML tree/BirdLife maps	0.05	0.92	0.146	0.205
ML tree/ENM maps	0.083	0.569	0.213	0.101
BI tree/BirdLife maps	0.061	0.603	0.055	0.62
BI tree/ENM maps	0.043	0.874	0.095	0.419
JT tree/BirdLife maps (68 species)	0.033	0.868	$6.62 \times 10^{-5}$	1

overdispersed community of birds and their sister taxa, in addition to HWI, all the traits tested as explanatory variables had statistically significant phylogenetic signal (electronic supplementary material, tables S5–S9). We looked for collinearity among the explanatory variables by examining generalized variance inflation factor (GVIF) values, but all values were smaller than 4, showing no correlation among predictors. Considering all dataset combinations and based on AICc model selection, HWI was positively correlated with range size and significantly correlated in most models (electronic supplementary material, table S4), indicating that better dispersers tend to have larger ranges (figure 1*a,b*). In two cases (JT/BirdLife and BI/BirdLife), the best model also included habitat association (electronic supplementary material, table S4). Models that included habitat association or bill depth in addition to HWI explained more of the variation in range size and also were good candidate models ( $\Delta\text{AICc} < 2$ ; table 3). While beak depth was not significantly correlated with range size, models including beak depth in addition to HWI and habitat association, or with HWI only, explained more of the variation in range size (table 3; figure 1*e,f*; electronic supplementary material, tables S11–S15). The null model was included in the best set of models ( $\Delta\text{AICc} < 2$ ) in all analyses involving ENM range size, and in one model involving the ML tree and BirdLife ranges (table 3; electronic supplementary material, tables S11–S15). In general, white-sand species have smaller ranges than their sister taxa, although this pattern is more evident in models with BirdLife maps (figure 1*c,d*). The models performed poorly when other traits (weight, percentage of fruits/seeds in diet and foraging strata) were included and those variables were not observed to be significantly correlated with range size (table 3; figure 1*g–i*; electronic supplementary material, tables S11–S15).

### 4. Discussion

We found evidence that dispersal ability (here measured as the HWI) is associated with range size of white-sand species and their sister taxa, and probably played a significant role in determining current distributions (figure 1*a,b*). This association was found for all dataset combinations, including different phylogenetic hypotheses (JT, ML and BI) and map sources (BirdLife and ENM). Such an association between better dispersers and larger ranges has been previously



**Figure 1.** The correlation between range size for the BirdLife (BL) and Ecological Niche Model (ENM) maps and the studied traits using the complete species pool: (a,b) dispersal ability measured as the hand-wing index (HWI); (c,d) habitat association as white-sand ecosystems (WSE) and non-white-sand ecosystems (N); (e,f) beak depth; (g,h) body size as bird weight in grams; (i,j) proportion of fruits and seeds in the bird diet and (k,l) the proportion of foraging in the understorey and ground strata.

**Table 3.** Regression coefficients and standardized errors (between parenthesis) for the explanatory variables, AICc,  $\Delta$ AICc, AICc weight and evidence ratio (ER) in the PGLS models based in the ML tree and ENM range size. Significant variables ( $p < 0.05$ ) and the best model are shown in italic.

