

## Research



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## Community ecology

## Tropical bird species have less variable body sizes

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Ecologists have often predicted that species' niche breadths should decline towards the Equator. Dan Janzen arrived at this prediction based on climatic constraints, while Robert MacArthur argued that a latitudinal gradient in resource specialization drives the pattern. This idea has some support when it comes to thermal niches, but has rarely been explored for other niche dimensions. Body size is linked to niche dimensions related to diet, competition and environmental tolerance in vertebrates. We identified 68 pairs of tropical and nontropical sister bird species using a comprehensive phylogeny and used the VertNet specimen database to ask whether tropical birds have lower intraspecific body-size variation than their nontropical sister species. Our results show that tropical species have less intraspecific variability in body mass ( $\bar{d}_{CV} = 0.0092$ ;  $p = 0.009$ ). Variation in body-size variability was poorly explained by both abiotic and biotic drivers; thus the mechanisms underlying the pattern are still unclear. The lower variation in body size of tropical bird species may have evolved in response to more stable climates and resource environments.

## 1. Introduction

Globally, some of the most striking patterns in species diversity and physiological adaptation exist along latitudinal gradients [1,2]. In a seminal paper [3], Dan Janzen proposed a climatic–physiological model wherein tropical mountains prevent organismal dispersal more than temperate mountains of similar height. Janzen reasoned that tropical species, being adapted to lower seasonal variation in temperature, have narrower thermal physiological tolerances (thermal niches). Mountain ranges were therefore more likely to impede dispersal of low-elevation tropical organisms, resulting in smaller geographic distributions of tropical species [4] and higher species turnover in response to topography [5]. Later, Robert MacArthur offered an alternative explanation for species distributions. He argued that greater stability of resources in warmer lower-latitude habitats permits more opportunities for resource specialization and niche partitioning [6]. Narrower niches in the tropics thus enable coexistence of more species, providing a general mechanism for the latitudinal diversity gradient.

Both the theoretical grounding and the empirical validity of the latitudinal niche-breadth gradient have spawned debate. The presumption that tropical species are more specialized in their resource-use niches has come into question [7], although recent work has demonstrated that tropical bird communities with higher species richness tend to consist of species with smaller diet breadths [8]. Furthermore, seasonal variation in precipitation tends to be higher in the tropics

than in temperate areas [9]. Thus, while the tropics are more stable in temperature, precipitation provides another climate stability axis that is inverse to temperature and may influence niche breadth across latitudes. Trait databases, which have become increasingly available at global scales, hold promise for exploring latitudinal patterns in traits across species and shedding light on this long-running debate.

Here, we use publicly available data on bird body mass to explore niche variation of tropical and nontropical sister species pairs. Body size is linked to thermal and resource-use niche dimensions owing to its covariation with climate [10], diet breadth [11], competition [12] and thermal tolerance in endotherms [13]; thus, increased intraspecific variation in body size may suggest broader niche width. Furthermore, differences in climatic stability, competition and resource use have all been invoked in hypotheses explaining latitudinal [14] and elevational [15] diversity gradients. We specifically ask the following:

- (1) Do nontropical birds have greater body-size variability than their tropical sister species?
- (2) Is the difference in body-size variability within species pairs related to differences in their biotic and abiotic environments?

## 2. Methods

### (a) Identifying sister species pairs

Using a consensus tree generated from 100 trees randomly sampled from the posterior distribution of trees in a global bird phylogeny [16], we calculated a pairwise distance matrix consisting of total branch length between all pairs of species. We defined a sister species pair as two species A and B for which both the following are true: species A is species B's single nearest neighbour by branch length, and species B is species A's single nearest neighbour. The phylogeny contained 2119 such pairs.

