University of Birmingham
Research at Birmingham

Scale-dependent effects of niche specialisation

Huang, Shan; Tucker, Marlee A.; Hertel, Anne G.; Eyres, Alison; Albrecht, Jörg

DOI:
10.1111/ele.13759

License:
Creative Commons: Attribution (CC BY)

Document Version
Publisher's PDF, also known as Version of record

Citation for published version (Harvard):
Huang, S, Tucker, MA, Hertel, AG, Eyres, A & Albrecht, J 2021, 'Scale-dependent effects of niche specialisation: the disconnect between individual and species ranges', *Ecology Letters*, vol. 24, no. 7, pp. 1408-1419. https://doi.org/10.1111/ele.13759

Link to publication on Research at Birmingham portal

General rights
Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- •Users may freely distribute the URL that is used to identify this publication.
- •Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- •User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- •Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy
While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Download date: 09. May. 2024

Received: 18 February 2021 | Revised: 15 March 2021 | Accepted: 25 March 2021

DOI: 10.1111/ele.13759

ECOLOGY LETTERS WILEY

LETTER

Scale-dependent effects of niche specialisation: The disconnect between individual and species ranges

Shan Huang[1] | **Marlee A. Tucker**[2] | **Anne G. Hertel**[1,3] | **Alison Eyres**[1,4,5] | **Jörg Albrecht**[1]

[1]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt, Germany

[2]Department of Environmental Science, Radboud University, Nijmegen, Netherlands

[3]Behavioural Ecology, Department of Biology, Ludwig-Maximilians University of Munich, Planegg-Martinsried, Germany

[4]Department of Biological Sciences, Goethe-University Frankfurt, Frankfurt, Germany

[5]RSPB Centre for Conservation Science, Cambridge, UK

Correspondence
Shan Huang, Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, SBiK-F, 60325, Frankfurt, Germany.
Email: shan.huang@senckenberg.de

Funding information
Radboud Universiteit, Grant/Award Number: Excellence Initiative Fellowship; Deutsche Forschungsgemeinschaft, Grant/Award Number: FR 3246/2-2, GO1221/25-2 and HU 2748/1-1; German-Israeli Foundation for Scientific Research and Development, Grant/Award Number: I-1465-413.13/2018; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 793077; Alexander von Humboldt-Stiftung

Editor: Amanda Bates

Abstract

One of the most general expectations of species range dynamics is that widespread species tend to have broader niches. However, it remains unclear how this relationship is expressed at different levels of biological organisation, which involve potentially distinctive processes operating at different spatial and temporal scales. Here, we show that range sizes of terrestrial non-volant mammals at the individual and species level show contrasting relationships with two ecological niche dimensions: diet and habitat breadth. While average individual home range size appears to be mainly shaped by the interplay of diet niche breadth and body mass, species geographical range size is primarily related to habitat niche breadth but not to diet niche breadth. Our findings suggest that individual home range size is shaped by the trade-off between energetic requirements, movement capacity and trophic specialisation, whereas species geographical range size is related to the ability to persist under various environmental conditions.

KEYWORDS
diet breadth, geographical range size, habitat breadth, home range, movement, niche breadth, resource availability, scale-dependent processes, terrestrial mammals

INTRODUCTION

Identifying what drives the dynamics of species distribution is a fundamental question in ecology and evolution, especially for understanding how species interact with their environment in a changing world (Grinnell, 1917; Holt, 2003; Sutherland et al., 2013). In particular, generalist species, which have a wide niche, are often expected to occupy large geographical ranges (Böhm et al., 2017; Brown, 1984; Jocque et al., 2010; Olalla-Tárraga et al., 2015; Slatyer et al., 2013). However, a disconnect between the range dynamics at different levels of biological organisation is suggested by contrasting expectations. While species range size is expected to increase with niche breadth, average individual home range size is expected to decrease with increasing niche breadth, because larger home range and niche specialisation have respectively been found to be associated with larger average body size in previous comparative work (Costa et al., 2008; Lindstedt et al., 1986; McNab, 1963). With potentially distinctive processes operating at different spatial and temporal scales, the reconciliation of the individual- and species-level dynamics is essential for identifying scale-dependent mechanisms, but rarely done (McGill, 2010). Here, we present a global study to compare the role of niche breadth in shaping distribution at the individual and species level in terrestrial mammals, a classic model system in macroecology owing to their critical roles in ecosystems and the abundant data for their geographic distribution and biological traits (Fritz et al., 2009; Jones et al., 2009; Tucker et al., 2018).

Niche breadth generally refers to the range of abiotic and biotic conditions under which a species is able to persist (Elton, 1927; Grinnell, 1917; Hutchinson, 1957; MacArthur & Levins, 1967). This idea is often conceptualised as the fundamental niche (i.e. the full range of conditions for persistence given physiological constraints) but empirically represented by the realised niche (i.e. the range of conditions with actual occurrence), especially in macroecological studies (Soberón, 2007). Although individuals of the same species might differ in their physiological tolerance and resource requirements, the collective species niche is an important concept in ecology and evolution (Wake et al., 2009), fundamental to understanding the distribution and diversity of life (Colwell & Rangel, 2009; Leibold, 1995; Levine & HilleRisLambers, 2009; Wake et al., 2009). Motivated by the urgent need to anticipate the impact of projected climate change, climatic tolerance (most often represented by the realised climatic niche) has been intensively studied for its role in shaping species distribution patterns (e.g. Comte & Olden, 2018; Eyres et al., 2017; Hawkins & Felizola Diniz-Filho, 2006; Saupe et al., 2019; Tomašových et al., 2016). In comparison, ecological specialisation, that is, the range of resources or habitats a species can use, has received relatively little attention, but is also crucial for understanding species persistence in changing environments (Fernández & Vrba, 2005; Harcourt et al., 2002; Pyron, 1999; Schleuning et al., 2020; Sol et al., 2002). The loss of preferred resources and habitats might intensify climatic impacts (Peters et al., 2019; Pineda-Munoz et al., 2021), or pose bigger threats to biodiversity than climate change per se, especially to endotherms like mammals (Khaliq et al., 2017). Therefore, we intend to fill this gap by directly focusing on ecological specialisation of terrestrial mammals along two niche axes related to the use of resources and habitats: the diet and habitat niche breadth.

Specialisation on specific resources and habitats can play various roles in shaping patterns of distribution at the individual and species level. The geographical range of a species is shaped by the collective distribution of its individuals (Jablonski, 2000), and the movement of individuals maintaining gene flow (Burgess et al., 2016; Kokko & López-Sepulcre, 2006; Stevens et al., 2014). These movements can range from daily foraging within home ranges to natal dispersals and migrations, driven by a variety of factors including resource distribution, mating partners, competitors and predators (Alerstam & Bäckman, 2018; Altizer et al., 2011; Riotte-Lambert & Matthiopoulos, 2020; Stevens et al., 2014) and thus might show strong relationships with diet and habitat specialisation. For example, classic cost-benefit theory predicts a specialisation-dispersal trade-off, in which dispersal ability (e.g. ability of moving among habitats) is expected to be higher in generalists than in specialists, with higher costs for specialists (e.g. for finding suitable resources), but higher benefits for generalists (e.g. for avoiding competition) (Jacob et al., 2018; Jocque et al., 2010; Nurmi & Parvinen, 2011; Vasconcelos & Rueffler, 2020). However, empirical evidence of this trade-off is mixed (e.g. Jakobsson & Eriksson, 2003; Laube et al., 2015; Martin & Fahrig, 2018; Stevens et al., 2014), potentially due to the lack of clade-wide comparisons to display broad-scale patterns not apparent for subsets of taxa (Jablonski, 2007).

