

## REVIEW AND SYNTHESIS

# Niche breadth predicts geographical range size: a general ecological pattern

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### Abstract

The range of resources that a species uses (i.e. its niche breadth) might determine the geographical area it can occupy, but consensus on whether a niche breadth–range size relationship generally exists among species has been slow to emerge. The validity of this hypothesis is a key question in ecology in that it proposes a mechanism for commonness and rarity, and if true, may help predict species' vulnerability to extinction. We identified 64 studies that measured niche breadth and range size, and we used a meta-analytic approach to test for the presence of a niche breadth–range size relationship. We found a significant positive relationship between range size and environmental tolerance breadth ( $\bar{r} = 0.49$ ), habitat breadth ( $\bar{r} = 0.45$ ), and diet breadth ( $\bar{r} = 0.28$ ). The overall positive effect persisted even when incorporating sampling effects. Despite significant variability in the strength of the relationship among studies, the general positive relationship suggests that specialist species might be disproportionately vulnerable to habitat loss and climate change due to synergistic effects of a narrow niche and small range size. An understanding of the ecological and evolutionary mechanisms that drive and cause deviations from this niche breadth–range size pattern is an important future research goal.

### Keywords

Extinction risk, geographical range, meta-analysis, niche breadth, rarity, specialisation.

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## INTRODUCTION

A species' niche breadth describes the suite of environments or resources, in the broadest sense, that it can inhabit or use (Gaston *et al.* 1997). Brown (1984) argued that, by utilising a greater array of resources and maintaining viable populations within a wider variety of conditions, a species should become more widespread – this would lead to a positive correlation between niche breadth and geographical range size. This intuitively appealing hypothesis has been discussed, debated and tested in numerous studies and books (e.g. Brown 1984; Gaston *et al.* 1997, 2000; Gaston & Blackburn 2000; Arribas *et al.* 2012; Boulangeat *et al.* 2012), yet a general consensus on the presence or magnitude of such a relationship has been slow to emerge. Nevertheless, the validity of this niche breadth–range size hypothesis is a key question in ecology in that it proposes a mechanism for commonness and rarity, and if true, may help predict species' vulnerability to extinction under rapid environmental change (Harcourt *et al.* 2002; Boyles & Storm 2007; Heim & Peters 2011).

The hypothesised niche breadth–range size relationship is one of several suggested mechanisms explaining commonness and rarity. For example, it has been invoked to explain the common observation that local abundance is positively correlated to geographical range size (Brown 1984; reviewed in Gaston & Blackburn 2000). It has also been applied to the evolution of resource utilisation. For example, Janz & Nylin (2008) suggested that diversification among

herbivorous insects is driven by alternating evolutionary periods of dietary generalisation (associated with range expansion) and specialisation (associated with local adaptation to new hosts).

Evolutionary mechanisms might also play a role in niche and range size determination. Among closely related species, variation in traits such as dispersal ability (e.g. Lester *et al.* 2007; Arribas *et al.* 2012), evolutionary age (e.g. Willis 1922; Webb & Gaston 2000) and niche position (the availability of resources within a species' niche) (Hanski 1993; Gregory & Gaston 2000) have been used to explain differences in geographical range size. Increased dispersal ability and time since species inception should increase the likelihood of filling available niche space, and thus attaining a larger range size. However, recent reviews have failed to find evidence of consistent relationships (Lester *et al.* 2007) between the above factors and range size or have shown that predicted associations can arise purely through stochastic range size evolution (Pigot *et al.* 2012). For instance, if range size evolves randomly and if species with small ranges are more likely to go extinct, then a positive association between species age and range size could result because of loss of the small-ranged species, rather than because range size increases with species age (Pigot *et al.* 2012). Thus, variation in range size among species might be more strongly mediated by other factors such as niche characteristics (Laube *et al.* 2013).

In a comprehensive study on British birds, Gregory & Gaston (2000) found that niche position was closely associated with geo-

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graphic range size. This supported earlier, more anecdotal reports, that widespread species were those that utilised widespread resources (reviewed in Gaston & Blackburn 2000), and Pither (2003) showed that tolerance of cold extremes (rather than the range of temperatures tolerated) was the most important factor determining the geographical ranges of trees and shrubs in North America. Yet, the niche breadth and niche position hypotheses for range size are not mutually exclusive; e.g. a species with a broader niche might be more likely to have widespread resources included within that niche.

Studies that have looked for evidence for a niche breadth–range size relationship have been limited by problems of sampling bias, spatial extent and niche definitions, making it difficult to discern the evidence for or against its generality. If, e.g. resource use is determined for more individuals or at more locations for common and widespread species than for scarce and restricted species, then apparent niche breadth is likely to be greater in the former simply by chance (i.e. sampling effects; Burgman 1989). A positive relationship would therefore come about purely as a sampling artefact. The mechanisms determining range size might also vary with spatial scale. For example, Brändle *et al.* (2002a) found that as the spatial scale increased, the importance of dietary niche breadth in predicting range size decreased, while physiological tolerance became more important. Specialisation itself is also highly scale dependent, such that a local specialist might be a generalist at a regional scale and *vice versa* (Gaston *et al.* 1997; Hughes 2000).

Finally, accurate niche measures (whether breadth or position) are obscured by the n-dimensional nature of the Hutchinsonian niche (Hutchinson 1957; Colwell & Futuyma 1971). Niche breadth can be measured in many ways (see Table S1 in Supporting Information) and niche breadths along different axes are not necessarily correlated (e.g. Berkström *et al.* 2012); so, the presence or absence of a statistical relationship between niche breadth and range size might be dependent on the niche axis measured (Harcourt *et al.* 2002). Inevitably, if enough niche axes are measured, some will be found that correlate positively with range size and others will be found that do not. In the absence of a clear rationale for choosing one component of the niche over another, most studies measure multiple niche axes. Habitat use, diet and environmental tolerance (here considered a niche component and typically defined as thermal limits in animals and germination traits in plants) are the most frequently measured niche subsets. Despite these difficulties, a strong, positive relationship between niche breadth and range size among multiple, independent systems would provide general support for the niche breadth–range size hypothesis.