model	intercept	HWI	habitat	Bill depth	weight	diet	Foraging strata	HWI * Habitat	F	p	R <sup>2</sup>	AICc	$\Delta$ AICc	AICcw	ER
Range.size ~ HWI.mean + Bill Depth + Weight + Diet + Foraging Strata + Habitat	8.98 (2.06)	0.14 (0.06)	−0.27 (0.51)	1.46 (1.27)	−0.43 (0.60)	−0.73 (0.99)	0.71 (0.74)	—	1.623	0.17	0.083	168.3	8.873	0.004	84.46
Range.size ~ HWI.mean + Bill Depth + Diet + Foraging Strata + Habitat	8.79 (2.03)	0.14 (0.06)	−0.35 (0.50)	0.71 (0.75)	—	−0.62 (0.97)	0.76 (0.73)	—	1.866	0.124	0.095	166.1	6.606	0.012	27.19
Range.size ~ HWI.mean + Bill Depth + Foraging Strata + Habitat	9.45 (1.73)	0.12 (0.05)	−0.36 (0.49)	0.57 (0.71)	—	—	0.65 (0.71)	—	2.268	0.08	0.11	163.8	4.344	0.036	8.77
Range.size ~ HWI.mean + Bill Depth + Habitat	9.26 (1.71)	0.13 (0.05)	−0.29 (0.49)	0.84 (0.65)	—	—	—	—	2.748	0.056	0.113	162.2	2.721	0.081	3.89
Range.size ~ HWI.mean + Habitat	10.68 (1.60)	0.12 (0.06)	−0.31 (0.48)	—	—	—	—	—	2.457	0.098	0.066	161.3	1.857	0.125	2.53
Range.size ~ HWI.mean × Habitat	10.89 (2.26)	0.11 (0.08)	−0.66 (2.92)	—	—	—	—	0.01 (0.11)	1.564	0.213	0.039	163.8	4.292	0.037	8.55
Range.size ~ HWI.mean + Bill Depth	9.06 (1.66)	0.13 (0.05)	—	0.88 (0.64)	—	—	—	—	4.007	0.026	0.127	160.1	0.669	0.226	1.39
Range.size ~ HWI.mean	10.55 (1.59)	0.12 (0.05)	—	—	—	—	—	—	4.384	0.042	0.076	159.5	0.000	0.316	1.00
Range.size ~ 1	13.84 (0.45)	—	—	—	—	—	—	—	—	—	—	160.8	1.313	0.164	1.92

reported but is not ubiquitous in the literature. While there are studies that demonstrate a positive relationship between range size and dispersal ability [20,22,26–28], others have shown no effect [21,75] or a reduced effect compared to post-dispersal survivorship traits [76]. The absence of a relationship has been explained by the small effect dispersal has when considering the evolutionary time scale in which ranges are attained [21]. Lester *et al.* [21] argued that dispersal ability will exhibit greater importance when ranges were attained in the recent past and when habitats are more fragmented. White-sand ecosystems are believed to have a dynamic history and local extinctions during the last glacial cycle are hypothesized based on phylogeographic patterns [17,18]. Thus, current ranges likely reflect the ability of species to move between white-sand ecosystems patches and colonize more distant ones. It appears that recent dynamics and the patchiness of white-sand ecosystems underlie the relationship we observed between dispersal ability and range size.

A highly dispersed, patchy habitat and the presence of wide Amazonian rivers would seem ideal conditions for developing population subdivision, and eventually allopatric speciation [77]. Speciation events influence the distribution pattern of geographical range sizes as bigger ranges become split into smaller ranges [1,78]. With one notable exception (*Galbula leucogastra*) [42], white-sand species for which phylogeographic data are available do not show the strong regional genetic structure reported for many *terra-firme* forest taxa [16]. The shallow genetic structure of white-sand birds might reflect the recent attainment of distributions or ongoing gene flow across potential barriers, including major rivers and intervening forest types, both argue for an important role for dispersal in shaping white-sand birds range size.

White-sand birds have on average smaller ranges than their sister taxa (figure 1a,b). The scattered and fragmented nature of white-sand ecosystems might be driving this pattern, as white-sand bird distributions are embedded in a matrix of lowland Amazonian *terra-firme* and flooded forests. Based on our results, dispersal ability is limiting species' ability to reach new patches and establish new populations. If given sufficient time, dispersal limitation might be overcome and species could expand their distributions to occupy white-sand ecosystems patches across the whole Amazonian region [21,79]. By contrast, white-sand sister taxa generally occur in more continuous ecosystems, like savannahs and *terra-firme* forests, where range expansion probably occurs faster than in fragmented ecosystems [80].