### (b) Compiling body-mass measurements

We downloaded all bird body-mass records for the sister species identified using the methods above from a dataset of specimen measurements [17]. We excluded all anomalous records differing by a factor of  $\geq 10$  from the median species value and measurements taken on non-adult birds, retaining pairs in which both species had at least 10 valid body-mass measurements. Next, we used the median absolute value of latitude of the breeding and year-round ranges of each species (electronic supplementary material, appendix S1) to classify each species as either tropical ( $|\text{lat}| < 23.5^\circ$ ) or nontropical ( $|\text{lat}| > 23.5^\circ$ ). We excluded all pairs except for tropical–nontropical pairs, leaving 68 species pairs.

### (c) Comparing body-mass variability

We  $\log_{10}$ -transformed the body-mass measurements and calculated the coefficient of variation (CV), an unbiased variance estimator, for each species. We ran a paired, one-sided  $t$ -test on these CV values. The null hypothesis was that the CV of the tropical species is not lower than the CV of nontropical species. To ensure that there was no effect of differing sample sizes within species pairs, we used a bootstrap procedure: we sampled, without replacement, mass measurements from the species with more records equal to the number of measurements in the species with fewer records. We calculated the CV of the subsample and ran the  $t$ -test. We repeated this procedure 999 times to get a bootstrap distribution of  $t$ -statistics.

### (d) Testing the influence of covariates

We compiled the following covariates (electronic supplementary material, appendix S1): latitudinal, phylogenetic and geographic distances within each species pair, seasonal and interannual variation in temperature and precipitation, average body mass of the species pair, range size, migratory status, predatory status, richness of co-occurring species and co-occurring congeners. For covariates other than body mass, migratory status and trophic status, we regressed the difference in body-mass CV of each species pair against the difference in the covariate within each species pair (tropical value subtracted from nontropical value). For body mass, we used the mean value for the pair, and for migratory and trophic status, we used a single categorical variable describing both species in the pair. If at least one member of the pair was migratory or predatory, we classified the pair as such. We conducted a multiple regression, selecting the best model using forward selection, and using corrected Akaike information criterion (AICc) to determine which predictor to add at each step.

### (e) Controlling for dataset artefacts

To ensure that any potential results were not due to systematic sampling differences between tropical and nontropical birds, we also regressed the difference in body-mass variability against the within-pair difference of the following covariates, representing potential sampling artefacts: convex hull area and elevational range of specimen collection locations, spatial variability of temperature and precipitation among collection locations, and number of distinct populations sampled (electronic supplementary material, appendix S1). We used R software version 3.3.3 for all our analyses; data are archived at [18].