Individual-level distribution patterns can be captured by the average individual home range size (Bowman et al., 2002; Whitmee & Orme, 2013), which is maintained by short-term (e.g. daily) movements of individuals (Tucker et al., 2018; Tucker et al., 2019). Collectively, individual home ranges form a species' geographical range yet might be shaped by different mechanisms specific to the individual level. In particular, the average home range size of a species has long been recognised as a strong correlate with average body size (Lindstedt et al., 1986; McNab, 1963). It is possible that body size is a metabolic proxy (see their tight link studied by Brown et al., 1993; West et al., 1997) that connects the ecological niche to individual and species ranges through energetic mechanisms (Brown & Maurer, 1989; Jetz et al., 2004; Teitelbaum et al., 2015; Tucker et al., 2019). For example, the capacity for a specialised species to efficiently use a narrow range of resources, combined with a larger body size, might provide a large energy budget for the movement necessary to maintain large home ranges (McNab, 1963; Ofstad et al., 2016). Higher specialisation might only be possible for larger bodied species which can obtain specific resources across larger areas. The resulting pattern of larger home ranges in specialists contradicts the specialisation-dispersal trade-off, but it remains unclear whether such individual-level dynamics affect the species geographical range size, given the opposite effect from dispersal (increasing species range size in generalists).

In this study, we investigated the relationship between (realised) ecological niche breadth and range size at the individual and species level to identify the potential mechanisms acting at these two levels of biological organisation. Specifically, we compared species geographical range size and average individual home range size to first assess their relationship across mammal species. We then evaluated the role of species ecological specialisation, focusing on diet and habitat breadth, while controlling for species body size, in shaping species and average individual range size. Considering the dramatic spatial variation in abiotic conditions at broad scales (Anderegg & HilleRisLambers, 2019; McGill, 2010; Slatyer et al., 2013), we expected habitat breadth to be more related to geographical range size than to average home range size, while species' diet breadth could be related to common behaviours and physiological characteristics shared across individuals and thus more related to average individual home range size (Hertel et al., 2018; McNab, 1963; Ofstad et al., 2016; Tucker et al., 2018). Within the same context, we also assessed the links of ecological specialisation to two important modes of movements, which respectively support species geographical range size and average individual home range size: the average distance of natal dispersals and the average distance of more regular (or routine) movement (in adults) on an hourly to 10-day basis. Overall, our study demonstrates a complex role of the ecological niche in terms of resource and habitat use in driving spatial dynamics of animal species, suggesting strong dependency of the mechanisms on the level of biological organisation, where different biological processes act at different spatial and temporal scales.

MATERIALS AND METHODS

Data and variables for range size and niche breadth

We combined data of mammalian species traits from multiple sources that are publicly available (summarised in Table 1). In particular, our focal response variables, average individual home range size and species' geographical range size (both in km^2), were available for 626 and 4668 mammalian species respectively. Following Fritz et al., (2009), we re-assigned species identities in the Red List database by the International Union for Conservation of Nature (Schipper et al., 2008; IUCN 2020), to follow the mammalian taxonomy by Wilson and Reeder (2005), which is also followed by all the other data sources. We excluded the order Cetacea and families Phocidae, Otariidae and Odobenidae to focus on primarily terrestrial mammals. Information on home range size was not available for bat species (Order Chiroptera) in the PanTHERIA database (Jones et al., 2009).

The original datasets on species diet and habitat use included a total of 10 types of dietary materials (from Wilman et al., 2014) and 17 primary habitat categories (from IUCN 2020). We did not use spatial datasets of global habitat distribution that can be overlaid by species range maps to estimate species habitat occupancy (e.g. Tuanmu & Jetz, 2015) due to recently raised concerns over the accuracy and precision of range maps based on expert opinions (e.g. Herkt et al., 2017; Hurlbert & Jetz, 2007).

We summarised the number of different types of dietary materials (originally measured in percentage of total diet) and primary habitats observed to be used by each species (hereafter, diet count and habitat count), as commonly done in broad-scale comparative analyses (e.g. Forister et al., 2015). This is to avoid overinterpreting the precision of proportional diet composition data, which were based on semiquantitative estimates from verbal description (Wilman et al., 2014; but see below on additional measures). The mammalian species in our dataset consumed 1–6 different dietary materials and occurred in 1–12 different primary habitats. Although habitat use is partly related to the use of specific food resources, it is also driven by factors such as nesting and mating

TABLE 1 A summary of our data sources for terrestrial mammal species and the sample sizes (*N*) in the original datasets and in our final analyses (after excluding non-terrestrial species)

Data	Unit	Original *N*	Focal *N*	Data sources
Individual home range size	km^2	626	573	PanTHERIA by Jones et al., (2009)
Geographical range size	km^2	4668	4175	
Adult body mass	g	3542	3117	
1-hour &10-day movement distance	km	44[a]	44	Tucker et al., (2018)
Natal dispersal distance	km	75	75	Whitmee and Orme (2013)
Diet type	%	5400	4483	EltonTraits by Wilman et al., (2014)
Habitat type	binary	4598[b]	4483	The IUCN Red List (IUCN 2020)
Phylogeny	myr	5020	4483	Bininda-Emonds et al., (2007); Fritz et al., (2009)

[a]The original data were at the individual level, including 784 individuals from 57 species.

[b]The sample size after converting the IUCN Red List taxonomy for terrestrial mammals to the more widely respected taxonomy by Wilson and Reeder (2005), which is followed by all the other data sources.

opportunities (Brown, 1999; Morris, 2003; Rosenzweig, 1991). The two measures of ecological niche breadth do not covary among species (confirmed based on phylogenetic generalised least square analysis [PGLS, see below]; $N = 543$, $\lambda = 0.57$ [0.39, 0.71], $R^2 = 0.00$, $p = 0.84$).

Most species used a limited number of dietary materials and primary habitats causing heterogeneity in model residuals and variance. For statistical robustness, we created binary categorical variables from diet and habitat count. We used the median diet count (two dietary materials) and the median habitat count (three primary habitats) to classify species as specialists (< median) or generalists (≥ median). To assess the robustness of our conclusions, we evaluated several alternative metrics of diet and habitat niche breadth (see *Sensitivity analyses*).

We focused our main analyses on the final dataset containing 543 species of terrestrial non-volant mammals from 91 families in 21 orders in which data for all focal variables were available. By excluding missing values in the data sources, this subset represents those mammalian species that have received intense study effort (see comparison and sensitivity tests of our main results in Supporting Information). We did not estimate missing values using imputation in light of recently raised concern over the reliability of such estimation when data coverage is not randomly distributed (Johnson et al., 2021).

Statistical analyses of range size and niche breadth

To investigate the relationships between individual-level and species-level range size as well as their respective associations with niche breadth, we fitted four multivariate models in a Bayesian framework (BM). In all four models, average individual home range size and species geographical range size were treated as a bivariate response (both transformed to their natural logarithm to achieve homoscedasticity). We incorporated the phylogenetic relationship among species by including the variance–covariance matrix as a random factor (Hadfield & Nakagawa, 2010; Housworth et al., 2004; de Villemereuil & Nakagawa, 2014).

We first fitted two simple models (SBM) without predictor variables to estimate the variance attributable to phylogeny in the two range variables and their covariance owing to shared evolutionary history. Both models included an unstructured phylogenetic variance–covariance matrix, with the phylogenetic covariance constrained to be zero in SBM1 but estimated in SBM2.