A lack of strong empirical evidence and studies that appropriately controlled for sampling effects led Gaston & Blackburn (2000) to conclude that there was little support for a general, positive relationship between niche breadth and range size. In the decade since their review, many more studies have investigated this relationship and a large proportion of these made efforts to account for the aforementioned confounding effects. Here, we use a meta-analytic framework to test the relationship between niche breadth and range size. We consider three broad niche dimensions – habitat, diet and environmental tolerance – and test for differences in strength of the relationship between taxonomic groups and the spatial scale being considered. We find a consistent positive relationship between niche breadth and range size, which is strongest for environmental tolerance breadth. This relationship is present across all taxonomic

groups examined and at different spatial scales and even holds when only studies that control for sampling effects are included.

## METHODS

### Data compilation

We used four approaches to compile our data set. First, we searched the literature using the ISI Web of Science database, with the search terms [niche breadth or niche width or tolerance breadth or diet breadth or habitat breadth or resource breadth] and [range size or geographical × range] in October 2012. Second, we identified original papers outlining commonly used metrics for niche breadth (Pielou 1974; Hurlbert 1978; Feinsinger *et al.* 1981; ter Braak 1986; Dolédec *et al.* 2000; Fridley *et al.* 2007; Warren *et al.* 2008) and used Web of Science to retrieve all publications citing each of these. Third, we identified two recent reviews of niche breadth (specifically thermal tolerance breadth) and geographical range (Bozinovic *et al.* 2011; Sunday *et al.* 2011) and scanned their reference list to locate additional, potentially relevant, papers. Finally, after identifying relevant studies (see Inclusion criteria) by the first three methods, we retrieved the publications cited in each of these. Combined, these yielded a total of 2670 unique references. To reduce the risk of sampling bias, we did not include papers that were encountered by chance outside the search parameters. The titles and abstracts of all references were scanned and those that were clearly outside the scope of this meta-analysis were discarded, leaving a total of 180 references.

### Inclusion criteria

We had three inclusion criteria: (1) does the study measure both niche breadth and range size? (2) Does the study use four or more species (see below)? (3) Does the study include extractable data? For Criterion 1, studies that reported niche breadth and/or range size as a categorical variable (e.g. wide vs. narrow niche; large vs. small range size) were included, in addition to those using other metrics for niche breadth and range size. We classified niche measures into three broad categories: habitat, diet and environmental tolerance. Range size measurements were divided into two categories, defined by whether estimates covered the entire geographical distribution of the species ('comprehensive') or only part of its distribution ('partial'). Where a study measured range size at both scales, we excluded the partial measure so that each study had only one effect size per niche breadth measure. We chose to do this because we were primarily interested in the relationship between niche breadth and geographical range size, although we were able to test the niche breadth–range size hypothesis for both categories. For criterion 2,  $n \geq 4$  is required for calculations of the effect size variance ( $v_s$ ) (Borenstein *et al.* 2009). Criterion 3 meant that we sometimes excluded studies that measured both niche breadth and range size but where it was not possible to calculate the effect size. Exclusion was usually due to ambiguous information about the direction of the effect or data that were not reported in such a way that effect sizes could be extracted (see Table S2 in Supporting Information). Meta-analytic models assume statistical independence of effect sizes, and inclusion of multiple studies covering the same species would violate this assumption. If two or more studies covered the same species group, we included data from the study with

the higher number of species. Two studies (Brändle *et al.* 2003; Thompson & Ceriani 2003) measured the temporal germination niche breadth, which cannot readily be assigned to one of the three niche categories we examined. These studies were consequently excluded from the analysis, but the results are included in Table S2.

### Meta-analysis statistical methods

The common effect size we calculated was Fisher's  $\bar{z}$ , which is the standard effect size measure used for correlational data (Borenstein *et al.* 2009). We preferentially calculated  $\bar{z}$  using the correlation coefficient  $r$ , extracted from summary tables, the text or figures (using *Image J v. 1.46r*; Schneider *et al.* 2012). When this approach was not possible, we converted test statistics ( $t$ ,  $F$ ) or  $P$ -values (Borenstein 2009). We then calculated the variance using the number of species as the sample size.

If there was more than one effect size per niche category (diet, habitat or tolerance) within a study, we calculated the study mean and its associated variance by following a hierarchical approach to combining data (see Slatyer *et al.* 2012). First, we calculated the mean effect if the same individuals contributed two or more effects to the same response (e.g. niche breadth calculated using two different indices). Second, if there was still more than one effect size per niche category (e.g. the study was carried out in multiple regions, with some species overlap), we calculated the weighted mean for the study for that category, using a standard fixed-effects model. For both steps, the variance of the mean of  $m$  effects (denoted  $X_i$  or  $X_j$ ) each with a variance of  $V_i$  or  $V_j$  and  $r_{ij}$  representing the correlation between  $X_i$  and  $X_j$  is:

$$V_{mean} = \left( \sum_{i=1}^m m_i V_i + 2 \sum_{i,j} (r_{ij} \sqrt{V_i} \sqrt{V_j}) \right) / m^2$$

(modified from Borenstein *et al.* 2009, p. 228).

When the variance differed between effect size estimates, we multiplied each  $V_i$  in the first sum by  $(W_i/W_{mean})$  and each term in the second sum by  $(W_i \times W_j)/(W_i \times W_j)_{mean}$ , where  $W_i \times = 1/V_i$  and  $W_{mean} = (\sum W_i)/m$  (see Slatyer *et al.* 2012).  $r_{ij}$  was either provided in the publication or calculated as the proportion of species shared between data sets.

