



## BIOGEOGRAPHY

# Birds optimize fruit size consumed near their geographic range limits

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Animals can adjust their diet to maximize energy or nutritional intake. For example, birds often target fruits that match their beak size because those fruits can be consumed more efficiently. We hypothesized that pressure to optimize diet—measured as matching between fruit and beak size—increases under stressful environments, such as those that determine species' range edges. Using fruit-consumption and trait information for 97 frugivorous bird and 831 plant species across six continents, we demonstrate that birds feed more frequently on closely size-matched fruits near their geographic range limits. This pattern was particularly strong for highly frugivorous birds, whereas opportunistic frugivores showed no such tendency. These findings highlight how frugivore interactions might respond to stressful conditions and reveal that trait matching may not predict resource use consistently.

All animals feed on a subset of available resources. This range of resources defines an important dimension of species' niches (1, 2), determines species' ability to obtain essential nutrients and energy (3), and influences the overall structure and stability of food webs (4, 5). Optimal foraging theory predicts that natural selection should drive species to select a diet that optimizes energy or nutritional intake per unit effort or time (6, 7), which can lead to patterns of consumer-resource trait matching across different trophic guilds (8, 9). However, local contexts such as environmental stress could theoretically alter the pressure to optimize diet. For example, oystercatchers can be forced to optimize foraging and consume the largest resources available under harsh environmental conditions, even when this increases the chance of damaging their beak (10).

Although species can exist across large geographic extents, environmental suitability

varies within these ranges, potentially affecting species' fitness (11) and physiology (12). For example, temperature and interspecific competition have been shown to influence energy costs (13, 14) and delimit species' ranges (15–17), such that populations near range edges might exist at their niche limits (11). Feeding interactions are affected not only by dietary efficiency and environmentally driven energy costs but also by the availability of resource species (18), which could change across a consumer's range. The absence of suitable food resources may even be a biotic determinant of species' range limits (15), such that the location of range boundaries could be a cause of diet selection (e.g., if environmental conditions near range limits lead species to change their diet) or a consequence of it (e.g., if low resource availability determines species' range limits).

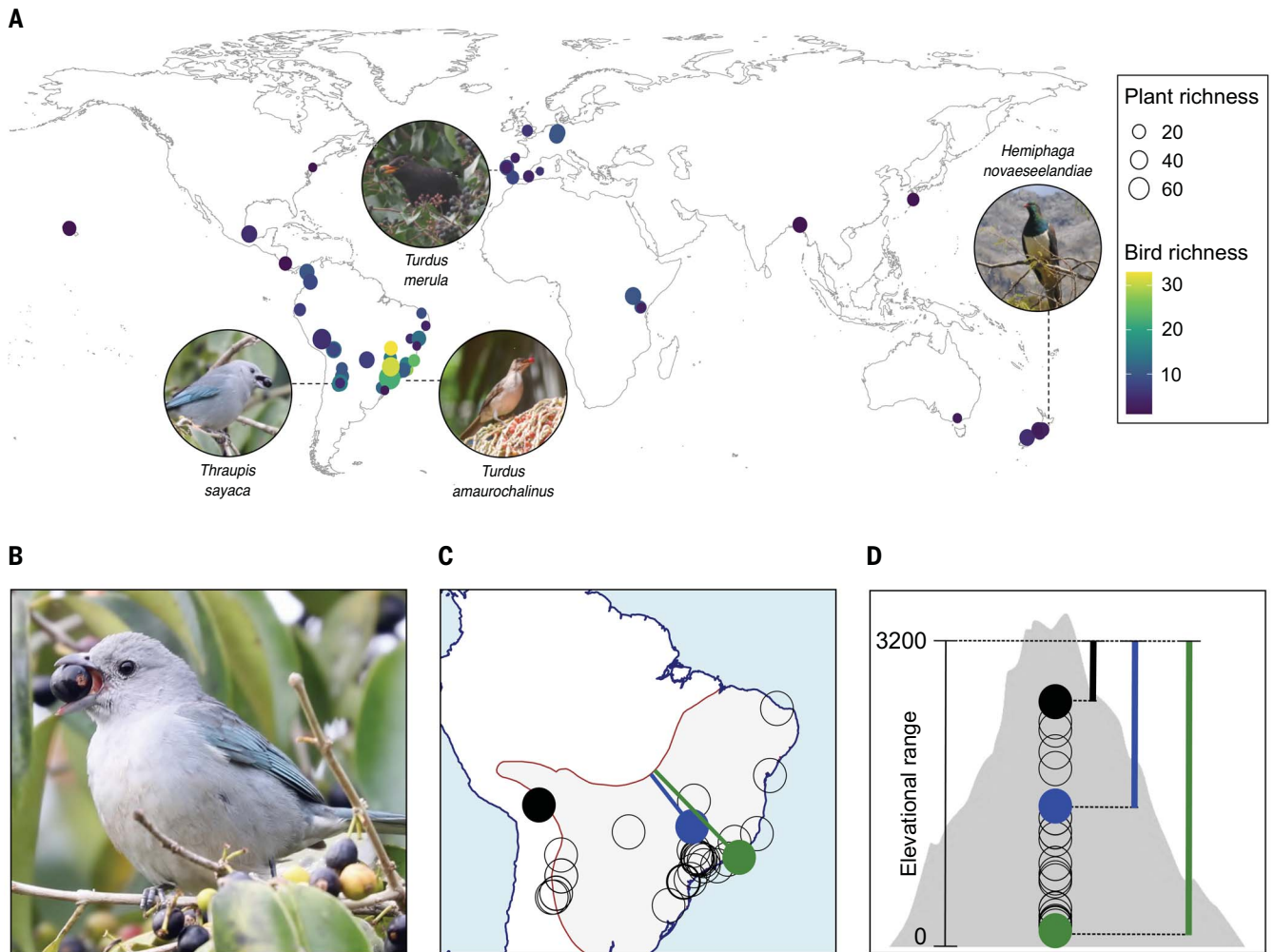
Whereas previous studies have evaluated how diet breadth might change within a species' range (19, 20), it remains unclear whether