To evaluate the effects of ecological niche breadth, we fitted two full models (FBM) that include three predictors as fixed effects: diet breadth (binary variable), habitat breadth (binary variable) and body mass (natural-log-transformed and z-standardised), as well as their pairwise interactions in explaining home range size and geographical range size. Similar to SBMs above, both FBMs included the phylogenetic variance–covariance matrix but only FBM2 assessed the phylogenetic covariance between average individual home range size and species geographical range size, and the covariance was constrained to 0 in FBM1.

We used weakly informative normal priors (N(0,1)) for all fixed effects (when included) and random effects, and an LKJ correlation prior (Lewandowski et al., 2009) for the correlation of random effects (McElreath, 2020). For each model, we ran four chains of 6,000 iterations, excluding the first 2,000 as warm-up in each chain and applied a thinning interval of 10. Therefore, all estimated model coefficients and credible intervals were based on a total of 1,600 posterior samples, and all estimates showed satisfactory convergence ($\hat{R} < 1.05$), and had effective sample sizes >400. Posterior predictive checks recreated the underlying distribution of the response variables. We compared the performance of the models using the widely applicable information criterion (WAIC, Watanabe, 2010).

Sensitivity analyses for range size and niche breadth

To assess the robustness of our findings, we conducted a series of sensitivity analyses. We reanalysed the patterns with (a) several alternative quantifications of niche breadth including measures based on counts (log-transformed), Shannon's index and distance-based diversity (Figure S1–3, Table S1–3), (b) larger sample sizes for the effect of niche breadth on geographical range size (up to 4175 species; Table S4) including a comparison of bats and non-bat species (Table S5; Figure S6) and (c) counter-factual maps of inferred natural distribution of species without human influence (Faurby et al., 2018; Tables S6). We complemented (c) with analyses of the species with low extinction risk according to the IUCN Red List (Tables S7 & S8), thereby excluding species whose geographical ranges might have contracted due to human impact (Cardillo et al., 2008; Schipper et al., 2008; see comparisons in Figure S6 & S7). We found consistent patterns across all supplementary assessments (Supporting Information).

We also compared the BM analyses with the more widely used and computationally less demanding phylogenetic generalised least squares analysis (PGLS; see more discussion by Freckleton et al., 2011; Housworth et al., 2004) and found consistent results (Tables S9 & S10, Figure S4 & S5). Because it is not straightforward to use PGLS models to explicitly account for the correlation between individual-level and species-level range size in an integrative framework, we highlight the results from the BM analyses in the main text. We used PGLS for most of our supplementary analyses to ensure robustness of our results with computational efficiency (Supporting Information).

Links of ecological specialisation to two types of individual movement

We also assessed the links of ecological specialisation to two important modes of movements, which, respectively, support species geographical range size and average individual home range size. Specifically, we analyzed the average distance of natal dispersals and the average distance of more regular movement (in adults) on an hourly to 10-day basis (see details in Supporting Information). Data for these two factors are limited (Table 1), but our results, when interpreted with caution, can illuminate how niche breadth is related to range size at the individual and species level.

We fitted PGLS models to the subsets of species for which the traits of interest were available (Tables S11 to S14), with natal dispersal distance and short-term (hourly and 10-day) movement distance (displacement) as response variables. We assessed diet and habitat niche breadth, adult body mass, individual home range size or species geographical range size as the predictor variables (Tables S11 to S14). The phylogenetic structure was estimated in Pagel's λ based on maximum likelihood and was found to be significantly different from 0 in all models.

All data organisation and analyses were conducted in R 3.5.3 (R Development Core Team, 2020), with the packages 'ape' (Paradis et al., 2004), 'phytools' (Revell, 2012) and 'tidyr' (Wickham & Henry, 2019) for dataset visualisation and transformation, 'caper' (Orme, 2012) for PGLS analyses, 'brms' (Bürkner, 2017, 2018) for BM analyses and 'loo' for model comparison (Vehtari et al., 2016).

RESULTS

Average individual home range size and species geographical range size in terrestrial (non-volant) mammals are positively correlated, with a major effect of phylogeny (SBM2: phylogenetic correlation r_{phylo} =0.3 [0.05, 0.51]; see all parameter estimates and model comparisons in Table 2). Phylogeny also accounts for 91% ($R^2_{\text{HR-phylo}}$ =0.91 [0.87, 0.94]) of the variance in average individual home range size and 49% ($R^2_{\text{GR-phylo}}$ =0.49 [0.36, 0.62]) of the variance in species geographical range size. These results suggest that variation in average individual home range size and geographical range size is constrained by the evolutionary history of the species.

Including niche breadth and body size in the model weakened the phylogenetic correlation between average individual home range size and geographical range size (FBM2, phylogenetic correlation r_{phylo} = 0.28 [−0.04, 0.54]) and improved model performance (ΔWAIC =34 between FBM2 and SBM2; Table 2). Moreover, including the phylogenetic correlation parameter only slightly improved the performance of models after accounting for the effects of niche breadth and body mass (ΔWAIC =4 between FBM1 and FBM2). Therefore, the phylogenetic correlation between average individual home range size and geographical range size is likely mediated by adult body mass and other traits related to resource and habitat use.

Based on our best model (FBM2), average individual home range size and species geographical range size are associated with niche breadth in different niche dimensions (Figure 1, see consistent results across all supplementary analyses in Tables S1–S10, Figures S4 & S5). Average individual home range size is shaped by the interactive effects of diet breadth and body size but not related to habitat breadth, while species geographical range size is related to habitat breadth but not to diet breadth or body size.

Specifically, average individual home range size increases with body size, but this increase was more pronounced for dietary specialists than for generalists, so that among small-bodied species, dietary generalists have larger home ranges than dietary specialists, whereas the opposite is the case among large-bodied species (Figure 2a). In addition, average individual home range size was positively associated with all measures of short-term movement distance (more closely with displacements over 10 days than 1 h; $p < 0.01$ in all PGLS

TABLE 2 Comparison of, including two simple models (SBM) based on phylogenetic structure alone and two integrated models (FBM) based on phylogeny, niche breadth and average adult body mass. Model performance was summarized in the marginal R^2 (R^2_{m}), the conditional R^2 (R^2_{c}), the variance explained by the phylogeny (R^2_{phy}), the Watanabe-Akaike Information criterion (WAIC) and the difference in WAIC to the best model (ΔWAIC). For the phylogenetic and residual correlation between the two response variables (r_{phy} and r_{res} respectively), the mean and 95% credible intervals are given. The sample size in this analysis was n = 543

	Model performance						**Correlation estimates**		**Model comparison**	
	Home range size			**Geographical range size**						
Models	R^2_{m}	R^2_{c}	R^2_{phy}	R^2_{m}	R^2_{c}	R^2_{phy}	r_{phy}	r_{res}	**WAIC**	**ΔWAIC**
BM1	0	0.90	0.91	0	0.40	0.47	0	0.23 [0.11, 0.35]	1895	42
BM2	0	0.90	0.91	0	0.41	0.49	0.3 [0.05, 0.51]	0.16 [0.02, 0.29]	1887	34
FBM1	0.53	0.88	0.71	0.11	0.44	0.44	0	0.18 [0.07, 0.27]	1857	4
FBM2	0.53	0.88	0.72	0.11	0.45	0.45	0.28 [−0.04, 0.54]	0.12 [0, 0.24]	1853	0