Finally, we ran separate random-effects models in the R package *Metafor* (Viechtbauer 2010), using study-level effects for each niche category (i.e. the effect sizes calculated after combining data if required, as described above). The null hypothesis for each analysis was that the mean effect size was zero and effect sizes were always calculated such that a positive value indicated that species with a broader niche occupied a larger geographical range. Heterogeneity was estimated using the  $I^2$  statistic (Higgins & Thompson 2002; Higgins *et al.* 2003), which is less sensitive to study number than the commonly quoted Cochran's  $Q$  (Borenstein *et al.* 2009). To examine the influence of the scale of range measurement and taxonomic grouping on the relationship, we ran separate mixed-effects models for each niche category using the effect size as the response variable and scale of range measurement (comprehensive vs. partial) and taxonomic group as explanatory factors. Finally, we used a mixed-effects model to test whether control of sampling effects influenced mean effect size by including sampling design (with or without some control for sampling effects) as an explanatory factor. We classified a study as having controlled for sampling effects if they (1) used equal sampling to measure niche breadth

for each species, (2) used a well-studied set of species for which sampling bias has been determined to not be influential (e.g. Cowley *et al.* 2001) or (3) statistically adjusted for potential sampling bias.

### Publication bias

Several methods are commonly used to test for publication bias and its potential impact on the results of the meta-analysis and we employed three methods. First, we tested for funnel plot asymmetry using a weighted regression and standard error as the predictor (Egger *et al.* 1997; Rothstein *et al.* 2005). A funnel plot, with study effect size on the  $x$ -axis and sample size (or standard error) on the  $y$ -axis, will tend to have a cluster of large studies around the mean effect, whereas smaller studies are spread across the base of the graph (Borenstein 2009). If there is no publication bias, studies are expected to be distributed symmetrically around the mean effect size. Asymmetry in the funnel plot is therefore an indicator of publication bias and most commonly involves the absence of studies from the lower left of the graph – i.e. small studies with non-significant or negative effect (Borenstein 2009).

Our second approach was to use a 'trim and fill' method, which suppresses the most extreme positive studies to generate a symmetrical funnel plot and re-calculates the effect size without these studies (Duval & Tweedie 2000a,b). The method also provides an estimate of the number of hypothetically 'missing' studies, based on asymmetry in the funnel plot (Duval & Tweedie 2000a,b). This method therefore estimates what impact potential publication bias might have on the results of the analysis.

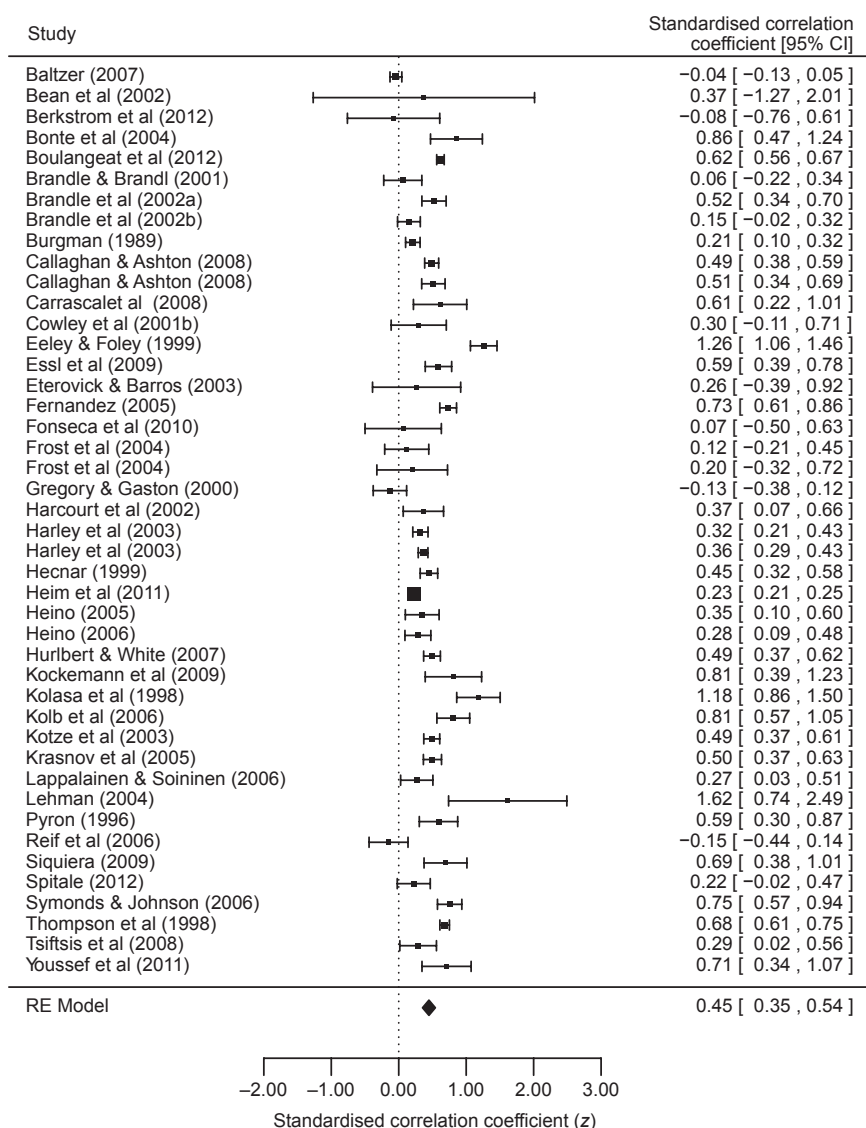
Finally, we examined how robust our results are to the effects of publication bias using Rosenberg's fail-safe number. This is the number of new studies with a mean effect size of zero necessary to reduce the observed significance level to  $\alpha = 0.05$  (Rosenberg 2005). Fail-safe numbers are often considered robust if they are greater than  $5n + 10$ , where  $n$  is the original number of studies (Rosenthal 1991). That is, when the fail-safe number is large relative to the number of studies, publication bias (if it exists) is unlikely to alter the conclusions of the analysis (Rosenberg 2005).

