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Independent variation of avian sensitivity to climate change and trait-based adaptive capacity along a tropical elevational gradient

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Abstract

Aim: How species respond to climate change is influenced by their sensitivity to climatic conditions (i.e. their climatic niche) and aspects of their adaptive capacity (e.g. their dispersal ability and ecological niche). To date, it is largely unknown whether and how species' sensitivity to climate change and their adaptive capacity covary. However, understanding this relationship is important to predict the potential consequences of a changing climate for species assemblages. Here, we test how species' sensitivity to climate change and trait-based measures of their ecological adaptive capacity (i) vary along a broad elevational gradient and (ii) covary across a large number of bird species.

Location: A Neotropical elevational gradient (300–3600 m.a.s.l.) in the Manú Biosphere Reserve, south-east Peru.

Methods: We focus on 215 frugivorous bird species along a Neotropical elevational gradient. We approximate species' sensitivity to climate change by their climatic niche breadth, based on species occurrences across South America and bioclimatic variables. In addition, we use a trait-based approach to estimate the dispersal ability of species (approximated by their wing pointedness), their dietary niche breadth (approximated by bill width) and their habitat niche breadth (the number of used habitat classes).

Results: We found that (i) species' climatic niche breadth increased with elevation, while their trait-based dispersal ability and dietary niche breadth decreased with elevation, and (ii) sensitivity to climate change and trait-based adaptive capacity were not related across species.

Main conclusions: These results suggest different mechanisms of how species in lowland and highland assemblages might respond to climate change. The independent variation of species' sensitivity to climate change and their trait-based adaptive capacity suggests that accounting for both dimensions will improve assessments of species'

susceptibility to climate change and potential impacts of climate change on diverse species assemblages.

KEYWORDS
birds, climate change, climatic niche, dietary niche, dispersal, frugivory, functional traits, habitat niche, mountain, vulnerability

1 | INTRODUCTION

Species can respond in different ways to climate change. For example, species might persist locally if changing climates lie within their climatic niche or if they adjust to changing climates *in situ* (Bellard et al., 2012). Moreover, species might shift their geographical ranges to track their suitable climate under climate change (Chen et al., 2011; Lenoir et al., 2020). In addition, species need to respond to climate-induced changes in food resource or habitat availability (Jackson et al., 2015; Maron et al., 2015). Therefore, understanding and predicting the potential impacts of climate change on species assemblages likely requires accounting for the different ways in which species may respond to the changing conditions.

To understand species' responses to climate change, we can draw upon a framework that has been described by the Intergovernmental Panel on Climate Change (IPCC, 2007) and is commonly applied in assessments of species' vulnerability to climate change (Foden et al., 2013, 2018). According to this framework, species' susceptibility to climate change comprises three dimensions: the exposure of species to climate change (i.e. the direction and extent to which the physical environment of the species changes), their sensitivity to any exposure and their adaptive capacity to counteract exposure effects (Foden et al., 2013). Here, we explicitly focus on the sensitivity and the adaptive capacity, which relate to intrinsic properties of species. First, the sensitivity of a species to climate change is defined as the degree to which it is affected by any kind of climate change (Foden et al., 2018; IPCC, 2007). Species' sensitivity to climate change is influenced by their climatic niche, that is the climatic conditions in which species can maintain evolutionary fitness and stable populations (Algar & Tarr, 2018). Second, the adaptive capacity of a species is defined as its ability to adjust to any kind of climate change, respond to its consequences and moderate potential damage (Foden et al., 2018; IPCC, 2007, 2014). Species' adaptive capacity is related to several ecological and evolutionary attributes of the species, for example their dispersal ability, phenotypic plasticity and evolutionary potential (Foden et al., 2018; Pacifici et al., 2015).

Studies on potential impacts of climate change on species assemblages often focus on species' sensitivity to climate change, for example by assessing occurrence-based or physiologically derived measures of species' climatic niche (Khaliq et al., 2014; Nunez et al., 2019; Thuiller et al., 2006). In contrast, aspects of the adaptive capacity of species have mostly been accounted for in integrated vulnerability measures (Culp et al., 2017; Foden et al., 2013) and are only recently being incorporated into projection models (Di Musciano et al., 2020; Razgour et al., 2019). Given the difficulty in quantifying the different aspects of species' adaptive capacity, it remains largely unclear how the sensitivity of species to climate change is related to adaptive capacity.

One way towards a more integrative understanding of species' susceptibility to climate change is to apply trait-based approaches (Schleuning et al., 2020; Willis et al., 2015). Response traits influence how species respond to environmental change and can approximate their sensitivity and adaptive capacity under climate change (Foden et al., 2018; Luck et al., 2012). First, the climatic niche breadth influences the persistence of species under climate change and can therefore be used to approximate species' sensitivity to climate change (Botts et al., 2013; Foden et al., 2018; Herrera et al., 2018; Figure 1a). Second, several response traits influence critical ecological aspects of species' adaptive capacity. For example, species' body size or wing shape influences their ability to disperse and shift their ranges under climate change (Dawideit et al., 2009; Sheard et al., 2020; Figure 1b). Furthermore, the ecological niche breadth of species influences their ability to adjust to changes in resource availability (Slatyer et al., 2013). For instance, the ecological niche breadth of species is related to their habitat niche breadth and their dietary niche breadth (Figure 1c,d). While dietary flexibility is difficult to quantify, response traits related to food handling and uptake may be used to estimate the flexibility of species to switch between dietary resources (Bender et al., 2017).