these shifts systematically alter diet optimization rather than simply reflect changes to diversity or identity of exploited resources according to their availability. Thus, testing whether diet optimization varies consistently across species' ranges while accounting for resource availability can improve our understanding of the processes that determine range limits and provide insights into how food-resource selection affects community organization and functioning (4, 5). Moreover, efforts to predict resource use on the basis of consumer and resource traits (21, 22) implicitly assume that species' food preferences are consistent across their ranges—an assumption that remains untested.

In this work, we hypothesized that species may systematically vary their use of different resources across their ranges because lower environmental suitability can increase their energy requirements, thereby influencing trait matching (i.e., the use of resources that closely match their own morphology) to achieve diet optimization. Frugivorous birds, in particular, might optimize their caloric intake by consuming the largest fruits that can fit easily in their beaks with little handling, such that energy intake is maximized for each consumption event (23). Beak size and handling costs might set an upper limit to the size of fruits consumed by birds (24, 25), whereas fruit profitability tends to increase with its size [e.g., owing to increasing pulp rewards (26, 27)]. Although we acknowledge that species may optimize their fitness in many different ways (7), measuring all dimensions of energetic and nutritional optimization is difficult for many bird and plant species. Therefore, we assume that, all else being equal, fruits that approach the maximum consumable size (i.e., those that closely match a bird's beak size) provide the greatest reward per fruit consumption event (23). Specifically, because conditions (biotic and/or abiotic) might be more energetically demanding to species near their range limits (11, 12), we hypothesize that birds will optimize their diet to favor the best-matched fruits

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**Fig. 1. Data-collection sites and measures of distance to range limits.**