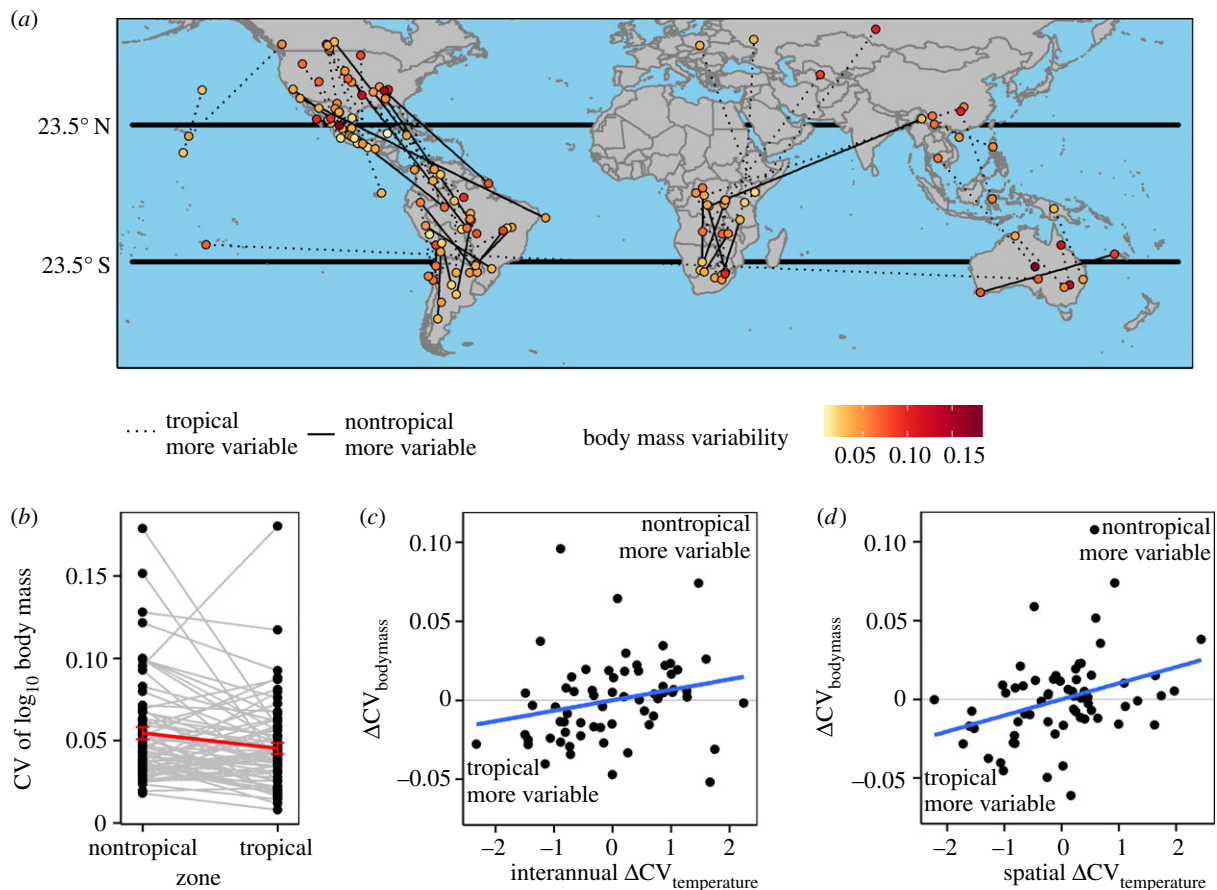
## 3. Results/discussion

### (a) Tropical birds have lower body-size variability

Across all tropical–nontropical bird species pairs, the tropical members tended to have lower body-size variability, indicated by lower average CV of body mass:  $t_{67} = 2.44$ ;  $p = 0.009$ , mean difference  $\bar{d}_{CV} = 0.0092$  (less in the tropics), CI = (0.0029,  $\infty$ ) (figure 1*a,b*). This pattern was not an artefact of lower sample sizes in the tropics (tropical species had lower average CV in 100% of bootstrap simulations, significantly in 72% of simulations). An unpaired phylogenetically corrected analysis confirmed this pattern (electronic supplementary material, appendix S2).

### (b) Body-size variability differences may be mediated by climate and range size

We found no evidence for the hypothesis that the latitudinal gradient in body-size variability is driven by decreased seasonal temperature variability closer to the Equator [3]. Five predictors were retained in the best model predicting the within-pair difference in body-mass variability (multiple  $R^2 = 0.32$ ; electronic supplementary material, table S1 and figures S1 and S2): spatial variability in temperature across locations where specimens were collected (positive relationship, standardized coefficient = 0.01;  $p = 0.007$ ; figure 1*c*), interannual temperature variability (marginally positive relationship, coefficient = 0.007;  $p = 0.07$ ; figure 1*d*), seasonal precipitation variability (marginally negative relationship, coefficient =  $-0.007$ ;  $p = 0.10$ ), predatory status (greater difference in predatory species pairs, coefficient = 0.02;  $p = 0.02$ ) and migratory status (greater difference in non-migratory species pairs, coefficient = 0.02;



**Figure 1.** (a) Range centroids of each bird species. Each point is coloured by the CV of that species' body-mass measurements. Tropical–nontropical species pairs are connected with a line. Pairs in which the nontropical species varies more (supporting the hypothesis) have solid lines, while pairs in which the tropical species varies more have dotted lines. (b) Difference in CV for each species pair, with the mean CV for each zone and its confidence interval plotted in red. (c) Positive relationship between the difference in interannual temperature variability and the difference in body-mass variability, controlling for all other predictors. (d) Positive relationship between the difference in spatial temperature variability and the difference in body-mass variability, controlling for all other predictors.