Knowledge on relationships between species' sensitivity and adaptive capacity at the assemblage level may inform us about the potential responses of entire species' assemblages to climate change. Previous work suggests that species' sensitivity and adaptive capacity differ among species assemblages depending on the environmental context. According to Janzen's climate variability hypothesis, species from variable climates have broader thermal niches than species from stable climates (Ghalambor et al., 2006; Janzen, 1967). Accordingly, the thermal tolerance of animal species tends to increase with increasing latitude and elevation (Fang et al., 2019; Khaliq et al., 2014; Shah et al., 2017). Similarly, geographical patterns of species' dispersal ability and ecological niche breadth have been investigated. For instance, a recent study revealed a positive latitudinal trend of average wing pointedness, a proxy for dispersal ability, in avian assemblages globally, possibly driven by increasing climate variability with latitude (Sheard et al., 2020). Furthermore, the latitude–niche breadth hypothesis predicts an increase in species' ecological niche breadth with latitude, but studies that have tested for latitudinal gradients in species'

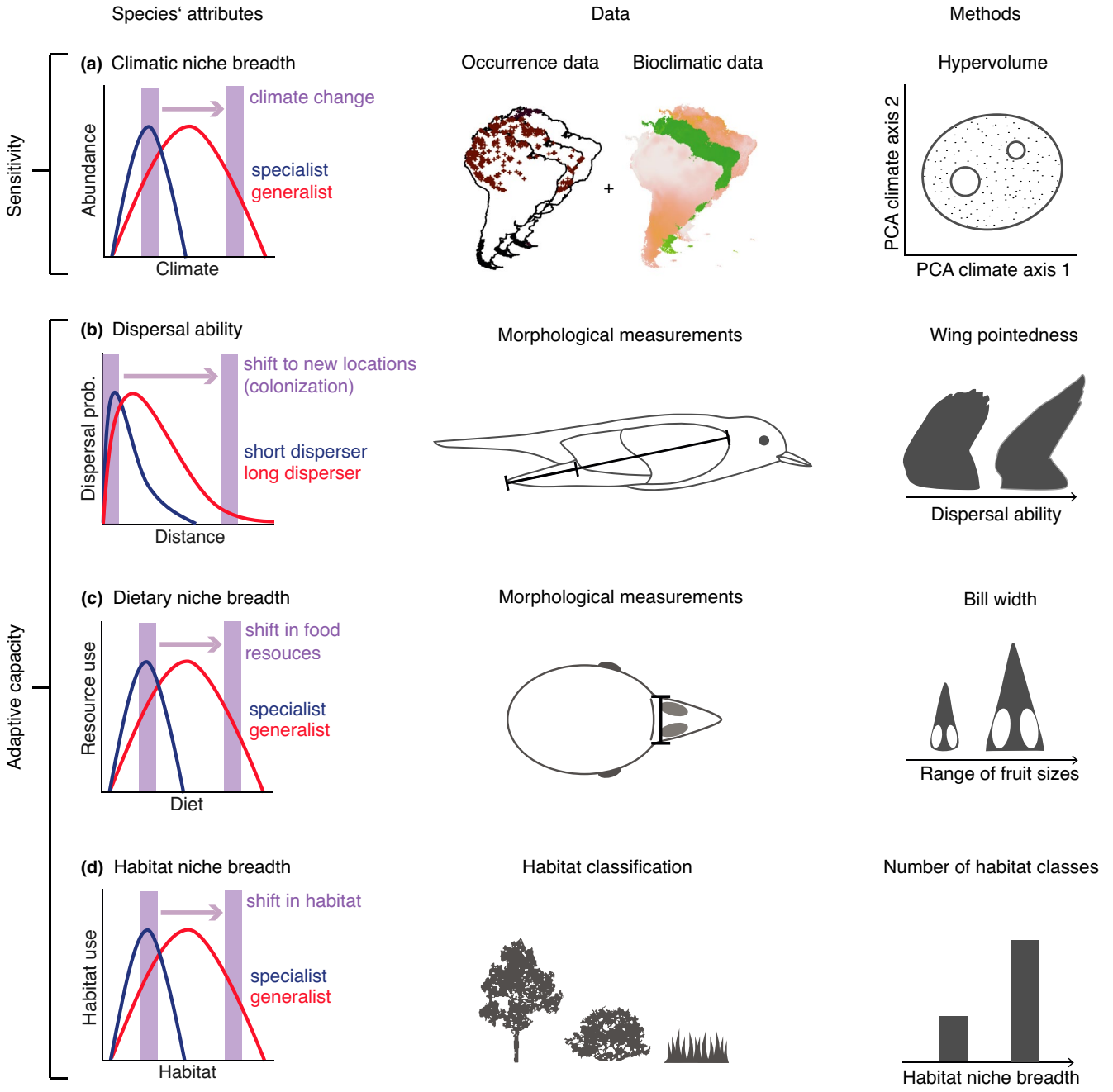

FIGURE 1 Response traits related to species' sensitivity to climate change, here climatic niche breadth, (a) and their ecological adaptive capacity, here dispersal ability, dietary niche breadth in terms of fruit choice and habitat niche breadth, (b–d). (a) A species' sensitivity to climate change can be approximated by its climatic niche breadth since a species with a broad climatic niche (generalist) has a higher chance that changing climates remain within its niche than a species with a narrow climatic niche (specialist). We estimated the climatic niche breadth of the avian frugivores based on species' current occurrences and climate data across South America as a hypervolume in a two-dimensional climate space. (b–d) Important aspects of a species' adaptive capacity are the species' ability to shift its range and to utilize a wide range of resources. (b) A species' ability to shift its range influences whether the species can track suitable conditions and relates to the species' dispersal ability. We approximated the dispersal ability of the avian frugivores by their wing pointedness measured on museum specimens. (c) A species' dietary niche breadth influences whether the species can tolerate shifts in food resources. For avian frugivores, this can be estimated by their bill width, which influences the range of fruit sizes the species can feed on. (d) Similarly, a species' habitat niche breadth influences whether the species can tolerate shifts in available habitat. We approximated the habitat niche breadth of the avian frugivores as the number of habitat classes the species are reported to occur in. The illustration of avian wing morphology is adapted from Sheard et al. (2020)

ecological niche breadth report inconsistent results (Schleuning et al., 2012; Vázquez & Stevens, 2004). Despite the few existing studies of large-scale variation in species' response traits, relationships between species' sensitivity to climate change and trait-based measures of their adaptive capacity have not yet been explicitly tested along environmental gradients.