## RESULTS

### Random-effects meta-analysis

We extracted 75 effect sizes from 64 studies that met our inclusion criteria (see Table S3 in Supporting Information). Of these studies, 36 controlled for sampling bias or provided data to support the argument that their study was free from sampling bias. Studies covered animals ( $n = 45$ ), plants ( $n = 17$ ), algae ( $n = 2$ ) and diatoms ( $n = 1$ ). Habitat breadth was the most common measure of niche breadth ( $n = 44$  studies; Fig. 1) followed by diet breadth ( $n = 20$ ; Fig. 2) and environmental tolerance range ( $n = 11$ ; Fig. 3) and several studies used two or more measures.

The mean effect size, 95% confidence intervals and results of tests for heterogeneity are given in Table 1. There was a significant positive relationship between niche breadth and geographical range size when niche breadth was measured as either habitat breadth ( $\bar{z} = 0.448$ ; Fig. 1) or environmental tolerance range ( $\bar{z} = 0.491$ ; Fig. 3). There was also a clear, but weaker, trend for a positive relationship between diet breadth and geographical range size



**Figure 1** Effect sizes and confidence intervals for studies measuring the relationship between habitat breadth and range size, and results of the random-effects meta-analysis (RE model) showing the mean effect size.

( $\bar{z} = 0.281$ ; Fig. 2). There was high variability in effect sizes between studies, with 83% (diet) to 95% (habitat) of the total variation in estimated effect sizes due to heterogeneity between studies.

### Mixed-effects meta-analysis: test of explanatory factors

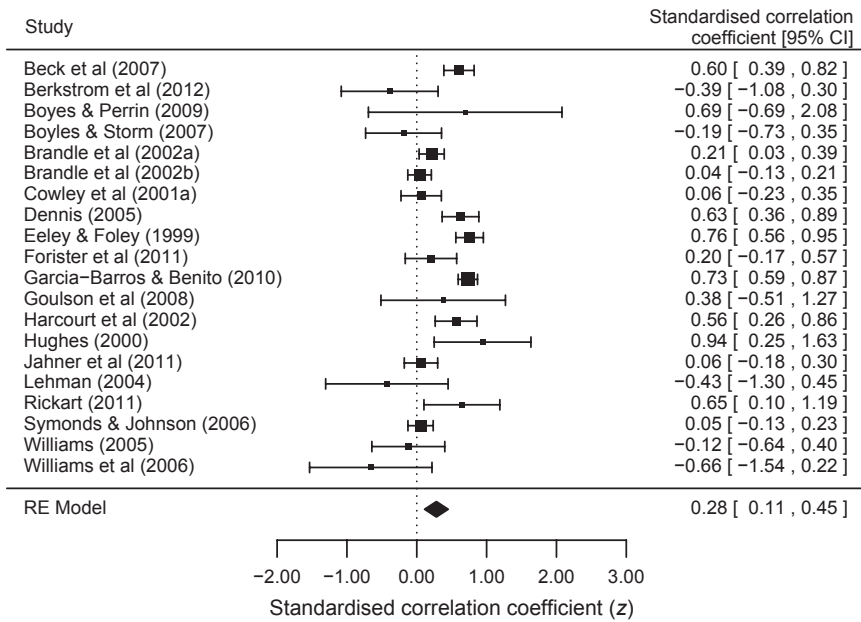
We used two mixed-effects models to examine the influence of taxonomic group and measurement scale, respectively. Results from these analyses are shown in Tables 2 (taxonomic group) and 3 (measurement scale). Neither explanatory factor had a statistically significant impact on the mean effect size, or accounted for a substantial amount of heterogeneity among studies (Tables 2 and 3). Nevertheless, dietary breadth was significantly correlated with range size only in arthropods and the association between tolerance breadth and range size was marginally non-significant in studies on animals (Table 2). Sample size was small ( $n = 5$ ) for the latter, however, and the effect size ( $\bar{z} = 0.489$ ) indicates a moderate to strong relationship.

Studies that controlled for sampling effects had lower average effect sizes than those that did not, although this difference was not statistically significant (Table 4). Whereas studies that did not control for sampling effects always had significant mean effects within each niche breadth measure (Table 4), of the controlled studies, only the habitat breadth–range size relationship had a mean effect significantly greater than zero. Although always positive, the mean effect size of studies that controlled for sampling effects was not statistically greater than zero when niche breadth was measured as diet ( $\bar{z} = 0.188$ ,  $P = 0.125$ ,  $n = 10$ ) or environmental tolerance ( $\bar{z} = 0.299$ ,  $P = 0.570$ ,  $n = 6$ ).

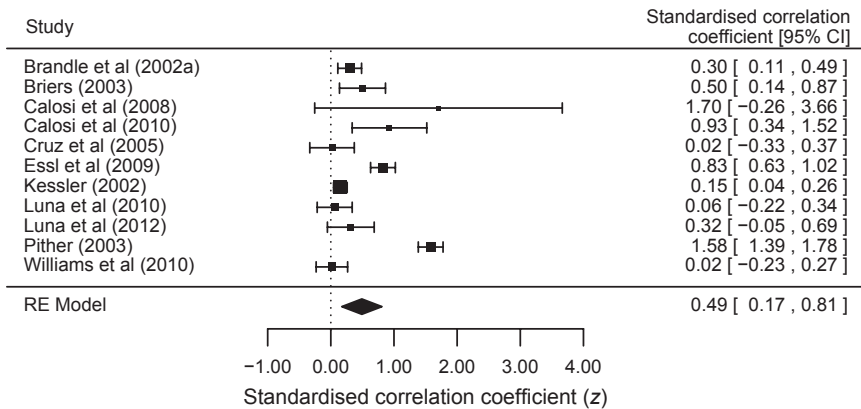
### Publication bias

We did not find evidence for publication bias through regression tests for funnel plot asymmetry (see Fig. S1 for funnel plots) or the trim-and-fill analysis (Table 5). For the latter, there were no putatively missing studies for any niche breadth measure, and ‘corrected’





**Figure 2** Effect sizes and confidence intervals for studies measuring the relationship between diet breadth and range size, and results of the random-effects meta-analysis (RE model) showing the mean effect size.