(A) Map showing the distribution of 126 locations in which avian frugivory interactions were recorded. Colors represent the number of bird species used for analyses in each location, and circle size is proportional to the number of fruiting plant species in the site. Photos depict some of the bird species analyzed. (B) The Sayaca tanager *Thraupis sayaca* (synonym *Tangara sayaca*) was the most ubiquitous species in our dataset. (C) Map showing all locations where *T. sayaca* was recorded (circles) across its range (gray polygon). Filled circles represent locations with different distances to the species' geographic range

edge (brown line): close to the edge (black), intermediate to the edge (blue), and far from the edge (green). Lines connected to filled circles represent the shortest path between the site and the bird's geographic range edge. Coastal edges (blue line) were not used for estimating distances to geographic range edge. (D) Illustrative example of how distance to elevational range limit was calculated. Lower elevation bounds at sea level (0 m) were not used for estimating distance to elevational limit (33). [Photo credits: *T. sayaca* (M.G.); *Turdus amaurochalinus* (R. B. Missano); *Turdus merula* (J.M.C.); *Hemiphaga novaeseelandiae* (L.P.M.)]

near their range boundaries and relax this dimension of diet optimization toward their range core (while potentially optimizing other dimensions of their fitness). However, the alternative hypothesis is also plausible if stressful conditions of range limits make birds invest less time searching for preferred fruit (23) and instead consume whichever fruit resources they can find or if the low availability of well-matched fruits is a driver of birds' range limits.

Several ecological factors could moderate range-edge effects on trait matching. For example, a bird's degree of frugivory may affect its trait-matching patterns because highly frugivorous birds obtain most of their food re-

sources from fruits, whereas species with a lower degree of frugivory might invest more time searching for alternative, nonfruit food resources to achieve their energy requirements (28). Similarly, migratory birds are more likely to travel long distances and may thus be affected by wider environmental gradients within their ranges. Moreover, local human disturbance might represent an additional source of environmental stress for some bird species (29), potentially overwhelming larger-scale range drivers (30). Finally, both the abiotic environment (31) and the strength of plant-frugivore trait matching (32) may change with latitude. Therefore, we also tested whether the potential effect of distance to range edge on

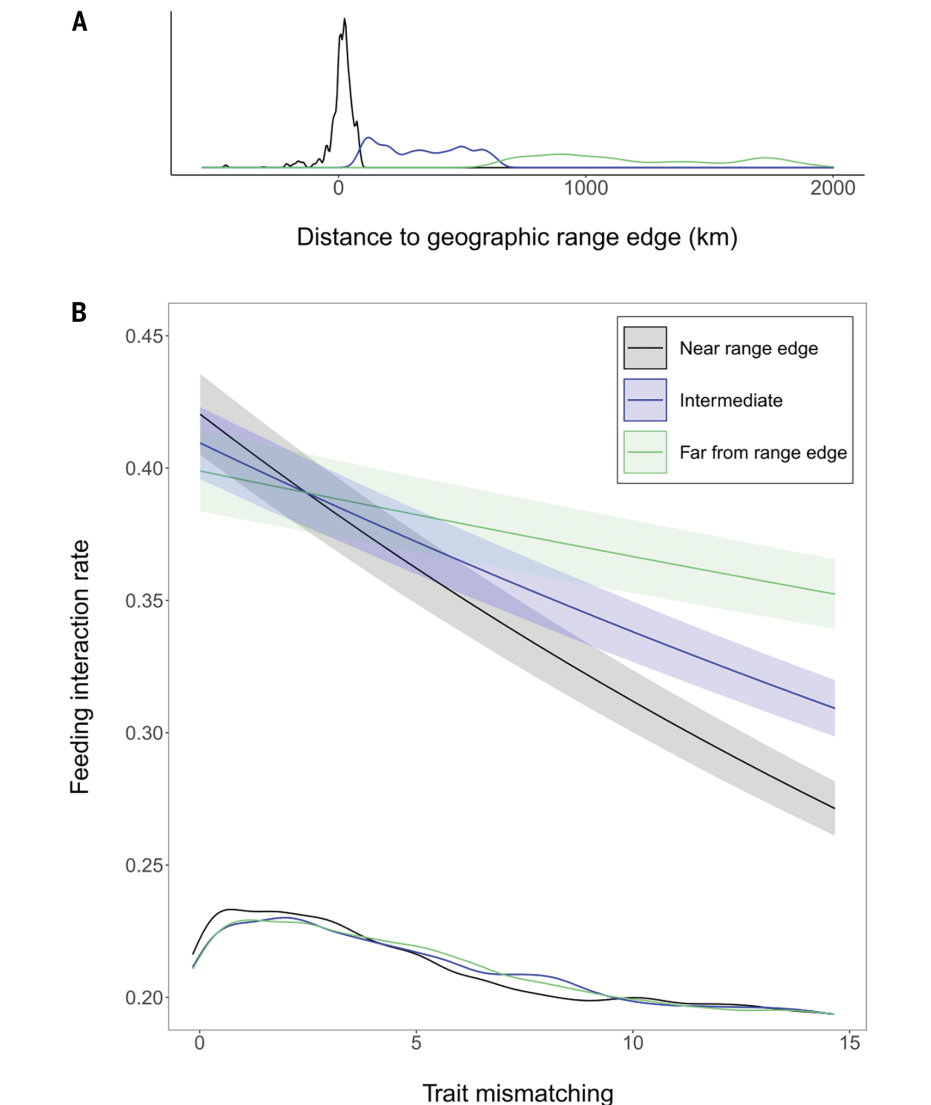
birds' fruit-consumption patterns is influenced by these moderator variables.