Evidence is mixed for relationships between sensitivity and adaptive capacity at the species level. For example, habitat niche breadth of European breeding birds has been reported to be positively related to their dietary niche breadth and negatively related to their climatic niche breadth (Reif et al., 2016), while habitat niche breadth and climatic niche breadth were positively related in a study focussing on French breeding birds (Barnagaud et al., 2012). Resolving such differences is important because the relationship between species' sensitivity and adaptive capacity determines potential trade-offs in species' overall ability to respond to climate change. For instance, if species that are highly sensitive to climate change also have a low adaptive capacity, then their overall susceptibility to climate change might be higher than estimated from their climatic niche alone (Foden et al., 2013).

Here, we aim to identify the relationship between species' sensitivity to climate change and response traits associated with species' ecological adaptive capacity. We assess this relationship (i) in different species assemblages along an elevational gradient and (ii) across the entire species pool. We focus on 215 avian frugivore species co-occurring along a Neotropical elevational gradient with a highly diverse avifauna. Our focus on avian frugivores, a functionally homogeneous ecological group, allows trait-based approaches to be applied across a large set of species. Furthermore, avian frugivores play crucial roles as seed dispersers, especially in the tropics (Jordano, 2014). To approximate species' sensitivity to climate change, we quantify species' climatic niche breadth as a hypervolume based on their current occurrences and climate conditions across South America. To approximate species' ecological adaptive capacity, we make use of avian morphological traits related to dispersal ability and dietary niche breadth in terms of fruit choice (Bender et al., 2017; Dawideit et al., 2009; Sheard et al., 2020). In addition, we include a measure of species' habitat niche breadth (Figure 1b–d).

(i) We expect species' climatic niche breadth in frugivore assemblages to increase with increasing elevation because increasing diurnal temperature variability should favour species with broad climatic niches at high elevations (i.e. the climate variability hypothesis; Ghalambor et al., 2006; Janzen, 1967). Furthermore, we expect species' dispersal ability and ecological niche breadth to decrease with increasing elevation because the low diversity and availability of fruit resources at high elevations might promote bird species with round wings and narrow ecological niches (Dehling, Töpfer, et al., 2014). (ii) Across species, we expect a negative relationship between climatic niche breadth and traits related to adaptive capacity. While there is no clear *a priori* support for this expectation, sensitivity and adaptive capacity might trade off in species that have survived past climate change; that is, species might either have a broad climatic niche or a high adaptive capacity.

2 | METHODS

2.1 | Study system and assemblages of frugivorous birds

Our study system was an elevational gradient ranging from 300 to 3600 m.a.s.l. located in the Manú biosphere reserve in south-east Peru. The gradient is covered in lowland rain forest (<500 m.a.s.l.), montane rain forest (~500–1500 m.a.s.l.), cloud forest (~1500–3000 m.a.s.l) and elfin forest (>3000 m.a.s.l.). At the tree line (~3500 m.a.s.l.), elfin forest is interrupted by patches of Puna grassland (Patterson et al., 1998). All forest types are intact primary forests. Precipitation is high along the entire gradient (annual rainfall approximately 1500–4800 mm, mean = 2709 mm), while temperature declines with increasing elevation (mean annual temperature ranges from 24.3°C at 500 m.a.s.l. to 7.3°C at 3500 m.a.s.l.; Girardin et al., 2010, 2013).

We focussed on frugivorous bird species, defined as those species who consume fruit as a main part of their diet (Dehling, Fritz, et al., 2014; obligate and partial frugivores as classified by Kissling et al., 2007). This classification implies that species may also use other food resources (e.g. invertebrates), but depend on fruits as their main diet at least in specific seasons or parts of their life. Based on this classification, we identified 245 frugivorous species along the Manú gradient. To ensure unbiased estimates of species' climatic niches (see description below), we excluded species with strong seasonal migrations. Furthermore, we excluded ground-dwelling species, because their dispersal behaviour cannot be approximated by wing shape (see the description below). These steps resulted in a set of 215 species, for which we recorded the local elevational ranges (i.e. minimum and maximum elevation) based on local checklists (Dehling, Fritz, et al., 2014; Dehling et al., 2013; Merkord, 2010; Walker et al., 2006). Frugivorous bird assemblages were determined every 300 m of elevation following previous work (Dehling, Fritz, et al., 2014).

2.2 | Sensitivity: climatic niche breadth

We estimated species' climatic niche breadth based on bioclimatic variables and species' occurrences across South America; that is, we quantified species' realized climatic niche breadth across the entire continent (Figure 1a). We downloaded occurrence data for each bird species from the Global Biodiversity Information Facility (GBIF.org, 2017) and subjected the data to a comprehensive quality check. First, we excluded data entries with a longitude of zero and data entries for which the country provided by the author of the data did not resemble the country in which the coordinates were located. Second, we compared the GBIF occurrences to species' extent-of-occurrence range maps (BirdLife International & Handbook of the Birds of the World, 2017) and removed outliers, that is occurrence points >500 km away from the range map margins. Finally, we only analysed species for which at least 20 spatially unique occurrence

points were available (every latitude–longitude combination was counted only once, regardless of how many observations were reported from that point) and where these points covered the species' range maps reasonably well.