**Figure 3** Effect sizes and confidence intervals for studies measuring the relationship between environmental tolerance breadth and range size, and results of the random-effects meta-analysis (RE model) showing the mean effect size.

**Table 1** Summary statistics from random-effects meta-analyses. *n* is the number of studies,  $Q_T$  is total heterogeneity and  $I^2$  is the amount of total heterogeneity attributable to differences among studies

Niche breadth	<i>N</i>	Mean effect ( $\bar{z}$ )	95% CI	<i>P</i>	Heterogeneity	
					$Q_T$ ( <i>P</i> )	$I^2$ (95% CI)
Habitat	44	0.448	0.353, 0.543	<0.001	667.681 (<0.001)	95.386% (92.899, 97.563)
Diet	20	0.281	0.110, 0.450	0.001	115.911 (<0.001)	83.482% (68.598, 94.234)
Tolerance	11	0.491	0.173, 0.810	0.003	203.411 (<0.001)	94.313% (87.445, 98.396)

effect sizes (calculated after suppressing extreme positive studies) were identical to those from the initial random-effects model. For all random-effects models, the fail-safe number was high ( $> 5n + 10$ ) relative to the number of studies in the analysis (Table 5), indicating that publication bias (if present) is unlikely to alter the conclusions of the analysis.

**DISCUSSION**

Brown (1984) suggested that species able to utilise a wider range of resources should be able to occupy a larger geographical area, leading to a positive relationship between niche breadth and range size. Yet, due to issues of sampling bias, methods of measuring niche

**Table 2** Results of a mixed-effects meta-analysis examining the influence of taxonomic group on the relationship between niche breadth and range size.  $Q_M$  and the associated  $P$ -value provide a test for the effect of taxonomic group on the mean effect size, while  $Q_E$  provides a test of residual heterogeneity, estimated by  $\tau^2$ . Results are only shown for taxonomic groups examined by more than one study

Taxonomic group	$N$	Mean effect ( $\bar{z}$ )	95% CI	$P$	$Q_M (P)$	$Q_E (P)$	$\tau^2$ (95% CI)
Habitat					1.692 (0.946)	449.133 (<0.001)	0.097 (0.058, 0.188)
Chordata	18	0.419	0.250, 0.589	<0.001			
Spermatopsida	9	0.503	0.284, 0.721	<0.001			
Arthropoda	8	0.478	0.240, 0.716	<0.001			
Bryophyta	3	0.414	0.044, 0.784	0.006			
Mollusca	2	0.276	-0.219, 0.770	0.275			
Diet					1.107 (0.293)	106.241 (<0.001)	0.106 (0.043, 0.324)
Arthropoda	10	0.363	0.130, 0.596	0.002			
Chordata	10	0.176	-0.082, 0.435	0.182			
Tolerance					0.001 (0.981)	201.289 (<0.001)	0.276 (0.112, 1.113)
Plants	6	0.497	0.065, 0.923	0.024			
Animals	5	0.489	-0.045, 1.022	0.073			

**Table 3** Results of a mixed-effects meta-analysis examining the effect of the spatial extent of measurement (across entire species range – 'Comprehensive'; across some of range – 'Partial') on the relationship between niche breadth and range size.  $Q_M$  and the associated  $P$ -value provide a test for the effect of spatial scale on the mean effect size, while  $Q_E$  provides a test of residual heterogeneity, estimated by  $\tau^2$

Scale	$n$ (studies)	Mean effect ( $\bar{z}$ )	95% CI	$P$	$Q_M (P)$	$Q_E (P)$	$\tau^2$ (95% CI)
Habitat					1.404 (0.236)	542.371 (< 0.001)	0.081 (0.051, 0.158)
Comprehensive	24	0.497	0.372, 0.621	<0.001			
Partial	20	0.381	0.235, 0.526	<0.001			
Diet					1.295 (0.255)	80.869 (< 0.001)	0.094 (0.039, 0.340)
Comprehensive	16	0.234	0.048, 0.419	0.014			
Partial	4	0.471	0.107, 0.835	0.011			

**Table 4** Comparison of effect sizes between studies that do and do not provide some control for sampling effects.  $Q_M$  and the associated  $P$ -value provide a test for the effect of sampling control on the mean effect size (i.e. whether effect sizes differ between the two types of study)

	$n$ (studies)	Mean effect ( $\bar{z}$ )	95% CI	$P$	$Q_M (P)$
All					0.449 (0.503)
With control	41	0.380	0.251, 0.508	<0.001	
Without control	34	0.502	0.378, 0.626	<0.001	
Habitat					1.090 (0.297)
With control	25	0.405	0.282, 0.529	<0.001	
Without control	19	0.508	0.361, 0.655	<0.001	
Diet					1.076 (0.300)
With control	10	0.188	-0.052, 0.428	0.125	
Without control	10	0.410	0.175, 0.645	<0.001	
Tolerance					0.149 (0.699)
With control	6	0.299	-0.775, 1.372	0.586	
Without control	5	0.617	0.133, 1.101	0.013	

breadth and spatial scale, it has taken nearly three decades to verify that this pattern exists generally. Here, we have shown a consistent relationship between niche breadth and range size, which is independent of broad taxonomic grouping and the scale of range measurement. That we found a highly significant mean effect suggests that the relationship between niche breadth and range size is a

general ecological pattern. However, what drives this pattern, and why certain species deviate from it, is in need of further exploration.