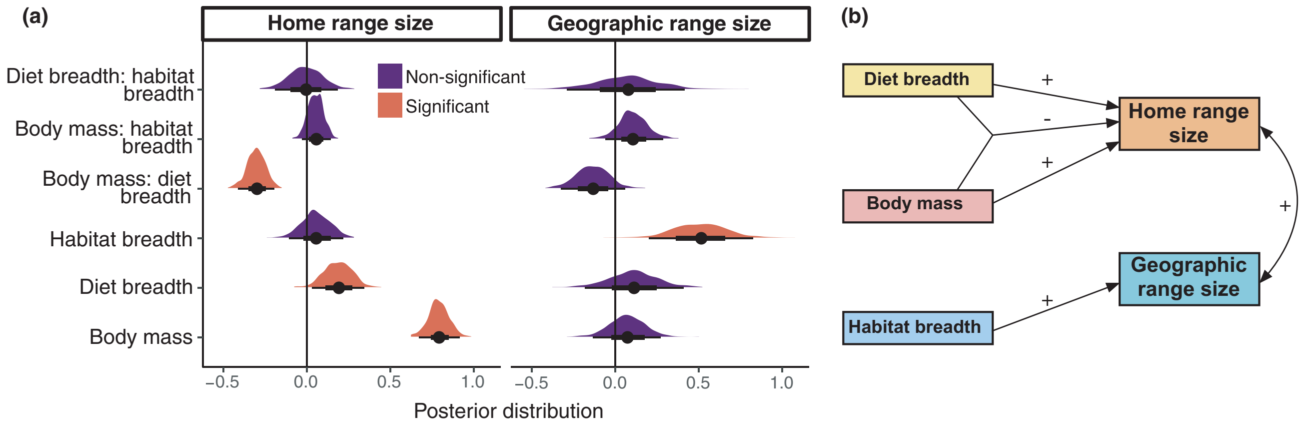

FIGURE 1 Comparison of the effect sizes based on 1600 posterior samples (a) from the best Bayesian multilevel model (FBM2, see model performance comparison in Table 2) shows that species average home range size (left) and geographical range size (right) are associated with the breadth on different niche axes. The results are also illustrated in a schematic diagram (b)

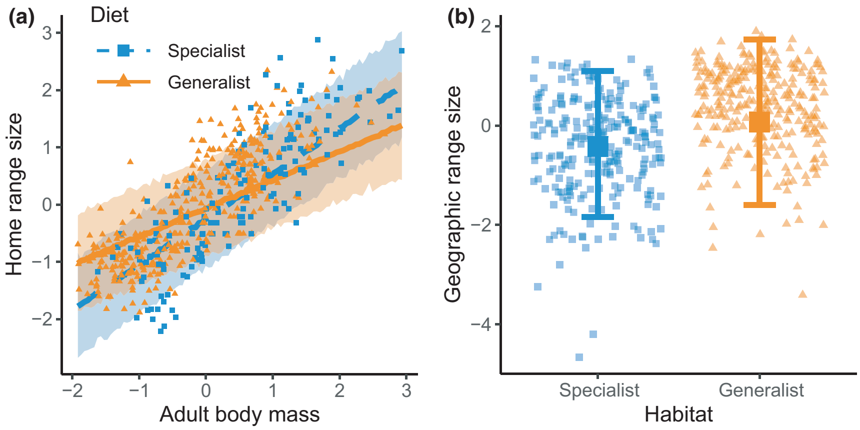

FIGURE 2 Illustration of (a) the interactive effect of body size and diet breadth on home range size and b) the effect of habitat breadth on geographical range size based on the best model (FBM2, see model performance comparison in Table 2). The points represent species data for comparing specialist species (blue squares) and generalists (orange triangles). The lines and shaded areas in a) respectively represent the estimated slopes and their credible intervals. Note that the slopes deviate slightly from the raw data because the model also accounts for the phylogenetic structure in the data and habitat niche breadth. The bars in b) indicate the mean and the 5–95% quantile of the data

analyses; Tables S11–S13), and thus can serve as an indicator of adult moving distance during regular routines. Species that show greater displacements over 10-day periods also tend to be dietary specialists ($N = 44$, $R^2 = 0.13$, $p = 0.010$), but 1-h displacement and long-distance displacements (95% quantile) at the two timescales show different patterns, suggesting that drivers of movement vary at different temporal, and likely spatial scales (see further details in Supporting Information).

Our best model (FBM2) also suggests that habitat generalists tend to have larger geographical range sizes than specialists (Figure 2b). Similarly, longer natal dispersal distances are only (weakly) associated with broader habitat niches ($N = 69$, $R^2 = 0.034$, $p = 0.069$) but not to diet breadth (Table S14). This is despite natal dispersal having a strong positive correlation with both home range size and geographical range size, as well as adult body mass, as indicated by previous studies (Bowman et al., 2002; Whitmee & Orme, 2013) (also see Table S14). The similarity in patterns suggests that our finding of a correlation between geographical range size and habitat niche breadth is likely to be biologically meaningful rather than an artefact due to an area effect. Nevertheless, further investigation through spatial simulations using high-resolution habitat distribution maps will be useful (e.g. following Saupe et al., 2019; Tomašových et al., 2014).

DISCUSSION

By comparing how diet and habitat niche breadth are related to range size at the individual and species level, we identified different ecological mechanisms depending on the level of biological organisation and the related spatial and temporal scale. In general, a large geographical range can be maintained through rare dispersal events (e.g. natal dispersal) by individuals that, on average, occupy small (or large) home ranges. This disconnect between range dynamics at the individual and species level is further emphasised by their respective associations with niche breadth in different ecological niche dimensions. For terrestrial mammals, we only found partial support for the general expectation that widely distributed species have broader niches, as species geographical range size was not related to diet niche breadth but only to habitat niche breadth. In comparison, average individual home range size was mainly shaped by the interplay between diet niche breadth and body mass, and generally unrelated to habitat niche breadth.

The positive association between geographical range size and niche breadth has received much attention partly because it was proposed as one of the mechanisms for the most pervasive biodiversity pattern, the latitudinal diversity gradient (Jocque et al., 2010; Stevens, 1989). Tropical species are often expected to have smaller ranges and narrower niches (reviewed in Mimet et al., 2019). However, our analyses showed that this apparent association only applies to habitat but not dietary niche breadth, complementing previous community network analyses that showed reduced rather than increasing animal dietary specialisation on flowering and fruiting plants towards lower latitudes (Schleuning et al., 2012; but see contrasting patterns at the assemblage level in Dalsgaard et al., 2017). The same association is also found with natal dispersal which can be a major factor for maintaining gene flow within a species' geographical range (Briscoe et al., 2019; Stevens et al., 2014; Whitmee & Orme, 2013). These results indicate that species occupying larger geographical ranges are not necessarily capable of using a larger variety of resources, at least not with regard to food, but they might be able to tolerate a larger variety of environmental conditions. Therefore, we do not consider our results as contradictory to the role of niche partitioning in explaining the rich biodiversity in the tropics, but rather, as an invitation for further investigation on additional niche axes. Fruitful directions may include specialisation with respect to symbiotic relationships, especially parasitism which is increasingly recognised as a key interaction in ecosystems (Dunne et al., 2013; Frainer et al., 2018; Lagrue et al., 2014).