The final set of 215 bird species had on average 437 ± 431 spatially unique occurrence points (mean ± SD) ranging from 24 to 3467 spatially unique occurrence points per species. Only 11 of these species had fewer than 50 spatially unique occurrence points, and those 11 species were mostly small-ranged. We computed range coverage and geographical bias scores of the cleaned GBIF data in comparison with geographical range maps from BirdLife applying the method of Meyer et al. (2016). These metrics are based on the great-circle distance (km) of 1000 random points, placed across each geographical range map, to their geographically closest GBIF occurrence records (Meyer et al., 2016). The average range coverage of the cleaned GBIF data was −125.7 ± 65.3 km (mean ± SD, $n = 215$ species), and their average geographical bias score was 67.1 ± 53.5. These values indicate reasonable range coverage and low geographical bias (see Figures S1 and S2, Table S3). For comparison, Meyer et al. (2016) reported a much larger bias across mammals globally (average range coverage −205.5 ± 375.5 km).

We downloaded current bioclimatic data (1979–2013) from the climatologies at high resolution for the Earth's Land Surface Areas data (CHELSA; Karger et al., 2017) at a resolution of 30 arcsec. We selected 17 bioclimatic variables that capture minimum, maximum and mean values, as well as diurnal and seasonal variation of temperature and precipitation across South America (Table S1). The CHELSA data have the advantage of including orographic predictors in the precipitation estimation, thereby enhancing rainfall estimates based on interpolated weather station data, especially in mountainous regions (Karger et al., 2017).

Using the cleaned set of occurrence points and the bioclimatic variables, we estimated each species' climatic niche breadth as a two-dimensional hypervolume following Blonder et al. (2014). To reduce the number of dimensions before the computation of the climatic niche breadth of each species (as suggested by Blonder et al., 2014), we performed a principal component analysis (PCA) across the values of the 17 bioclimatic variables at all spatially unique occurrence points of the 215 bird species across South America. We used the first two axes of this PCA (capturing 76.59% of the total variation in the occurrence data; Table S1) and computed each species' climatic niche breadth as a two-dimensional hypervolume in this PCA space (Blonder et al., 2014). The first principal component was positively correlated with bioclimatic variables related to mean annual temperature and annual precipitation, and negatively correlated with seasonality in temperature and precipitation, and with mean diurnal range (Table S1). The second principal component was positively correlated with variables related to annual precipitation and negatively correlated with variables related to mean annual temperature, seasonality in temperature and precipitation, and with mean diurnal range. The hypervolume function performs a kernel density estimation and volume measurement using a Monte Carlo importance sampling approach (Blonder et al., 2014). We applied Gaussian kernel density and Silverman's bandwidth estimation (default settings in R package "hypervolume").

To test whether the two-dimensional hypervolume is a robust estimate of species' climatic niche breadth, we compared it with the estimates based on three- and four-dimensional hypervolumes (including the first three and four principal component axes, respectively) and with the estimates based on a different method of climatic niche quantification (Broennimann et al., 2012; details in Supporting Information text S1). The estimates of species' climatic niche breadth based on these different approaches were strongly positively correlated (Pearson's r ranging from .54 to .92, $p < .001$; Table S2), indicating robust and consistent estimation of climatic niche breadth across species.

2.3 | Adaptive capacity: dispersal ability, dietary niche breadth, and habitat niche breadth

We estimated the dispersal ability and the dietary niche breadth of the 215 selected frugivorous bird species with a trait-based approach, that is based on their wing pointedness and bill width (Figure 1b,c). The wing pointedness of bird species is related to their natal dispersal distances and their capacity to fly long distances (Dawideit et al., 2009; Santini et al., 2019; Winkler & Leisler, 1992). Therefore, measures of wing pointedness can serve as a proxy for dispersal ability (Sheard et al., 2020). The dietary niche breadth of frugivorous birds is related to species' bill width since broad-billed frugivorous species can feed on a wider range of fruit sizes than narrow-billed species and are therefore more flexible in their fruit choice (Bender et al., 2017; Wheelwright, 1985). This trait-based approach is justified since all species in our dataset consume fruits as a main part of their diet (Dehling, Fritz, et al., 2014; Kissling et al., 2009). Wing pointedness and bill width were measured for each species on museum specimens following measurement protocols from Eck et al. (2011) aiming at measuring two female and two male specimens per species (dataset from Dehling, Fritz, et al., 2014). Wing pointedness was measured as Kipp's index, which is the distance from the tip of the first secondary feather to the tip of the longest primary feather (mm) divided by wing length (mm; equivalent to the hand-wing index; Eck et al., 2011; Sheard et al., 2020). The average number of specimens measured per species was 3.6 ± 0.9 (mean ± SD). Only for three of the 215 bird species, measurements were based on a single specimen (list of specimens in Supporting Information text S2). For all further analyses, we computed mean values of wing pointedness and bill width for each species (Table S3).

We estimated the habitat niche breadth of all 215 frugivorous bird species as the number of habitat classes in which a species was recorded. This reflects the difference between species that are spread across many habitats (habitat generalists) and those restricted to a few habitats (habitat specialists; Figure 1d). These data are based on species' habitat use (binary) among 11 habitat classes representing a gradient from forested to open habitats, derived from the International Union for Conservation of Nature (IUCN) habitat

classification version 3 (dataset from Barnagaud et al., 2017; additional information in Supporting Information text S3). The climatic niche breadth and the traits related to species' adaptive capacity were estimated at the species level and are not specific to the studied elevational gradient.