The strongest relationship was found when the niche axis examined related to environmental tolerance, suggesting that tolerance of a wide range of abiotic conditions facilitates occupancy of a larger area. Habitat breadth, the most commonly measured metric, was also a good predictor of range size, whereas the weakest relationship (marginally non-significant) was found for diet breadth. The average effect size we estimated for habitat breadth ( $\bar{z} = 0.45$ ) is remarkably similar to that found in a recent study using path analysis to test drivers of range size variation in passerine birds ( $\bar{z} = 0.43$ ) (Laube *et al.* 2013). That study also found that diet breadth had a negligible correlation with range size ( $\bar{z} = -0.06$ ), in broad agreement with our findings here.

In their comprehensive review, Gaston & Blackburn (2000) suggested that niche position is more important than niche breadth in determining range size. Under this hypothesis, widespread species are those that utilise the most common and widespread resources (Hanski 1993). Of the nine studies included in our analysis that reported relationships between niche position and range size, seven found that range size was more strongly related to niche position than niche breadth. In contrast, Passy (2012) tested modelled predictions of the relationship between niche breadth and range size using fish and microorganisms and found that adaptation to common environments was insufficient to confer a large geographical range in the absence of a broad niche. There is clearly a need for additional studies that simultaneously compare the strengths of the effects of niche breadth and position on range size and a systematic synthesis of current evidence for the niche position hypothesis.

**Table 5** Tests for publication bias for study-level analysis. Meta-analysis results are often considered robust if fail-safe numbers are greater than  $5n + 10$ , where  $n$  is the original number of studies (Rosenthal 1991)

Niche breadth	$n$ (studies)	$\bar{\tau}_{\text{bias}}$ ( $P$ )	Trim-and-fill		Rosenberg's Fail-safe $N$ ( $5n + 10$ )
			$L$	Corrected $\bar{\tau}$ (95% CI)	
Habitat	44	0.366 (0.715)	0	0.448 (0.353, 0.543)	19 391 (230)
Diet	20	-1.335 (0.182)	0	0.281 (0.111, 0.450)	549 (110)
Tolerance	11	1.054 (0.292)	0	0.491 (0.173, 0.810)	574 (65)

### Sampling and scale effects

A common criticism of the niche breadth–range size hypothesis is that sampling effects might produce a false positive correlation when niche breadth in widespread species is measured from more individuals or more locations (Brown 1984; Hanski 1993; Gaston *et al.* 1997). Burgman (1989) demonstrated the potential strength of this effect using two measures of niche breadth: one that did not control for sampling effects and one that used statistical methods to negate any potential influence of sampling frequency. While the former gave a significant positive relationship between niche breadth and range size, there was no significant correlation when sampling effects were controlled. Similarly, Kolb *et al.* (2006) found that a positive niche breadth–range size relationship disappeared after controlling for differences in sample size between widespread and restricted species.

Over the last decade, an increasing number of studies have taken steps to explicitly control for sampling effects (e.g. Boulangeat *et al.* 2012; Luna *et al.* 2012). In our analysis, there was no statistical difference in the average effect size for studies that did and did not control for sampling effects, although the latter tended to show a stronger relationship. When examined separately, the niche breadth–range size relationship did, however, lose statistical significance among controlled diet and tolerance studies. For tolerance breadth at least, the effect size remained moderate ( $\bar{\tau} = 0.3$ ) and loss of statistical significance might be due to reduced sample size – additional studies are required before we can confidently attribute the initially observed relationship entirely to sampling effects. It does, however, once again highlight the need to control for sampling effects through study design (e.g. Calosi *et al.* 2008) or statistical adjustment (e.g. Burgman 1989). In contrast, when all niche measures were analysed together, or when habitat breadth was considered, the niche breadth–range size relationship remained strongly significant for studies that controlled for sampling effects; habitat breadth had the largest number of studies ( $n = 25$ ) among different niche measures. Thus, the observed general niche breadth–range size relationship cannot be explained as a sampling artefact.

The strength of the relationship between niche breadth and range size varied widely among studies. This is not entirely surprising, given the taxonomic diversity (diatoms, algae, plants and animals) included in the data set, as well as the many different niche breadth indices (Table S1) and methods of measuring range size used by the studies. Although we found no statistical differences in the strength of the niche breadth–range size relationship across taxonomic groups, sample sizes for each group were small (only habitat breadth in chordates was measured in more than 10 studies) and we were unable to analyse taxonomic variation below the current

taxonomic levels. Intrinsic differences among taxonomic groups might be expected to contribute to variation in the niche breadth–range size pattern, if, e.g. the relationship is influenced by phylogenetically conserved traits (reviewed in Wiens *et al.* 2010). However, traits such as dispersal ability, which might influence the relationship, can evolve rapidly, even within a species (e.g. Phillips *et al.* 2006), potentially rendering broad taxonomic groupings of little use in explaining among-study heterogeneity. An investigation of the niche breadth–range size hypothesis in a phylogenetic framework, incorporating relevant life-history traits, would shed much-needed light on this issue.

The high diversity in niche breadth and range size measures resulted in substantial variation in both the grain (resolution) and extent (area encompassed) of spatial scale (Wiens 1989) used across studies that might have contributed to the high heterogeneity. For example, studies that measure dietary breadth using coarse categories such as insects and plants (e.g. Brändle *et al.* 2002b) might be less likely to find a positive relationship with range size than one that measures resource use at a finer grain (Shkedy & Safrieli 1992).