Alternatively, the smaller ranges of white-sand species might reflect the total area covered by white-sand ecosystems in Amazonia, which is small compared to other habitats (approx. 335 000 km<sup>2</sup>, 5% of total area) [81]. The lowland Amazonian *terra-firme* forests, savannahs and flooded forests ecosystems occupied by white-sand sister taxa cover larger and more connected areas than white-sand ecosystems, with rare exceptions such as the Pantepui region in Northern South America where one white-sand sister taxon is found (*Xenopipo uniformis*) [82,83]. Indeed, it has been reported that species will have bigger ranges simply because they occur in more widespread habitats [6], and there is a strong relationship between range size and the area of climate envelopes and biome domains [7,8]. This illustrates the circularity that can arise from niche breadth estimates (often measured as the climatic niche), that will usually be larger in species occupying more widespread habitats [7]. Our use of a suite of birds

adapted to a particular ecosystem shows that the relationship between dispersal ability and range size is not the product of habitat differences. Still, the model that accounted for the interaction between HWI and habitat association performed poorly, showing that dispersal ability can be considered to influence range sizes similarly in white-sand and non-white-sand birds in our dataset.

None of the organismal (body size, beak depth) and ecological (diet and habitat strata) traits showed significant correlations with range size in any of our models. Other studies have shown that traits related to population establishment and persistence in new areas have a significant correlation with range size, sometimes stronger than the relationship with dispersal ability [76,84]. At the community assembly level, dispersal and local extinction potentially generate the nested structure seen in white-sand ecosystems bird communities [9,19]. Because of the white-sand ecosystems' patchiness, traits like clutch size, home range and generation time might be important in the metapopulation dynamics [85], and hence in the expansion of ranges. Unfortunately, data on these traits do not exist for most Amazonian birds so could not be considered in our analyses [86].

Although we used different sources and methods to obtain the data for our models, the results are consistent across the dataset combinations (electronic supplementary material, table S4). It is nearly impossible to know the true range of a species at any given point in time. BirdLife range maps, drawn from species records and specialist knowledge, and ENMs, commonly based on the realized climatic niche, are approximations of the true, but potentially dynamic distributions. Despite observed differences in estimated species distributions, both BirdLife and ENM maps led to very similar results (electronic supplementary material, figures S7–S52 and table S4). Dispersal ability was significantly and positively correlated with range size in all the best models, except in the BI/BirdLife dataset where it had marginal significance and habitat association had a significant correlation (electronic supplementary material, table S4). Because the absence of phylogenetic signal in range sizes is unlikely to be a type II error [87], we assume these differences do not occur due to variation in the topology and branch lengths among the phylogenies.

Our findings indicate that dispersal ability is an important trait determining range size in white-sand bird species. Based on these results, dispersal ability in white-sand species affects how fast and how far a species is able to expand its range, a potential source of concern given that poor dispersers might not be able to track rapid climatic changes that are predicted to occur [3,88,89]. However, dispersal ability explained a relatively small fraction of the variation in range sizes as evidenced by low adjusted  $R^2$ -values ( $R^2$  range for models with HWI only and  $\Delta AICc < 2 = 0.059–0.122$ ; table 3; electronic supplementary material, tables S11–S15). Models that included habitat association increased the amount of variation explained ( $R^2$  range from best models = 0.066–0.164; table 3; electronic supplementary material, tables S11–S15). Additionally, there is potential uncertainty for the role of dispersal ability and the other traits as the null model was often included in the best set of models (models with  $\Delta AICc < 2$ ). Potentially important life-history and ecological traits that might affect range size evolution are not known for many of these species, including clutch size, generation time, longevity and abundance [1,2]. In addition, some of the data used here were inferred from sister groups for which data are known [64].

The lack of trait data prevents building and testing more robust models [90]. Because tropical regions also are the most biodiverse regions of the planet and are under threat, it is imperative that more natural history and ecological data be collected and that research programmes aiming to fill these knowledge gaps are incentivized [86,91]. Until we develop more robust models for range evolution and identify key drivers, we will have a limited understanding of how species will cope, adapt and change their distributions due to climate change.

**Data accessibility.** Code and data to replicate analyses are provided with the electronic supplementary material.

**Authors' contributions.** J.M.G.C. and J.M.B. designed the study; J.M.G.C. collected trait and morphological data; J.M.G.C. and B.R.T. collected occurrence data; B.R.T. and J.C.C. performed niche modelling; J.M.G.C. performed the analyses; J.M.G.C. and M.V.A. wrote the first draft of the manuscript and all authors contributed on revisions.

**Competing interests.** We declare we have no competing interests.

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