2.4 | Relationships of species' sensitivity and trait-based adaptive capacity with elevation

We assessed relationships of species' sensitivity and traits related to adaptive capacity with elevation by fourth-corner analyses. The fourth-corner analysis was developed to test for relationships between environmental variables (here elevation as a surrogate for changing abiotic and biotic conditions) and species' traits based on species' occurrences (here presence/absence of bird species at each of the 12 elevational levels, 300–3600 m.a.s.l.; Dray & Legendre, 2008). Specifically, the fourth-corner analysis assesses the relationships between species' occurrences, environmental variables at these sites and species traits. The environmental variables and species traits used in our analysis are continuous. Therefore, the relationship is assessed as a Pearson correlation coefficient. The significance of the relationship is tested with a permutation test, that is a randomization procedure; we applied permutation model 6 to avoid inflated type I error (Dray & Legendre, 2008). We performed a separate fourth-corner analysis for each of the traits. Since we expected saturating trends with increasing elevation, we ln-transformed elevation prior to the analyses. When elevation was not ln-transformed prior to the analysis, the fourth-corner analyses yielded similar results (Table S4).

2.5 | Relationships between sensitivity and trait-based adaptive capacity across species

We tested for associations between sensitivity and trait-based adaptive capacity across species with phylogenetic generalized least square (PGLS) models. PGLS models take into account the phylogenetic covariance among species (Freckleton et al., 2002). We based the phylogenetic analyses on a global phylogeny for bird species (Jetz et al., 2012; see details in Supporting Information text S4). We applied PGLS models since bill width and wing pointedness showed strong, significant phylogenetic signal (Pagel's lambda = 1.00, $p = .001$, respectively; Freckleton et al., 2002). For climate and habitat niche breadth, lambda was 0.35 ($p = .001$) and 0.30 ($p = .006$), respectively, suggesting not only a significant phylogenetic signal as lambda differed from 0 but also that these attributes evolved according to a process in which the effect of the phylogeny was weaker than in the Brownian motion model (as lambda is expected to be 1 under the Brownian motion model; Freckleton et al., 2002). We fitted a PGLS model each for wing pointedness, bill width and habitat niche breadth (as measures of a species' adaptive capacity) against climatic niche breadth (the sensitivity measure) to control for these phylogenetic signals. Since the habitat niche breadth is represented by count data, we ln-transformed it before fitting the model. In these PGLS models, we set delta and kappa to one and estimated lambda by maximum likelihood. For wing pointedness, the model was not able to yield a maximum-likelihood estimate for lambda due to a flat likelihood surface, so we set lambda to 1 in this model.

All analyses were performed in R version 3.5.0 (R Core Team, 2018).

TABLE 1 Relationships between elevation (ln-transformed) and traits related to species' sensitivity to climate change (climatic niche breadth) and their ecological adaptive capacity (wing pointedness, dietary niche breadth and habitat niche breadth)

Response variable	Pearson's *r*	*p*-Value
Climatic niche breadth	.35	.002
Wing pointedness	−.12	.046
Bill width	−.12	.046
Habitat niche breadth	.03	.598

Note: We performed a separate fourth-corner analysis for each of the traits; this tests the relationships based on species' occurrences at 12 elevational levels every 300 m along the Manú gradient (300–3600 m.a.s.l.). Elevation was ln-transformed prior to the analyses. See Table S4 for results when elevation was not transformed.

3 | RESULTS

3.1 | Relationships of species' sensitivity and trait-based adaptive capacity with elevation

The fourth-corner analyses revealed a significant positive relationship between elevation and species' climatic niche breadth (Table 1). Specifically, species' climatic niche breadth increased until about 1200 m.a.s.l. and showed only little change between 1200 and 3600 m.a.s.l. (Figure 2a). In contrast, wing pointedness and bill width (reflecting species' dispersal ability and dietary niche breadth) decreased significantly with increasing elevation (Table 1, Figure 2b,c). Species' habitat niche breadth showed no significant association with elevation (Table 1, Figure 2d). These results suggest that species' sensitivity to climate change and their trait-based adaptive capacity decrease with increasing elevation.

3.2 | Relationships between sensitivity and trait-based adaptive capacity across species

Across the species pool of the entire elevational gradient, there were no significant relationships between sensitivity and trait-based adaptive capacity when accounting for phylogenetic relationships among species (Table 2). Species varied widely in the traits related to adaptive capacity across the entire spectrum of species' climatic niche breadths (Figure 3). This indicates that sensitivity and trait-based adaptive capacity vary independently across species.