When considering differences in effect size among different niche axes, grain might also be important: in general, diet is necessarily measured at a finer spatial grain than habitat use. That is, an individual or species can typically access multiple food resources (e.g. different species of plants) within a single habitat type (e.g. forest). Environmental tolerance could be considered a coarser grain, as multiple habitat types (e.g. forest, grassland, heath) are often present within a given climatic zone. Considered in this way, our findings reflect a stronger niche breadth–range size relationship for coarser-grained niche breadth categories. If true, there could be a lower limit of spatial scale at which the relationship between niche breadth and range size no longer holds true.

Several authors (e.g. Cowley *et al.* 2001; Brändle *et al.* 2002b; Baltzer *et al.* 2007) have suggested that the strength or presence of a relationship between niche breadth and range size will be scale-dependent, with different processes determining geographical ranges as the spatial extent of the investigation changes. In contrast, other studies have found significant correlations between spatial scales (e.g. Briers 2003; Callaghan & Ashton 2008). We did not find any evidence for differences in the niche breadth–range size relationship between studies conducted at a local or regional scale and those that encompassed species' entire geographical ranges, suggesting that niche breadth–range size relationships are not limited to a single spatial scale. The most appropriate scale (in terms of either grain or extent) is not immediately clear. It is therefore important that future studies explicitly define the scale that they are using so that scale-dependency, if present, can be detected in the future.

## Evolutionary and historical effects

It is straightforward to understand a link between a species' niche breadth across its entire range and its range size. It would almost be surprising if such a pattern did not exist. What is less intuitive is whether factors influencing local population dynamics in a single habitat are also relevant for determining global distribution patterns. This is the question being asked when niche breadth is measured from populations or individuals and is at the heart of the niche breadth–range size hypothesis.

Species inhabit environmental (or ecological) space through adaptive differentiation among individuals, phenotypic plasticity within individuals, or both (Ackerly 2003). It is therefore difficult to disentangle whether niche breadth is maintained through an aggregate process of microevolution to multiple environments or broad tolerance (Ackerly 2003). If the former, species having larger niche breadths may be comprised of many locally adapted populations (e.g. Olsson *et al.* 2009), posing a greater risk of local extinction under climate change (Atkins & Travis 2010; Kelly *et al.* 2012). Alternatively, large-niche species may be comprised of individual 'generalists', having great environmental tolerance, in which case one would expect lower vulnerability. Of course, a continuum between the above scenarios likely exists, but is one pattern more prevalent than the other? Adaptive differentiation can also evolve quickly and this has been commonly observed during the process of invasion, allowing widespread species to extend their ranges even further (e.g. Phillips *et al.* 2006).

None of the studies we examined sought to disentangle these microevolutionary effects on niche breadth. Although some previous research has explored the underpinnings of niche breadth (e.g. Atkins & Travis 2010; Bolnick *et al.* 2010), further experiments that establish whether niche breadth is more strongly influenced by among-individual variation vs. within-individual performance (and equally, among-population vs. within-population variation) are sorely needed. Classification of specialists and generalists can depend on whether resource use is measured at the species, population or individual level (Roughgarden 1972). Thus, a species might be a local specialist but a regional generalist if it is comprised of locally adapted populations (Hughes 2000). In such a scenario, measuring niche breadth as the average population niche breadth, compared to the species niche breadth, will produce dramatically different results. Similarly, a generalist population can be composed of either specialist or generalist individuals with high among- and within-individual variation respectively (Roughgarden 1972; Bolnick *et al.* 2010). To date, such research has rarely been applied in the context of large-scale ecological patterns (but see Angert *et al.* 2011b) and consequently, the strength of the influence of adaptive differentiation on these patterns is unclear.

Evolutionary processes as discussed above can obscure the direction of causality in the niche breadth–range size relationship. The results presented here are unable to address the causal mechanisms driving the observed relationship. Although a broad niche is often assumed to allow expansion into a larger geographical area this direction of causality is not a given. If, e.g. species-level niche breadth is maintained through genetic variation in environmental tolerance (i.e. local adaptation), geographical range expansion (accompanied by spatially varying selection) might drive an increase in niche breadth. Similarly, recent work suggests that among butterflies, diet breadth might be influenced by range size, with widely dispersing species encountering a greater range of host plants and

thus evolving to utilise a greater variety of species, including exotic species (Jahner *et al.* 2011). Feedback mechanisms might also operate, making causality bi-directional with underlying genetic variation and dispersal capability allowing initial colonisation of new areas, where evolutionary processes promote differentiation and niche expansion. However, until there is research that can determine to what extent the relationship is driven by within vs. among-population variation, it will be impossible to identify the causal links between local niche breadth and geographical range size. With rapid, modern climate change, whether niche breadth is determined primarily through adaptive differentiation or phenotypic plasticity may produce very different outcomes for species' distributional responses.

Evolutionary effects might also be important if individual-based performance under varying conditions is predictable from close relatives. Phylogenetic conservatism – the tendency for closely related species to have more similar traits (e.g. ecological niche) than distantly related species – is a common observation in ecology (Wiens 2004). When testing ecological patterns, it is therefore important to take relatedness into account to be sure that observed patterns are not merely a phylogenetic artefact (Cooper *et al.* 2010). Although phylogenetic signal in various niche-based traits has been detected (reviewed in Losos 2008), we know of very few studies that have specifically tested for phylogenetic conservatism in niche breadth *per se* (but see Brändle *et al.* 2002b; Emery *et al.* 2012). Thirteen studies in our analysis used phylogenetically independent contrasts to control for potential effects of phylogenetic relatedness. None found a substantial difference in the magnitude of the niche breadth–range size relationship with and without independent contrasts, and two (Gregory & Gaston 2000; Thompson & Ceriani 2003) found that the strength of the relationship actually increased after controlling for phylogenetic effects. Nevertheless, the above studies are based mainly on descriptive estimates of niche breadth (but see Luna & Moreno 2010; Luna *et al.* 2012). There is a strong need for studies that experimentally compare niche breadth (e.g. environmental tolerance) among close relatives, especially to understand whether rarer relatives actually lack the physiological capacity or genetic variation to tolerate rapidly changing environments. Current evidence suggests that this is the case (e.g. Kellermann *et al.* 2009).