We assembled a large-scale dataset of fruit-feeding interactions of 97 bird species recorded in 126 locations across six continents to test our hypotheses [Fig. 1A; more details on our dataset are provided in (33) and fig. S1]. For each location, our data describe the number of observed feedings of fruit species by a bird species (henceforth referred to as "interaction frequency"). We used a synthesis of literature and trait databases to obtain trait data for the 97 bird and 831 fruiting plant species in our dataset (tables S1 and S2) and determined the degree of trait matching between birds and the fruits they consumed (33). We used

zero-inflated generalized linear mixed-effects models and a model selection approach (fig. S2) to evaluate (i) whether the frequency with which a given bird species consumes fruits that vary in how closely they match its beak size changes when it approaches or crosses its range limits (a statistical interaction between trait matching and distance to range limits) and (ii) how this effect might be influenced by a set of moderator variables. Bird species observed outside of their range edges (e.g., vagrant individuals or migratory species in their passage routes) were included in our main models but removed in an additional supplementary analysis (33). We estimated trait mismatching (the inverse of trait matching) as the absolute difference between a bird's gape size and fruit diameter (fig. S3). Therefore, a stronger negative effect of trait mismatching on interaction frequency toward birds' range limits would indicate that birds more frequently consume closely size-matched fruits near their range edges. Although our trait mismatching metric assumes that a precisely zero difference between gape and fruit size is "optimal," we evaluated how changing the threshold for optimal trait mismatching values affects the reported patterns [see sensitivity analyses in (33)]. We analyzed both horizontal (hereafter, "geographic") and vertical (hereafter, "elevational") range limits (Fig. 1, C and D, and fig. S4) because these two dimensions of range boundaries could represent regions of lower suitability for bird species (12, 34), though their relative importance might vary across species and regions. We also included the three-way statistical interaction among trait mismatching and both distance measures in our starting models because the effects of geographic and elevational range limits may be synergistic (e.g., if the two range limits are generated by different stressors) or antagonistic (e.g., if being close to any limit is stressful, but both limits is no more stressful). Because abundant fruits may be selected by many bird species, we accounted for the total number of fruits consumed of each plant species (estimated as the total number of feeding records involving each plant species in the local network) in our models. Thus, we modeled each bird species' consumption of fruits relative to those that were locally available for consumption.