$p = 0.02$ ). Multicollinearity was not an issue; all variance inflation factors were less than 1.33. Thus, the nontropical species with the most variable body sizes tend to experience greater variability in temperature across years and space, while their tropical sister species tend to experience more stable temperatures interannually and inhabit ranges with lower temperature variation [15].

Spatial and temporal variation in temperature may influence body-size variability via several plausible mechanisms. First, variation in temperature across a species' range is a well-known driver of body-size variation for many bird species [19]. Second, the influence of interannual temperature variation on body-size variation may reflect differences in food availability during the growth period [20] or may represent different evolutionary strategies for dealing with climate extremes experienced at high latitudes [21]. These mechanisms can result in variation in body size independent of spatial variation in temperature. Finally, differences in spatial temperature variation are partly an artefact of specimen collection locations but also may reflect differences in environmental variability experienced by nontropical and tropical birds. Climates outside the tropics may vary more spatially, potentially selecting for greater intraspecific variability in climatic tolerance and thus body size.

Precipitation tells a different story, with greater seasonal variation in the tropics associated with lower body-size variability. This suggests that while stable temperatures may lead to lower variability, stability of precipitation may influence

variability in different ways [22]. One possible explanation for the opposite effects of temporal precipitation and temperature variability on body-size variability is that nontropical sites with more variable temperatures ( $r = -0.42$ ) and lower mean precipitation ( $r = -0.24$ ) have lower temporal precipitation variability [21]. Despite the stable precipitation regime, such harsh environments may select for greater body-size variability in nontropical species. Disentangling the relationships between temperature variability, precipitation variability and body-size variability will require further exploration of multiple taxa across geographic regions.

Our results also show that life-history traits play a role in intraspecific body-size variation, with species pairs that are predatory or non-migratory tending to have a greater tropical–nontropical difference in body-size variability. It is not readily clear how these life-history traits contribute to our observed pattern. Migration has been shown to constrain bird morphology across species [23], but it is not clear if selective factors related to migration constrain intraspecific morphology (e.g. body mass) such that species that migrate out of the tropics are less variable in their body size. In terms of trophic status, carnivorous and insectivorous birds outside the tropics may experience higher variability in the availability of food [24], suggesting that food resource availability may be important for predicting body-size variability.

The other covariates and potential dataset artefacts did not have any relationship with pairwise difference in body-size variability. We found no support for the idea that lower

variability in the tropics arises because tropical species are constrained to specialize their resource use owing to competition from greater numbers of co-occurring species, as MacArthur's reasoning implies [25]. In addition, we found no evidence that body-size variability is driven by within-year temperature variation, as Janzen's conceptual model would predict [3].

The lack of standing body-size variation in tropical species is potentially related to a history of lower climatic variability and more stable resources. The present result supports our *a priori* hypothesis that tropical birds have narrower niche breadths than their respective nontropical sister species, but is limited by only indirectly considering one trait in one taxonomic group. Future study targeting traits that capture climatic and resource-use niches of multiple taxa will increase our understanding of global biodiversity gradients and our

ability to make physiologically based predictions of future global biodiversity trends.

**Data accessibility.** Data are archived at <http://doi.org/10.5061/dryad.gd290> [18].

**Authors' contributions.** Q.D.R. compiled and analysed data and led the writing. B.B. led the conceptualization of the study, and all other authors contributed equally to study conceptualization, design and writing. All authors approved the final version of the manuscript and are accountable for its accuracy and scientific integrity.

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

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