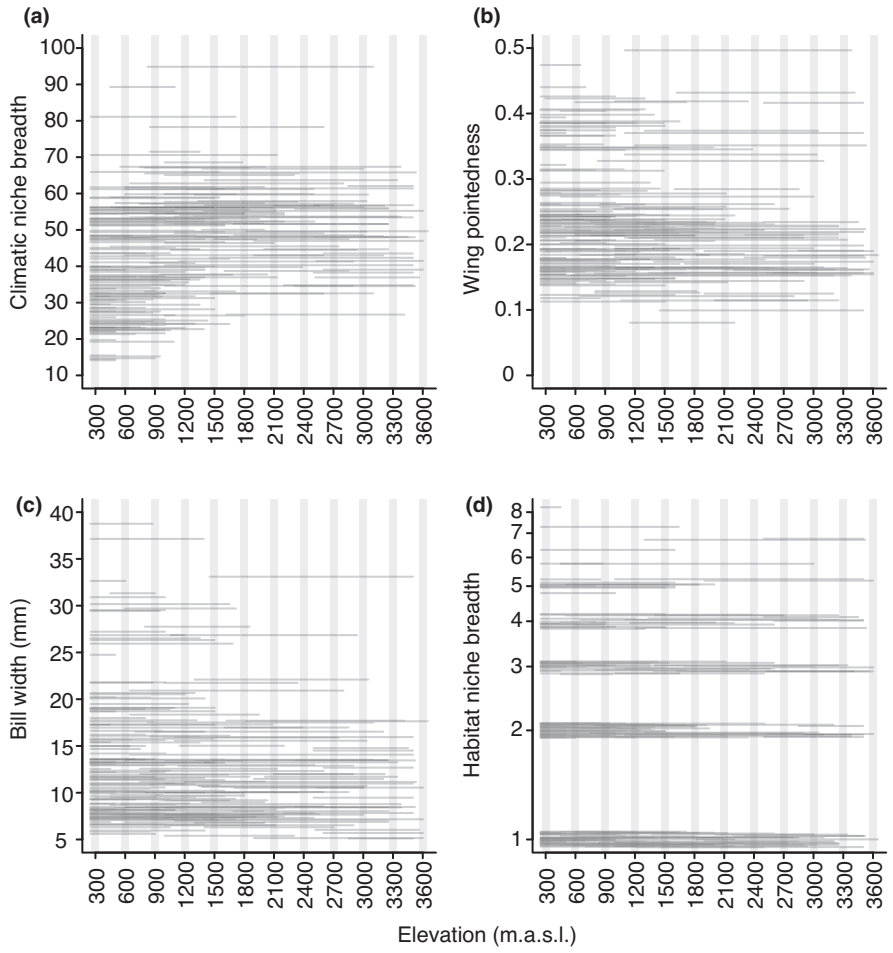

FIGURE 2 Elevational patterns of species' sensitivity to climate change (a) and of their trait-based ecological adaptive capacity (b–d). Shown are patterns of species' (a) climatic niche breadth, (b) wing pointedness (as a proxy for species' dispersal ability), (c) bill width (as a proxy for species' dietary niche breadth) and (d) habitat niche breadth (i.e. number of used habitat types) along elevation. Horizontal lines represent each species' elevational range in the study area (from minimum to maximum elevation; $n = 215$ avian frugivores). Vertical lines indicate the 12 species assemblages studied at the different elevations

TABLE 2 Results of phylogenetic generalized least square (PGLS) models fitted to test for associations between species' sensitivity (climatic niche breadth) and aspects of their ecological adaptive capacity (wing pointedness, bill width and habitat niche breadth) across species

Response variable	Intercept/predictor	Estimate	Std. error	*t*-Value	*p*-Value
Wing pointedness	Intercept	0.33	0.56	0.59	.56
	Climatic niche breadth	0.04	0.03	1.28	.20
Bill width	Intercept	0.48	0.66	0.73	.47
	Climatic niche breadth	−0.02	0.03	−0.67	.50
Habitat niche breadth	Intercept	0.04	0.37	0.10	.92
	Climatic niche breadth	0.06	0.07	0.87	.38

Note: All traits were scaled and centred before the analyses to ensure comparability of the model estimates. Adjusted R^2 of all models was <.01.

Interestingly, different bird orders differed in their sensitivity and trait-based adaptive capacity (Figure 3). For instance, the climatic niche breadth of Passeriformes (perching birds, $n = 148$ species) and Trogoniformes (trogons, $n = 9$) varied from narrow to broad. However, Passeriformes had round to moderately pointed wings and narrow to moderately broad bills, while Trogoniformes were characterized by pointed wings and moderate bill width. Contrastingly, Psittaciformes (parrots, $n = 26$) and Piciformes (woodpeckers, $n = 21$) displayed mostly narrow to moderately broad climatic niches. Yet, Psittaciformes were among the species with the most pointed wings, while Piciformes had more rounded wings.

4 | DISCUSSION

We tested how species' sensitivity to climate change (i.e. their climatic niche) and their trait-based ecological adaptive capacity vary along an elevational gradient and covary across species. We found that species' climatic niche breadth increased with increasing elevation, while trait-based dispersal ability and dietary niche breadth decreased with increasing elevation. This indicates that the sensitivity of avian frugivore species to changing climates might be highest in lowland assemblages, while highland assemblages host avian frugivore species that might have a comparatively low adaptive capacity in terms of their dispersal ability and fruit resource use. Across