It is worth pointing out that the positive relationship between geographical range size and environmental tolerance is found more often in terrestrial ecosystems than in the ocean (Olalla-Tárraga et al., 2015; Tomašových et al., 2016). This might indicate an important role of the type of ecosystem (i.e. aquatic or terrestrial) in shaping this pattern (e.g. due to fundamental differences in environmental heterogeneity). For instance, large geographical ranges in marine taxa are often achieved by niche tracking in the tropical seas (Tomašových et al., 2014), so that widely distributed marine species might still be at great risk of extinction under severe climate change scenarios. In contrast, we showed that widely distributed terrestrial species might have relatively high tolerance towards changes in the physical environment such as habitat loss (see also Khaliq et al. 2014; Khaliq et al., 2017; Lenoir et al., 2020). However, our results also indicate that many widely distributed species have a specialised diet and thus may still be prone to extinction when climate change and human activities alter the resource landscape within their habitats (Barnes et al., 2017; Di Marco & Santini, 2015; Sévêque et al., 2020), or induce fine-scale restructuring of local communities (e.g. see Blowes et al., 2019; Bowler et al., 2017; Piano et al., 2017). Geographical range size thus may not be a reliable predictor of species extinction probability (Bowler et al., 2019) as often expected (e.g. Cardillo et al., 2006; Collins et al., 2018; Finnegan et al., 2015; Fritz et al., 2009).

Moreover, our finding that habitat niche breadth was related to species geographical range size but not to individual home range size points to a mismatch between species and individual ability to tolerate a wide range of environmental conditions. In the absence of long-distance dispersal, the occurrence of individuals within a particular habitat is not only a result of habitat preference but also of historical contingency (Fukami, 2015; De Meester et al., 2016). Local adaptation over time might result in populations that are highly specialised to survive under specific conditions (Chardon et al., 2020; Kawecki & Ebert, 2004; Sanford & Kelly, 2010; Telfer & Kelsall, 1984). Therefore, a widely distributed species might actually possess large intraspecific variance in habitat preference rather than a general capability of persisting in a variety of conditions (Edelaar & Bolnick, 2019; Jaenike & Holt, 1991; Wiegand et al., 2008). Given the popularity of niche modelling in conservation biology (Guisan et al., 2013; Pacifici et al., 2015), we urge further studies to consider the environmental niche at the individual level to better predict future range dynamics under global changes (e.g. Benito Garzón et al., 2019; Tingley et al., 2016). We are also in great need of niche data resolved to the individual level for comparing intraspecific variation in niche breadth (e.g. Bolnick et al., 2003; Kernaléguen et al., 2015; Maldonado et al., 2019) across a wide range of taxa. This kind of data bears great potential for disentangling the niche-related mechanisms underlying distribution patterns at different levels of biological organisation (e.g. Sánchez-Tójar et al., 2020).

In contrast to the lack of relationship with habitat breadth, average individual home range size shows a strong albeit complex relationship with diet breadth, consistent with our expectation that the use of specific resources is more related to behaviours and physiological characteristics shared across individuals than habitat use is. We found that large-bodied specialists tend to have larger home ranges than generalists, whereas the opposite is the case for small-bodied specialists. Surviving on a limited variety of food resources likely comes with a generally higher demand than generalists in foraging success, which can be promoted through movements for searching (Jacob et al., 2018). This explanation is also supported by our finding that dietary specialisation is associated with larger body sizes (Figure S5), which tend to support longer distance movements in mammals (see also Bowman et al., 2002; Tucker et al., 2018). Importantly, we note that these effects strongly depend on the temporal scale at which movement is quantified. We found that the link to diet niche breadth breaks down both for hourly movements and the once-in-a-lifetime natal dispersal, which is not related to foraging.

The complex relationship we found between average individual home range and species diet breadth also suggests the availability of resources as a key factor for shaping distribution patterns. Resource availability evidently drives patterns of individual movement, as abundant resources reduce the need for animals to move (McLoughlin et al., 2000; Tucker et al., 2018; Teitelbaum et al., 2015). In this study, we were only able to explore this at the individual level, but the results provide additional support in that primary productivity explains a larger proportion of variance in movement distances than niche breadth and body mass (see Table S11–S13 summarising data from Tucker et al 2018). Yet, questions remain on how these patterns at the individual level might contribute to patterns at higher level of biological organisation, such as species geographical distribution and spatial variation in community structure, which are clearly affected by resource availability in a general sense (e.g. see Brun et al., 2019; Jetz et al., 2004; Jetz & Rahbek, 2002; Santini et al., 2018). In addition, resource limitation can also restrict the realised individual diet breadth in species that have a wider fundamental diet niche (Robinson & Strauss, 2020), an effect that needs to be evaluated for the same taxa in differential resource landscapes. Moreover, exposure to novel resource landscapes might alter a species' fundamental niche, such as the range of edible food types (Grant & Grant, 2006) through evolutionary processes. Therefore, the effect of distribution dynamics on species' niche breadth should also be considered when assessing human influence on biodiversity.

Some recent work has suggested that the spatial configuration and temporal fluctuation of resources may be more important than the overall resource availability in itself for shaping animal movement patterns (Fryxell et al., 2008; Riotte-Lambert & Matthiopoulos, 2020; Tucker et al., 2019), as well as the distribution of species. For example, migratory behaviour, which can effectively enlarge ranges at both the individual and species level, is often a consequence of animals tracking similar environments or resources (Eyres et al., 2017; Teitelbaum et al., 2018; Teitelbaum & Mueller, 2019). The role of resource tracking in shaping species geographical ranges might also explain the lack of direct correlation between species range size and diet breadth in our results. The diversity of habitats a species can occur in, and the resulting species distribution patterns, might be determined by the distribution of the particular resources needed and the species' ability to track them. Therefore, the development of realistic accounts for the resources available across a species' geographical range might be crucial for understanding larger scale distribution patterns of biodiversity.

Collectively, our results highlight the difficulty in synthesising empirical patterns concerning different levels of biological organisation. While we fully appreciate the complex interactions among individual- and species-level processes, we emphasise that specific biological mechanisms might only operate at particular biological (organisational and taxonomic), spatial and temporal scales. Our comparisons of range size at the individual and species level pointed to specialisation in different aspects of a species' ecological niche. We, thus, draw attention to an often-neglected challenge for transferring knowledge across scales, especially in inferring general patterns and processes of biodiversity from individual behaviours. For example, the use of individual-based models to identify key mechanisms of biodiversity dynamics has shown great promise in recent years (e.g. Grimm et al., 2017; Pachepsky et al., 2001). This approach will undoubtedly benefit from a better understanding of the extent to which the processes that shape biodiversity's responses to environmental changes are expressed at different levels of biological organisation, ranging from individuals and species to communities and ecosystems (Keil & Chase, 2019; Pos et al., 2019; van der Sande et al., 2019).

ACKNOWLEDGEMENTS

We thank the sELDiG working group, supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118) for initial discussion, and particularly L. Pellissier and F. Hartig for further feedback on the project. We also thank S. Edie and T. Price for discussion during the project as well as S. Fritz and T. Müller for comments on the manuscript. S.H. was supported by the Alexander von Humboldt Foundation (postdoctoral fellowship) and the German Science Foundation (DFG, HU 2748/1-1). M.A.T. was supported by a Radboud Excellence Initiative Fellowship. A.G.H. was supported by the European Union's Horizon 2020 research and innovation programme (Marie Skłodowska-Curie grant No 793077) and from the German-Israeli Foundation for Scientific Research and Development (I-1465-413.13/2018). A.E. was supported by DFG grants FR 3246/2-2 and GO1221/25-2. We thank the editor and two anonymous referees for their constructive feedback. Open Access funding enabled and organized by Projekt DEAL.