### Frugivorous birds consume more closely size-matched fruits near geographic range edges

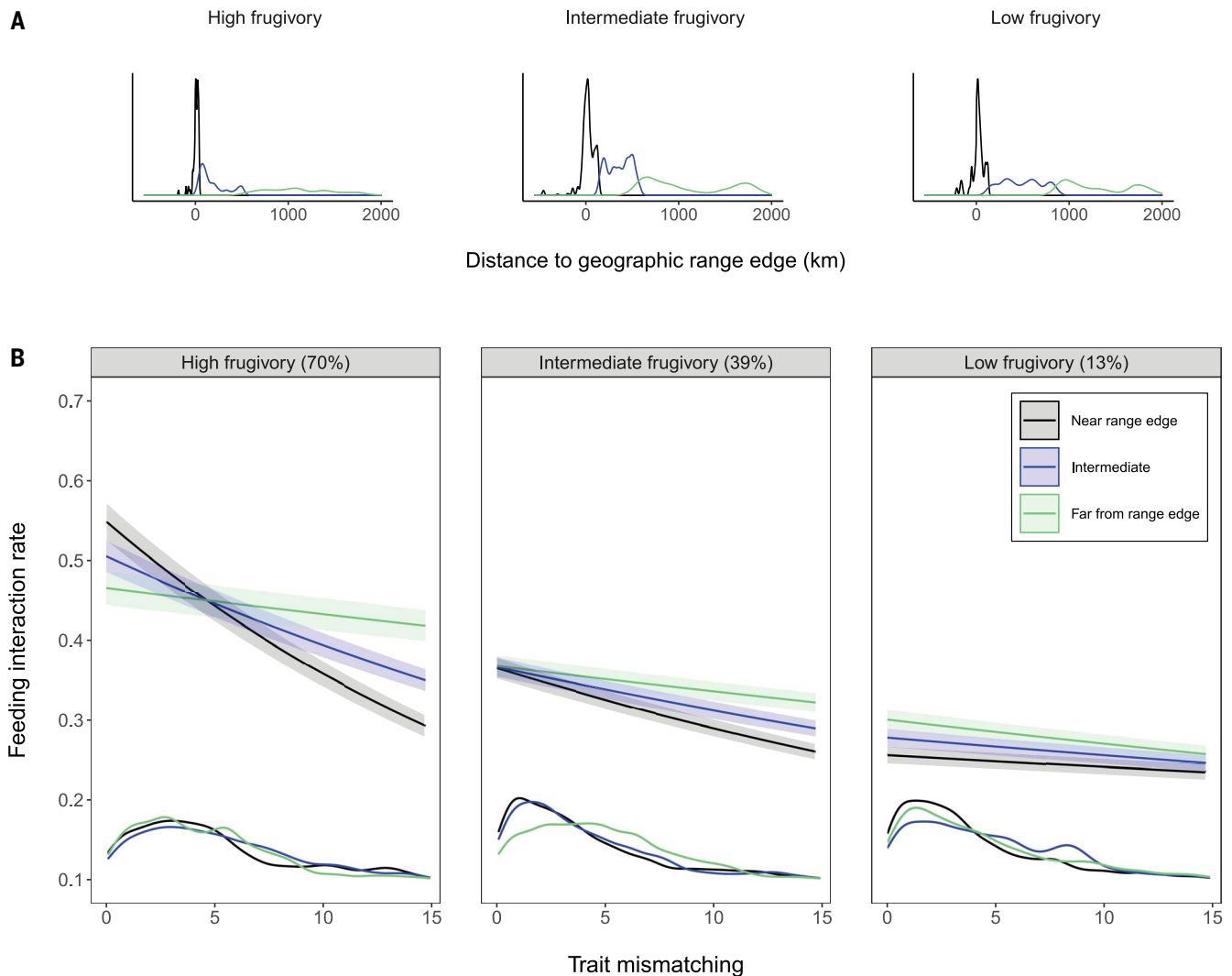
Birds more frequently consumed fruits matching their gape size near their geographic range edges (Fig. 2 and figs. S5 to S12), an effect that was strong for highly frugivorous birds but absent for species with a low degree of frugivory (Fig. 3). Our model selection retained the statistical interaction among trait mismatching, distance to geographic range edge, and degree of frugivory in all best-fitting models [difference



**Fig. 2. The impact of trait matching on feeding interaction rate changes near a bird's geographic range edge.** (A) Density plots show the distribution of distance to geographic range edge values, with each line color representing one of three equal-sized groups in the dataset used for plotting. (B) Model-predicted values of feeding interaction rate (consumption relative to a fixed number of fruits) across birds' geographic ranges (line colors). Predicted values (for an average bird species) were obtained from our best-fitting model and conditioned on the fixed effects and the zero-inflation component of the model while holding the nonfocal variables constant at their averages or reference level. Feeding interaction rates are representative of plants that would have received 11 interactions (the median number of fruits consumed of each plant species) from all frugivores present (33). Distance to geographic range edge was analyzed as a continuous predictor in our models, though, for visualization, we divided this variable into three categories (mean  $\pm$  SD). Shaded portions represent 95% confidence bands. Density plots within the panel show the distribution of trait mismatching values. The range of the x axis was defined between zero (perfect matching) and the 95th percentile of trait mismatching values.