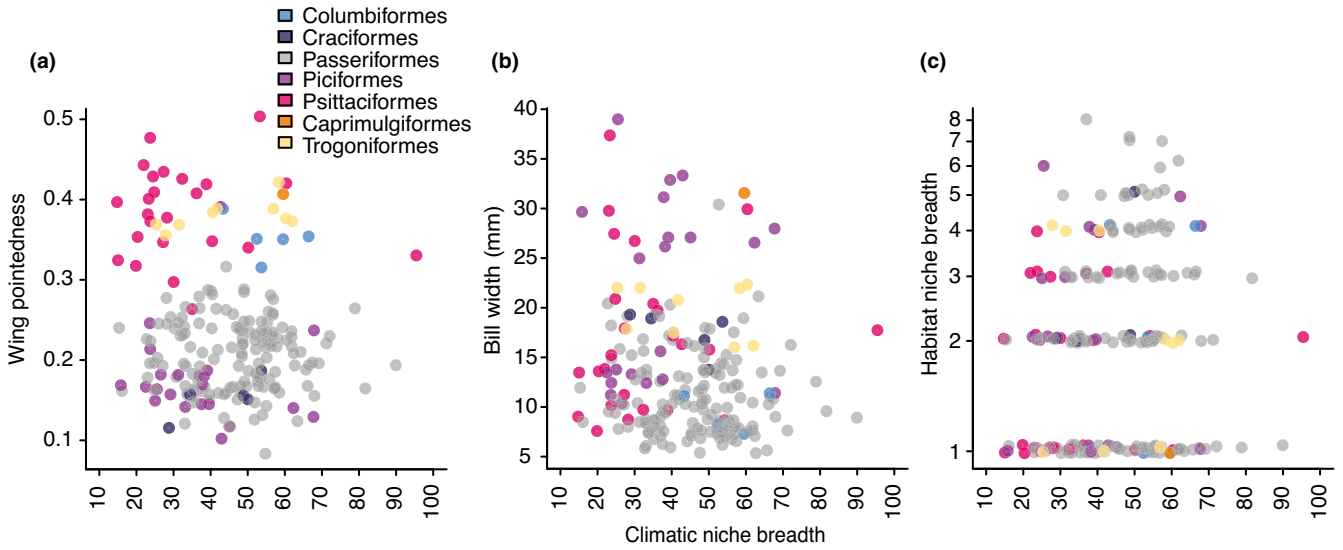

FIGURE 3 Associations between sensitivity to climate change (climatic niche breadth) and trait-based adaptive capacity across species. Shown are associations between climatic niche breadth and (a) wing pointedness (as a proxy for species' dispersal ability), (b) bill width (as a proxy for the dietary niche breadth of avian frugivores), and (c) habitat niche breadth (i.e. the number of used habitat types). Each dot represents a species (n = 215), and colours represent the different orders of frugivorous birds

the species pool and accounting for phylogenetic covariation, sensitivity to climate change and trait-based adaptive capacity varied independently.

4.1 | Relationships of species' sensitivity and trait-based adaptive capacity with elevation

In line with the climate variability hypothesis (Janzen, 1967) and our expectations, we found a positive relationship between species' climatic niche breadth and elevation. This relationship is also consistent with Rapoport's rule, which states that species' range sizes increase with increasing elevation because of a greater tolerance for climatic variation in highland species (Stevens, 1989, 1992). Along the Manú gradient, increasing diurnal temperature variation with elevation might favour avian frugivore species with broader thermal tolerances at higher elevations (Ghalambor et al., 2006; Rapp & Silman, 2012). Accordingly, high-elevation bird species in the Peruvian Andes have been reported to be more resistant to cold temperatures, but equally capable to withstand high temperatures compared with species from lower elevations (Londoño et al., 2015). The Glossy-black Thrush (*Turdus serranus*) and the Hooded Mountain Tanager (*Buthraupis montana*) are examples of high-elevation species at the Manú gradient with rather broad climatic niches. Among the lowland species with more narrow climatic niches are the Purple-throated Cotinga (*Porphyrolaema porphyrolaema*) and the Opal-rumped Tanager (*Tangara velia*).

The negative relationships of wing pointedness and bill width with elevation were in line with our expectations. Many tropical avian frugivore species are highly dependent on fruit in their diet (Kissling et al., 2009). Therefore, the significant but weak relationships we found might be due to bottom-up effects of the fruit plant assemblages on the avian frugivores and their traits (Vollstädt et al., 2017). Specifically, predominantly low plant heights and small fruit sizes at high elevations of the Manú gradient might promote the occurrence of round-winged and narrow-billed avian frugivores (Dehling, Töpfer, et al., 2014; Pigot et al., 2016). This likely relates to trait matching between interacting resource and consumer species, specifically a previously reported positive relationship between wing pointedness and plant height in plant–frugivore interactions (Bender et al., 2018; Dehling, Töpfer, et al., 2014). Similarly, bill width and fruit width of interacting avian frugivore and fruit plant species usually correspond closely (Bender et al., 2018; Burns, 2013). In addition, the decreasing availability of fruit resources with increasing elevation might lead to environmental filtering of bird traits resulting in low trait diversity of high-elevation bird assemblages (Hanz et al., 2019). Among the high-elevation species with rather round wings and narrow bills are the Blue-capped Tanager (*Thraupis cyanocephala*) and the Blue-winged Mountain Tanager (*Anisognathus somptuosus*), while the Red-bellied Macaw (*Orthopsittaca manilata*) is an example of a pointed-winged, broad-billed lowland species.

The opposing elevational patterns of climatic niche breadth on the one hand and trait-based dispersal ability and dietary niche breadth on the other hand suggest different mechanisms of how species from low- vs. high-elevation assemblages might respond to contemporary climate change. The narrow climatic niches of avian frugivore species from lowland assemblages suggest that lowland species might be sensitive to climate change. Therefore, lowland species may require shifting their elevational ranges upslope to track their suitable climate under contemporary climate change. Particularly, lowland species with pointed wings might be well equipped for such range shifts (Dawideit et al., 2009). Furthermore,

the flexibility in fruit choice of broad-billed lowland frugivores might enhance their ability to find matching fruit resources at higher elevations (Wheelwright, 1985). However, while upslope range shifts are a plausible strategy for species occurring at the base of the Andes, central Amazonian taxa would need to overcome several hundred kilometres to reach higher elevations. In comparison, the comparatively broad climatic niches of avian frugivores in assemblages at high elevations of the Manú gradient suggest that these species might be less sensitive to changing climates than species from low elevations. However, the ability of high-elevation species to disperse and shift their ranges might be limited due to their rather rounded wings (Dawideit et al., 2009). Moreover, their relatively narrow bills might restrict them to feed on small fruits making them less flexible to respond to changes in fruit resource availability (Wheelwright, 1985).