AUTHORSHIP

SH conceived the study. All authors contributed to the conceptual development and study design. JA provided guidance on the analytical strategy. MAT performed all the analyses on short-term individual movements, AGH performed all Bayesian regression analyses and SH performed all the other analyses. SH and MAT wrote the first draft of the manuscript and all authors contributed substantially to further development of the manuscript and revision.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13759.

DATA AVAILABILITY STATEMENT

All data used in the analyses are accessible from online databases that are publicly available, with references provided in Table 1. We have not generated any new data. The dataset combining all species-level variables, as well as the R code for conducting the main analyses, are archived on https://osf.io/f7hdq/.

ORCID

Shan Huang https://orcid.org/0000-0002-5055-1308
Marlee A. Tucker https://orcid.org/0000-0001-7535-3431
Anne G. Hertel https://orcid.org/0000-0001-7952-8243
Alison Eyres https://orcid.org/0000-0001-7866-7559
Jörg Albrecht https://orcid.org/0000-0002-9708-9413

REFERENCES

Alerstam, T. & Bäckman, J. (2018) Ecology of animal migration. *Current Biology*, 28, R968–R972.

Altizer, S., Bartel, R. & Han, B.A. (2011) Animal migration and infectious disease risk. *Science*, 331, 296–302.

Anderegg, L.D.L. & HilleRisLambers, J. (2019) Local range boundaries vs. large-scale trade-offs: climatic and competitive constraints on tree growth. *Ecology Letters*, 22, 787–796.

Barnes, A.D., Allen, K., Kreft, H., Corre, M.D., Jochum, M., Veldkamp, E. et al. (2017) Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. *Nature Ecology & Evolution*, 1, 1511–1519.

Benito Garzón, M., Robson, T.M. & Hampe, A. (2019) ΔTraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, 222, 1757–1765.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R. et al. (2007) The delayed rise of present-day mammals. *Nature*, 446, 507–512.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M. et al. (2019) The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339–345.

Böhm, M., Kemp, R., Williams, R., Davidson, A.D., Garcia, A., McMillan, K.M. et al. (2017) Rapoport's rule and determinants of species range size in snakes. *Diversity and Distributions*, 23, 1472–1481.

Bolnick, D., Svanbäck, R., Fordyce, J., Yang, L., Davis, J., Hulsey, C. et al. (2003) The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161, 1–28.

Bowler, D.E., Heldbjerg, H., Fox, A.D., de Jong, M. & Böhning-Gaese, K. (2019) Long-term declines of European insectivorous bird populations and potential causes. *Conservation Biology*, 33, 1120–1130.

Bowler, D.E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R. et al. (2017) Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution*, 1, 0067.

Bowman, J., Jaeger, J.A.G. & Fahrig, L. (2002) Dispersal distance of mammals is proportional to home range size. *Ecology*, 83, 2049–2055.

Briscoe, N.J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J.J., Camac, J.S., Giljohann, K.M. et al. (2019) Forecasting species range dynamics with process-explicit models: Matching methods to applications. *Ecology Letters*, 22, 1940–1956.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255–279.

Brown, J.S. (1999) Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, 1, 49–71.

Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: Consequences of an energetic definition of fitness. *American Naturalist*, 142, 573–584.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: The division of food and space among species on continents. *Science*, 243, 1145–1150.

Brun, P., Zimmermann, N.E., Graham, C.H., Lavergne, S., Pellissier, L., Münkemüller, T. et al. (2019) The productivity-biodiversity relationship varies across diversity dimensions. *Nature Communications*, 10, 5691.

Burgess, S.C., Baskett, M.L., Grosberg, R.K., Morgan, S.G. & Strathmann, R.R. (2016) When is dispersal for dispersal? Unifying marine and terrestrial perspectives. *Biological Reviews*, 91, 867–882.

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *2017*, 80, 28.

Bürkner, P.-C. (2018) Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, 10, 395–411.

Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J. & Purvis, A. (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B*, 275, 1441–1448.

Cardillo, M., Mace, G.M., Gittleman, J.L. & Purvis, A. (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 4157–4161.

Chardon, N.I., Pironon, S., Peterson, M.L. & Doak, D.F. (2020) Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. *Ecography*, 43, 60–73.

Collins, K.S., Edie, S.M., Hunt, G., Roy, K. & Jablonski, D. (2018) Extinction risk in extant marine species integrating palaeontological and biodistributional data. *Proceedings of the Royal Society B*, 285, 20181698.

Colwell, R.K. & Rangel, T.F. (2009) Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 19651–19658.

Comte, L. & Olden, J.D. (2018) Evidence for dispersal syndromes in freshwater fishes. *Proceedings of the Royal Society B*, 285, 20172214.

Costa, G.C., Vitt, L.J., Pianka, E.R., Mesquita, D.O. & Colli, G.R. (2008) Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecol. Biogeogr.*, 17, 670–677.

Dalsgaard, B.o., Schleuning, M., Maruyama, P.K., Dehling, D.M., Sonne, J., Vizentin-Bugoni, J. et al. (2017) Opposed latitudinal patterns of network-derived and dietary specialization in avian plant–frugivore interaction systems. *Ecography*, 40, 1395–1401.

De Meester, L., Vanoverbeke, J., Kilsdonk, L.J. & Urban, M.C. (2016) Evolving perspectives on monopolization and priority effects. *Trends in Ecology & Evolution*, 31, 136–146.

de Villemereuil, P. & Nakagawa, S. (2014) General quantitative genetic methods for comparative biology. In: Garamszegi, L.Z. (Ed.) *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. Berlin Heidelberg Berlin, Heidelberg: Springer, pp. 287–303.

Di Marco, M. & Santini, L. (2015) Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, 21, 2169–2178.

Dunne, J.A., Lafferty, K.D., Dobson, A.P., Hechinger, R.F., Kuris, A.M., Martinez, N.D. et al. (2013) Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biology*, 11, e1001579.

Edelaar, P. & Bolnick, D.I. (2019) Appreciating the multiple processes increasing individual or population fitness. *Trends in Ecology & Evolution*, 34, 435–446.

Elton, C.S. (1927) *Animal Ecology*. London: Sidgwick and Jackson.

Eyres, A., Böhning-Gaese, K. & Fritz, S.A. (2017) Quantification of climatic niches in birds: Adding the temporal dimension. *Journal of Avian Biology*, 48, 1517–1531.

Faurby, S., Davis, M., Pedersen, R.Ø., Schowanek, S.D., Antonelli, A. & Svenning, J.-C. (2018) PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology*, 99, 2626.

Fernández, M.H. & Vrba, E.S. (2005) Body size, biomic specialization and range size of African large mammals. *Journal of Biogeography*, 32, 1243–1256.

Finnegan, S., Anderson, S.C., Harnik, P.G., Simpson, C., Tittensor, D.P., Byrnes, J.E. et al. (2015) Paleontological baselines for evaluating extinction risk in the modern oceans. *Science*, 348, 567–570.

Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y., Butterill, P.T. et al. (2015) The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 442–447.

Frainer, A., McKie, B.G., Amundsen, P.-A., Knudsen, R. & Lafferty, K.D. (2018) Parasitism and the biodiversity-functioning relationship. *Trends in Ecology & Evolution*, 33, 260–268.

Freckleton, R.P., Cooper, N. & Jetz, W. (2011) Comparative methods as a statistical fix: The dangers of ignoring an evolutionary model. *American Naturalist*, 178, E10–E17.