in Akaike Information Criterion ( $\Delta$ AIC)  $< 2$ ], with the top best-fitting model explaining 67.9% of the total variance in interaction frequency [conditional coefficient of determination ( $R^2$ ), or 17.4% with fixed effects only (marginal  $R^2$ )]. By contrast, none of our other moderators influenced range-edge effects on trait matching (i.e., these moderating effects did not improve relative model fit; tables S3 to S5). Results were

qualitatively similar after the removal of observations outside a bird's geographic or elevational range edges from the dataset (fig. S13 and tables S6 to S8) and when changing what we treat as optimal trait mismatching values (fig. S14), either by shifting the "peak" of optimal fruit size in our analyses (such that fruits needed to be smaller than gape size to be optimal; figs. S15 and S16) or by sequentially increasing the



**Fig. 3. Range-edge effects on trait matching vary with a bird's degree of frugivory.** For plotting, we organized the dataset into three equal-sized groups according to birds' degree of frugivory. **(A)** Density plots show the distribution of distance to geographic range edge values within each frugivory category. **(B)** Predicted values of feeding interaction rate were obtained from our best-fitting model and plotted across different levels of frugivory (panels) and distances to a bird's geographic range edge (line colors) [see (33) for more

details on how predicted values were generated]. Shaded portions represent 95% confidence bands. Panels show predictions split according to the mean degree of frugivory of each group (with mean values shown in parentheses). Density plots within panels show the distribution of trait-mismatching values. Note that increasing trait matching (i.e., a more negative effect of trait mismatching on feeding interaction rate) toward geographic range edges was pronounced for highly frugivorous birds but absent for birds with a low degree of frugivory.

range of trait mismatching values that were considered optimal (figs. S17 and S18).

The statistical interaction between trait mismatching and distance to geographic range edge was also retained in the top and third best-fitting models obtained from an alternative model selection process that did not include moderators (to determine whether increased trait matching at range edges held across the entire dataset; fig. S19), with the second best-fitting model only having trait mismatching as a predictor (table S9). Although these results confirm the importance of trait matching for explaining plant-frugivore interactions (25, 35), they suggest that the effect of trait matching varies within species' ranges (best-fitting mod-

el: conditional  $R^2 = 0.678$ , marginal  $R^2 = 0.177$ ). Because a bird's beak width (33) is also likely to be associated with the diameter of the fruit consumed, we repeated our main analyses using a slightly higher number of bird species in our dataset for which beak-width data were available ( $n = 105$ ). We found that trait matching also increased with proximity to geographic range edge when replacing gape size by beak width to estimate trait mismatching (fig. S20), an effect that was not influenced by any moderator (best-fitting model: conditional  $R^2 = 0.673$ , marginal  $R^2 = 0.177$ ; tables S10 to S12).

Fruit profitability is partially determined by the reward-to-cost ratio associated with fruit size (23). From this perspective, our findings

may reflect higher energetic costs near species' geographic range edges, such that frugivorous birds could be forced to optimize their diet to the most profitable, closely size-matched fruits. Evidence suggesting that a bird's degree of frugivory is a key moderator of this effect indicates that opportunistic frugivores achieve their energy requirements by consuming complementary food resources (28, 36). By contrast, because highly frugivorous birds have a specialized digestive system (28), they are likely more constrained to achieve dietary efficiency by consuming the most profitable fruits available (note that the bird species used in our analyses tended to be more frugivorous than average; fig. S1B).