Bird species at tropical elevational gradients have already shifted their elevational ranges upslope under contemporary climate change (Forero-Medina et al., 2011; Freeman & Class Freeman, 2014). Thus far, tropical lowland bird species tend to *expand* their elevational ranges upslope (i.e. they shift their upper elevational range limit upslope, while their lower elevational range limit stays unchanged), suggesting that they are able to tolerate increasing temperatures, at least to some extent (Freeman, Scholer, et al., 2018). This might indicate that occurrence-derived thermal tolerances of tropical lowland species underestimate species' actual thermal tolerances, because the climatic niche estimates are truncated at the lowest elevations (Feeley & Silman, 2010). Recently reported high relative abundances of Bornean bird species at sea level further support the hypothesis of truncated climatic niches of tropical lowland species (Burner et al., 2019).

In line with our findings, a recent meta-analysis revealed that high-elevation species globally have shifted their elevational ranges upslope at a lower rate than low-elevation species under contemporary climate change. This finding indeed suggests broader climatic niches of high-elevation species compared with lowland species (Mamantov et al., 2021). However, avian frugivore assemblages at the highest elevations are restricted by abiotic and biotic barriers, such as the tree line. Therefore, species occurring close to such barriers have to contract their elevation ranges because they cannot easily expand their ranges to higher elevations (La Sorte & Jetz, 2010). This phenomenon, often termed "mountaintop extinctions," has been rather widely reported under contemporary climate change and suggests that highland species face an elevated risk from rapid global warming (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018; Pacifici et al., 2017). In addition, ongoing changes in plant assemblages at high elevations (Feeley et al., 2011; Morueta-Holme et al., 2015) could imply that highland frugivores might have to switch to other food resources than fruits, for example to invertebrates (Carnicer et al., 2009), given their apparently limited capacity to feed on various fruit types. Current evidence therefore suggests that despite their comparably broad climatic niches, high-elevation species are highly susceptible to adverse consequences from contemporary climate change.

4.2 | Relationships between sensitivity and trait-based adaptive capacity across species

Contrary to our expectation, the sensitivity to climate change and the three metrics of trait-based adaptive capacity were unrelated across the avian frugivore species at the Manú gradient. Accordingly, we could not identify trait syndromes of species with coherent patterns in terms of their sensitivity and trait-based adaptive capacity. This result was emphasized by the large variation in trait values within bird orders, for example the perching birds (Passeriformes). Generally, some species with pointed wings and broad bills were characterized by broad climatic niches, for example the Golden-Headed Quetzal (*Pharomachrus auriceps*) and the Military Macaw (*Ara militaris*). Other species had broad climatic niches, but round wings or narrow bills, for example the Bronze-Green Euphonia (*Euphonia mesochrysa*) and the Spotted Tanager (*Tangara punctata*). Some species with narrow climatic niches had pointed wings or broad bills, for example the Black-Tailed Trogon (*Trogon melanurus*) and the Green-Backed Trogon (*Trogon viridis*). These species-specific differences in sensitivity and trait-based adaptive capacity within the group of avian frugivores coincide with the observation that individual species can differ greatly in response to climate change (Chen et al., 2011; MacLean & Beissinger, 2017; Moritz et al., 2008). Our findings reveal that even within ecologically homogeneous groups of species, such as avian frugivores, responses to climate change are likely to be idiosyncratic.

Interestingly, our findings differ from a global study reporting increasing average wing pointedness with increasing climate variability (Sheard et al., 2020). This suggests differences in this relationship between global and local scales, possibly influenced by our exclusion of migratory species from the analysis. Furthermore, we could not confirm a positive or negative relationship between climatic niche breadth and habitat niche breadth across avian species (Barnagaud et al., 2012; Reif et al., 2016), suggesting that these relationships differ between tropical assemblages with a high trait diversity compared with less diverse European bird assemblages (Barnagaud et al., 2012; Kissling et al., 2009; Reif et al., 2016). Together, this indicates that relationships between species' sensitivity and trait-based ecological adaptive capacity are context-dependent. We encourage future studies to test whether species' sensitivity to climate change is associated with other aspects of species' adaptive capacity, for example with other parts of species' ecological niches, or traits related to their evolutionary potential (Boutin & Lane, 2014). Moreover, applying comprehensive trait-based assessments to other taxonomic groups might yield a more general understanding of the relationship between species' sensitivity to climate change and adaptive capacity.

5 | CONCLUSIONS

We show that the sensitivity of avian frugivores to climate change (i.e. their climatic niche breadth) and their trait-based ecological adaptive capacity vary independently along elevation and across species. Our results emphasize that focussing only on the

sensitivity of species to climate change can be insufficient to predict potential effects of future climate change on species assemblages. Trait-based approaches can provide a ready way to assess other ecological dimensions of species' susceptibility to climate change. Such integrated trait-based assessments of climate change impacts on diverse species assemblages can be applied to other species groups and can inform measures of biodiversity conservation in a changing world.

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CONFLICT OF INTEREST

The authors state no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the results (Table S3) have been archived at Dryad: https://doi.org/10.5061/dryad.ksn02v766.

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BIOSKETCH

Larissa Nowak is interested in understanding how global change affects interacting species and how these effects are mediated by species functional traits. This study is part of her dissertation at Senckenberg Biodiversity and Climate Research Centre and Goethe University Frankfurt.

Author contributions: LN, MS, WDK, and SF conceptualized the research. LN and IMAB curated the data. LN analysed the data and wrote the manuscript with input from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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