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecology Letters*, 12, 538–549.

Fryxell, J.M., Hazell, M., Borger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M. et al. (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19114–19119.

Fukami, T. (2015) Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46, 1–23.

Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in darwin's finches. *Science*, 313, 224–226.

Grimm, V., Ayllón, D. & Railsback, S.F. (2017) Next-generation individual-based models integrate biodiversity and ecosystems: Yes we can, and yes we must. *Ecosystems*, 20, 229–236.

Grinnell, J. (1917) Field tests of theories concerning distributional control. *American Naturalist*, 51, 115–128.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T. et al. (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, 16, 1424–1435.

Hadfield, J.D. & Nakagawa, S. (2010) General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23, 494–508.

Harcourt, A.H., Coppeto, S.A. & Parks, S.A. (2002) Rarity, specialization and extinction in primates. *Journal of Biogeography*, 29, 445–456.

Hawkins, B.A. & Felizola Diniz-Filho, J.A. (2006) Beyond Rapoport's rule: Evaluating range size patterns of New World birds in a two-dimensional framework. *Global Ecology and Biogeography*, 15, 461–469.

Herkt, K.M.B., Skidmore, A.K. & Fahr, J. (2017) Macroecological conclusions based on IUCN expert maps: A call for caution. *Global Ecology and Biogeography*, 26, 930–941.

Hertel, A.G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J.E. et al. (2018) Berry production drives bottom–up effects on body mass and reproductive success in an omnivore. *Oikos*, 127, 197–207.

Holt, R.D. (2003) On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research*, 5, 159–178.

Housworth, E.A., Martins, E.P. & Lynch, M. (2004) The phylogenetic mixed model. *American Naturalist*, 163, 84–96.

Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13384–13389.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, 22, 415–427.

IUCN. (2020). The IUCN. Red List of Threatened Species. Version 2020-2. http://www.IUCN.redlist.org. ISSN 2307-8235. International Union for Conservation of Nature and Natural Resources.

Jablonski, D. (2000) Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology*, 26(sp4), 15–52.

Jablonski, D. (2007) Scale and hierarchy in macroevolution. *Palaeontology*, 50, 87–109.

Jacob, S., Laurent, E., Haegeman, B., Bertrand, R., Prunier, J.G., Legrand, D. et al. (2018) Habitat choice meets thermal specialization: Competition with specialists may drive suboptimal habitat preferences in generalists. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 11988–11993.

Jaenike, J. & Holt, R.D. (1991) Genetic variation for habitat preference: Evidence and explanations. *American Naturalist*, 137, S67–S90.

Jakobsson, A. & Eriksson, O. (2003) Trade-offs between dispersal and competitive ability: A comparative study of wind-dispersed Asteraceae forbs. *Evolutionary Ecology*, 17, 233–246.

Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science*, 306, 266–268.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, 297, 1548–1551.

Jocque, M., Field, R., Brendonck, L. & De Meester, L. (2010) Climatic control of dispersal–ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, 19, 244–252.

Johnson, T.F., Isaac, N.J.B., Paviolo, A. & González-Suárez, M. (2021) Handling missing values in trait data. *Global Ecology and Biogeography*, 30, 51–62.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L. et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090–184. *Ecology*, 90, 2648.

Kawecki, T.J. & Ebert, D. (2004) Conceptual issues in local adaptation. *Ecology Letters*, 7, 1225–1241.

Keil, P. & Chase, J.M. (2019) Global patterns and drivers of tree diversity integrated across a continuum of spatial grains. *Nature Ecology & Evolution*, 3, 390–399.

Kernaléguen, L., Arnould, J.P.Y., Guinet, C. & Cherel, Y. (2015) Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals. *Journal of Animal Ecology*, 84, 1081–1091.

Khaliq, I., Böhning-Gaese, K., Prinzinger, R., Pfenninger, M. & Hof, C. (2017) The influence of thermal tolerances on geographical ranges of endotherms. *Global Ecology and Biogeography*, 26, 650–668.

Khaliq, I., Hof, C., Prinzinger, R., Böhning-Gaese, K. & Pfenninger, M. (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20141097–https://doi.org/10.1098/rspb.2014.1097.

Kokko, H. & López-Sepulcre, A. (2006) From individual dispersal to species ranges: Perspectives for a changing world. *Science*, 313, 789–791.

Lagrue, C., Poulin, R. & Cohen, J.E. (2014) Parasitism alters three power laws of scaling in a metazoan community: Taylor's law, density-mass allometry, and variance-mass allometry. *Proceedings of the National Academy of Sciences of the United States of America*.

Laube, I., Graham, C.H. & Böhning-Gaese, K. (2015) Niche availability in space and time: migration in Sylvia warblers. *Journal of Biogeography*, 42, 1896–1906.

Leibold, M.A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology*, 76, 1371–1382.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J. et al. (2020) Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, 4, 1044–1059.

Levine, J.M. & HilleRisLambers, J. (2009) The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.

Lewandowski, D., Kurowicka, D. & Joe, H. (2009) Generating random correlation matrices based on vines and extended onion method. *Journal of Multivariate Analysis*, 100, 1989–2001.

Lindstedt, S.L., Miller, B.J. & Buskirk, S.W. (1986) Home range, time, and body size in mammals. *Ecology*, 67, 413–418.

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101, 377–385.

Maldonado, K., Newsome, S.D., Razeto-Barry, P., Ríos, J.M., Piriz, G. & Sabat, P. (2019) Individual diet specialisation in sparrows is driven by phenotypic plasticity in traits related to trade-offs in animal performance. *Ecology Letters*, 22, 128–137.

Martin, A.E. & Fahrig, L. (2018) Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. *Ecology*, 99, 2058–2066.

McElreath, R. (2020) *Statistical rethinking: A Bayesian course with examples in R and Stan*, 2nd edition. New York, USA: CRC Press.

McGill, B.J. (2010) Matters of scale. *Science*, 328, 575–576.

McLoughlin, P.D., Ferguson, S.H. & Messier, F. (2000) Intraspecific variation in home range overlap with habitat quality: A comparison among brown bear populations. *Evolutionary Ecology*, 14, 39–60.

McNab, B.K. (1963) Bioenergetics and the determination of home range size. *American Naturalist*, 97, 133–140.

Mimet, A., Buitenwerf, R., Sandel, B., Svenning, J.-C. & Normand, S. (2019) Recent global changes have decoupled species richness from specialization patterns in North American birds. *Global Ecology and Biogeography*, 28(11), 1621–1635.

Morris, D.W. (2003) Toward an ecological synthesis: A case for habitat selection. *Oecologia*, 136, 1–13.

Nurmi, T. & Parvinen, K. (2011) Joint evolution of specialization and dispersal in structured metapopulations. *Journal of Theoretical Biology*, 275, 78–92.

Ofstad, E.G., Herfindal, I., Solberg, E.J. & Sæther, B.-E. (2016) Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proceedings of the Royal Society B*, 283, 20161234.

Olalla-Tárraga, M.Á., Torres-Romero, E.J., Amado, T.F. & Martinez, P.A. (2015) Phylogenetic path analysis reveals the importance of niche-related biological traits on geographic range size in mammals. *Global Change Biology*, 21, 3194–3196.

Orme, D. (2012). The caper package: comparative analysis of phylogenetics and evolution in R.

Pachepsky, E., Crawford, J.W., Bown, J.L. & Squire, G. (2001) Towards a general theory of biodiversity. *Nature*, 410, 923–926.

Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M. et al. (2015) Assessing species vulnerability to climate change. *Nature Climate Change*, 5, 215–224.

Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A. et al. (2019) Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, 568(7750), 88–92.

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D.E., Isaia, M. et al. (2017) Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23, 2554–2564.

Pineda-Munoz, S., Wang, Y., Lyons, S.K., Tóth, A.B. & McGuire, J.L. (2021) Mammal species occupy different climates following the expansion of human impacts. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e1922859118.

Pos, E., Guevara, J.E., Molino, J.-F., Sabatier, D., Bánki, O.S., Pitman, N.C.A. et al. (2019) Scaling issues of neutral theory reveal violations of ecological equivalence for dominant Amazonian tree species. *Ecology Letters*, 22, 1072–1082.

Pyron, M. (1999) Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. *Journal of Biogeography*, 26, 549–558.

R Development Core Team (2020) *R: A language and environment for statistical computing*. Austria: R Foundation for Statistical Computing Vienna.

Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.

Riotte-Lambert, L. & Matthiopoulos, J. (2020) Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology & Evolution*, 35, 163–174.

Robinson, M.L. & Strauss, S.Y. (2020) Generalists are more specialized in low-resource habitats, increasing stability of ecological network structure. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 2043–2048.

Rosenzweig, M.L. (1991) Habitat selection and population interactions: The search for mechanism. *American Naturalist*, 137, S5–S28.

Sánchez-Tójar, A., Moran, N.P., O'Dea, R.E., Reinhold, K. & Nakagawa, S. (2020) Illustrating the importance of meta-analysing variances alongside means in ecology and evolution. *Journal of Evolutionary Biology*, 33, 1216–1223.

Sande, M.T., Gosling, W., Correa-Metrio, A., Prado-Junior, J., Poorter, L., Oliveira, R.S. et al. (2019) A 7000-year history of changing plant trait composition in an Amazonian landscape; the role of humans and climate. *Ecology Letters*, 22, 925–935.

Sanford, E. & Kelly, M.W. (2010) Local adaptation in marine invertebrates. *Annual Review of Marine Science*, 3, 509–535.

Santini, L., Isaac, N.J.B., Maiorano, L., Ficetola, G.F., Huijbregts, M.A.J., Carbone, C. et al. (2018) Global drivers of population density in terrestrial vertebrates. *Global Ecology and Biogeography*, 27, 968–979.

Saupe, E.E., Myers, C.E., Peterson, A.T., Soberón, J., Singarayer, J., Valdes, P. et al. (2019) Non-random latitudinal gradients in range size and niche breadth predicted by spatial patterns of climate. *Global Ecology and Biogeography*, 28(7), 928–942. https://doi.org/10.1111/geb.12904.

Schipper, J., Chanson, J.s., Chiozza, F., Cox, N.a., Hoffmann, M., Katariya, V. et al. (2008) The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science*, 322, 225–230.

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M. et al. (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, 22, 1925–1931.

Schleuning, M., Neuschulz, E.L., Albrecht, J., Bender, I.M.A., Bowler, D.E., Dehling, D.M. et al. (2020) Trait-based assessments of climate-change impacts on interacting species. *Trends in Ecology & Evolution*, 35, 319–328.

Sévêque, A., Gentle, L.K., López-Bao, J.V., Yarnell, R.W. & Uzal, A. (2020) Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, 95(6), 1689–1705.

Slatyer, R.A., Hirst, M. & Sexton, J.P. (2013) Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, 16, 1104–1114.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10, 1115–1123.

Sol, D., Timmermans, S. & Lefebvre, L. (2002) Behavioural flexibility and invasion success in birds. *Animal Behavior*, 63, 495–502.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: How so many species coexist in the tropics. *American Naturalist*, 133, 240–256.

Stevens, V.M., Whitmee, S., Le Galliard, J.-F., Clobert, J., Böhning-Gaese, K., Bonte, D. et al. (2014) A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters*, 17, 1039–1052.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D. et al. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101, 58–67.

Teitelbaum, C.S., Fagan, W.F., Fleming, C.H., Dressler, G., Calabrese, J.M., Leimgruber, P. et al. (2015) How far to go? Determinants of migration distance in land mammals. *Ecology Letters*, 18, 545–552.

Teitelbaum, C.S., Huang, S., Hall, R.J. & Altizer, S. (2018) Migratory behaviour predicts greater parasite diversity in ungulates. *Proceedings of the Royal Society B*, 285, 20180089.

Teitelbaum, C.S. & Mueller, T. (2019) Beyond migration: Causes and consequences of nomadic Animal movements. *Trends in Ecology & Evolution*, 34, 569–581.

Telfer, E.S. & Kelsall, J.P. (1984) Adaptation of some large North American mammals for survival in snow. *Ecology*, 65, 1828–1834.

Tingley, M.W., Wilkerson, R.L., Howell, C.A. & Siegel, R.B. (2016) An integrated occupancy and space-use model to predict abundance of imperfectly detected, territorial vertebrates. *Methods in Ecology and Evolution*, 7, 508–517.

Tomašových, A., Jablonski, D., Berke, S.K., Krug, A.Z. & Valentine, J.W. (2014) Nonlinear thermal gradients shape broad-scale patterns in geographic range size and can reverse Rapoport's rule. *Global Ecology and Biogeography*, 24, 157–167.

Tomašových, A., Kennedy, J.D., Betzner, T.J., Kuehnle, N.B., Edie, S., Kim, S. et al. (2016) Unifying latitudinal gradients in range size and richness across marine and terrestrial systems. *Proceedings of the Royal Society B: Biological Sciences*, 283(1830), 20153027–https://doi.org/10.1098/rspb.2015.3027.

Tuanmu, M.-N. & Jetz, W. (2015) A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 24, 1329–1339.

Tucker, M.A., Alexandrou, O., Bierregaard, R.O., Bildstein, K.L., Böhning-Gaese, K., Bracis, C. et al. (2019) Large birds travel farther in homogeneous environments. *Global Ecology and Biogeography*, 28, 576–587.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C. et al. (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359, 466–469.

Vasconcelos, P. & Rueffler, C. (2020) How does joint evolution of consumer traits affect resource specialization? *American Naturalist*, 195, 331–348.

Vehtari, A., Gelman, A. & Gabry, J. (2016) loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 1.0.0. https://github.com/stan-dev/loo.

Wake, D.B., Hadly, E.A. & Ackerly, D.D. (2009) Biogeography, changing climates, and niche evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 19631–19636.

Watanabe, S. (2010) Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, 11, 3571–3594.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122–126.

Whitmee, S. & Orme, C.D.L. (2013) Predicting dispersal distance in mammals: a trait-based approach. *Journal of Animal Ecology*, 82, 211–221.

Wickham, H. & Henry, L. (2019) tidyr: Easily tidy data with 'spread' and 'gather' functions. R package version 0.8.3. https://CRAN.R-project.org/package=tidyr.

Wiegand, T., Naves, J., Garbulsky, M.F. & Fernández, N. (2008) Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecological Monographs*, 78, 87–103.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

Wilson, D. & Reeder, D. (2005) *Mammal species of the world: A taxonomic and geographic reference*, 3rd edition. Baltimore, MD, USA: Johns Hopkins University Press.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Huang S, Tucker MA, Hertel AG, Eyres A, Albrecht J. Scale-dependent effects of niche specialisation: The disconnect between individual and species ranges. *Ecology Letters*. 2021;24:1408–1419. https://doi.org/10.1111/ele.13759