### Standardizing by range and gape size

It is plausible that small-ranged birds may only be stressed at shorter distances from their range edge or that small-gaped birds consume fruits with a relatively narrower clearance. To test whether the effects of trait matching and distance to range edge are relative, rather than absolute, we standardized trait mismatching, distance to geographic range edge, and distance to elevational limit by a bird's gape size, geographic range size, and elevational range size, respectively (hereafter, "standardized models"). These models assume that a given trait mismatching value (e.g., 2 mm) is greater for small-gaped birds than for large-gaped birds and that small-ranged species are relatively unstressed throughout all of their range except at the edge. Again, the statistical interaction effect between trait mismatching and distance to geographic range edge was retained in the top best-fitting model (conditional  $R^2 = 0.675$ , marginal  $R^2 = 0.164$ ), yet this effect was only apparent for migratory species (fig. S21). However, several models had a similar fit ( $\Delta\text{AIC} < 2$ ), including some in which statistical interactions involving trait mismatching and distance to range limits were not included as predictors (tables S13 to S15). Therefore, range-edge effects on trait matching were not consistently retained in our best-fitting standardized models.

We interpret these standardized model results being weaker than those from our main analyses as indicating that the effects of distance to range edge are absolute, rather than relative to range size. Indeed, large-ranged species might experience very different biotic and/or abiotic conditions within their ranges (37, 38) and thus be forced to adjust their diet accordingly. By contrast, small-ranged species (which occur largely or entirely near their range edge) are more likely to have narrow niches (37, 38) and be threatened (39), suggesting that these species may be under relatively high stress throughout their entire range. Although exceptions to this pattern do, of course, exist (37), the fact that migratory status was only an important moderator of range-edge effects on trait matching in our standardized models corroborates this interpretation; migratory birds tended to have larger geographic ranges than nonmigratory species (Wilcoxon rank-sum test:  $w = 1725$ ,  $P < 0.001$ ), such that the moderating effect of migratory status might already be partly captured in (unstandardized) models that use absolute distance values. Conversely, trait mismatching was a good predictor of plant-frugivore interactions in both standardized and unstandardized models (tables S3 and S13), suggesting that birds similarly optimize both absolute and relative fruit size.

### Multiple factors influence birds' fruit consumption

Besides trait matching (25, 35), other factors influence fruit consumption by birds, such as

handling techniques (40) and fruit nutritional content (41). In particular, fruit size may constrain consumption by "gulpers" (species that consume fruits whole) more than "mashers" (species that process fruits in their beak) (28, 40). Nevertheless, species' differences in handling technique are unlikely to have driven our results, because range-edge effects on trait matching were observed even when we assumed that only fruits smaller than gape size could be optimal [by penalizing the consumption of larger fruits (i.e., interactions that likely involved mashers) in our analyses (33)].

We focused our hypotheses around diet optimization but acknowledge that other factors may influence birds' foraging behavior. For example, consumers might forage suboptimally to mitigate predation risk (42) and behavioral interference (23). The latter may partly explain why birds near elevational range limits [which are often determined by territoriality in tropical montane regions (16, 43)] did not substantially increase their consumption of optimally sized fruits. Moreover, whereas elevational range limits can be stressful for species inhabiting montane regions (34, 43), geographic range edges are likely a more consistent proxy of environmental stress when considering all the species in our dataset (33), such as those with no high-elevation areas within their ranges. Importantly, fruit trait composition may vary across a bird's range and affect fruit selection (44), though our models controlled for this possibility by testing for trait matching relative to fruit availability at a given site. The fact that most of our sites were located in the tropics and South America, combined with evidence that birds from nontropical zones tend to be less frugivorous than tropical birds (45), might also have influenced the observed patterns. Indeed, most nontropical birds in our dataset fall at the lower half of the frugivory continuum (fig. S22), where range-edge effects on trait matching are less pronounced (Fig. 3). Finally, we highlight that the hypotheses we tested pertain to species-level ranges and traits. Although it could be interesting to explore how different individuals of a species select food resources, this would require measurement of fruits and beaks before consumption, and such experimental conditions would face different limitations.

Our findings indicate that variation in trait matching is associated with changes in resource use across space. This knowledge may contribute to improving present efforts to predict species interactions and quantify how they respond to global change (46). Biogeographic patterns in trait matching may also have implications for coevolutionary processes because interaction frequency can indicate selective pressure (9, 47), which could create positive feedback with trait matching near species' range edges. By showing that birds consume

more closely size-matched fruits near geographic range limits, our study provides insights into how frugivore interactions might respond to shifts in geographic range. This understanding is especially important as global changes cause range shifts and contractions, forcing many populations to live near or outside their historic range limits (48).

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#### ACKNOWLEDGMENTS

We thank all our colleagues in the Tyljanakis and Stouffer lab groups for their insightful comments on this manuscript, as well as the researchers who collected field data and assembled the databases used in this study. We acknowledge BirdLife International and *Handbook of the Birds of the World* for providing the species' range data and the Cornell Lab of Ornithology for developing and maintaining the Birds of the World research platform. We are indebted to S. Nakagawa for his advice on the method used for calculating the variance explained by our models. **Funding:** We acknowledge the following funding: University of Canterbury Doctoral Scholarship

(L.P.M.); The Marsden Fund grant UOC1705 (J.M.T., L.P.M.); New Zealand's Biological Heritage National Science Challenge (J.M.T., L.P.M.); The São Paulo Research Foundation grants FAPESP 2014/01986-0, 2022/09561-4, and 2021/10639-5 (M.G., C.E.), 2015/15172-7 and 2016/18355-8 (C.E.), and 2004/00810-3 and 2008/10154-7 (C.I.D., M.G., M.A.P.); CEPID-FAPESP (CBioClima, Proc. 2021/10639-5) (M.G.); Earthwatch Institute and Conservation International (C.I.D., M.G., M.A.P.); Carlos Chagas Filho Foundation for Supporting Research in the Rio de Janeiro State – FAPERJ grant E-26/200.610/2022 (C.E.); Brazilian Research Council grants 540481/01-7 and 304742/2019-8 (M.A.P.) and 300970/2015-3 (M.G.); Rufford Small Grants for Nature Conservation nos. 22426–1 (J.C.M.-F., Í.M.) and 11042-1 (M.C.M.); Universidade Estadual de Santa Cruz (Propp-UESC no. 00220.1100.1644/10-2018) (J.C.M.-F., Í.M.); Fundação de Amparo à Pesquisa do Estado da Bahia – FAPESB no. 0525/2016 (J.C.M.-F., Í.M.); Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq 303302/2022-4 (J.C.M.-F.); ARC SRIEAS grant SR200100005 Securing Antarctica's Environmental Future (D.M.D.); German Science Foundation – Deutsche Forschungsgemeinschaft PAK 825/1 and FOR 2730 (K.B.-G., E.L.N., M.Q., V.S., M.S.), FOR 1246 (K.B.-G., M.S., M.G.R.V.), and HE2041/20-1 (F.S., M.S.); Portuguese Foundation for Science and Technology – FCT/MCTES contract 10.54499/CEECIND/02064/2017 (L.P.d.S.), 10.54499/UIDB/04004/2020, 10.54499/LA/P/0092/2020 (J.M.C., R.H.), and 10.54499/CEECINST/00152/2018/CP1570/CT0014 (R.H.); National Scientific and Technical Research Council, PIP 592 (P.G.B.); and a doctoral fellowship by the National Scientific and Technical Research Council (CONICET, Argentina) (R.A.R.). **Author**

**contributions:** Conceptualization: L.P.M., J.M.T.; Methodology: L.P.M., J.M.T., D.B.S.; Data collection: P.G.B., K.B.-G., J.M.C., D.M.D., C.I.D., C.E., M.G., R.H., Í.M., J.C.M.-F., M.C.M., E.L.N., M.A.P., M.Q., R.A.R., F.S., V.S., M.S., L.P.d.S., F.R.d.S., J.A.T., A.T., M.G.R.V.; Writing – original draft: L.P.M., J.M.T.; Writing – review and editing: All authors. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** The data and code necessary to reproduce the analyses of this manuscript are available at Dryad (49). We do not have rights to redistribute the BirdLife range polygon data (50), but this dataset can be requested by all qualified researchers at <http://datazone.birdlife.org/species/requestdis> and is available for use under license for conservation purposes, scientific analysis, or research. **License information:** Copyright © 2024 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

#### SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.adj1856](https://doi.org/10.1126/science.adj1856)

Materials and Methods

Figs. S1 to S22

Tables S1 to S15

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MDAR Reproducibility Checklist

Submitted 12 June 2023; accepted 13 May 2024

10.1126/science.adj1856