Previous studies have not detected (or only detected weak) phylogenetic signal for range size – sister taxa often have dissimilar range sizes (reviewed in Waldron 2007). Indeed, there are many well-known examples where closely related species vary greatly in their geographical range extent (e.g. the widespread common dandelion (*Taraxacum officinale*) has a congener (*Taraxacum pankhurstianum*) restricted to a single Scottish island; Richards & Ferguson-Smyth 2012). A similar lack of phylogenetic signal in niche breadth would suggest that this trait is evolutionarily labile. This is supported by recent evidence of rapid shifts in habitat specificity among birds (Barnagaud *et al.* 2011) and niche expansion following invasion in mites (Hill *et al.* 2013).

Invasive species that flourish in new regions are clear evidence that limited dispersal ability can prevent range expansion and filling of the fundamental niche. Similarly, Dullinger *et al.* (2012) suggest that post-glacial migration lags among Austrian alpine flora have caused nearly a third of species to occupy less than half of their predicted suitable range. Historical processes such as these are thus likely to add noise to the observed niche breadth–range size relationship. Dullinger *et al.* (2012) also showed that dispersal capacity



greatly increased the amount of range filling, suggesting that incorporating dispersal ability into niche breadth–range size analyses might provide insights into the underlying variation in this pattern.

### Niche breadth, range size and extinction risk

Climate change and habitat loss are key threats to biodiversity worldwide (Schipper *et al.* 2008). Many ecological traits have been shown to correlate with a species' vulnerability to these threats including body size (e.g. Cardillo *et al.* 2005), dispersal ability (e.g. Kotiaho *et al.* 2005) and plant pollination strategy (e.g. Pilgrim *et al.* 2004). Models predict that specialists should decline more quickly than generalists (Thuiller *et al.* 2005), with a greater likelihood of disrupted interspecific interactions (e.g. predator–prey relationships) and loss of required resources. Furthermore, species with broader niches might be able to respond more quickly to climate change (Dullinger *et al.* 2012) and have a faster rate of niche evolution (Lavergne *et al.* 2013). Such rapid niche evolution is associated with lower recent population declines (Lavergne *et al.* 2013).

There is substantial recent evidence, from a variety of taxa, supporting the theory that specialists are declining more quickly, or are more vulnerable to climate change and habitat loss than their broader niche relatives (e.g. fish: Munday 2004; bats: Boyles & Storm 2007; birds: Seoane & Carrascal 2008; frogs: Botts *et al.* 2013; plants: Ozinga *et al.* 2013; see also Heim & Peters 2011). However, most models predicting vulnerability to climate change assume static niches in both time (i.e. no evolutionary response) and space (i.e. species averages or extrapolation from population traits) (Lavergne *et al.* 2010). Failure to take temporal and spatial variation into account will tend to cause over- and under-estimation of extinction risk respectively (see Atkins & Travis 2010; Harte *et al.* 2004). For example, the widely distributed copepod *Tigriopus californicus* has an upper temperature limit of approximately 38 °C, but some populations near the northern (high latitude) edge of its distribution have upper limits of less than 35 °C with limited potential for adaptation to higher temperatures (Kelly *et al.* 2012). This species might therefore be more vulnerable to climatic changes than what would be predicted based on species' averages or overall tolerance breadth.

Geographical range size has similarly been identified as a predictor of species' vulnerability to climate change and disturbance and is perhaps the trait most commonly correlated with extinction risk (see Angert *et al.* 2011a). A recent model predicts a negative relationship between range size and extinction, independent of other intercorrelated traits (Birand *et al.* 2012). Large-range species might be less vulnerable to extinction through two non-exclusive mechanisms. First, species with a larger range size might be more resilient to change since they are better able to recolonise areas following localised extinctions (Gaston 2003). Second, large-ranged species might be more resistant to disturbance because they are more likely to occupy 'refuge' habitats (Gaston 2003). However, as discussed above, if widely distributed species also show strong local adaptation, range size alone might seriously underestimate extinction risk (Atkins & Travis 2010).

The abundance–occupancy relationship – one of the most general patterns in ecology (reviewed in Gaston *et al.* 2000) – means that species with small range sizes also tend to be locally rare and *vice versa*. Our results suggest that these same species are most likely to be specialised and these separate effects could disproportionately magnify their extinction risk (Davies *et al.* 2004; Munday 2004;

Williams *et al.* 2006; but see Hobbs *et al.* 2010). Consequently, while the presence of a niche breadth–range size relationship provides an initial indicator of potential vulnerability, experiments are urgently needed to understand rarity, especially field experiments under changing conditions where abiotic and biotic factors may interact strongly. Such experiments might also help to explain heterogeneity in the niche breadth–range size relationship, with some species likely to be rare by, e.g. low tolerance and others by specialisation (e.g. local mutualisms).

### CONCLUSIONS

Here, we have shown a positive relationship between niche breadth and range size that is maintained across niche breadth measurements, taxonomic groups and spatial scales. This result challenges earlier claims that such a relationship does not exist and is purely a statistical artefact. Instead, we suggest that it is a general ecological pattern and that niche breadth can explain at least some of the variation in geographical range size among taxa. Other species traits, such as niche position, might also be important in determining range size, but systematic review of the current evidence is required. Understanding the underlying causes of this pattern, especially in a phylogenetic context, can tell us about the evolution of niche breadth, the importance of population structure to climate tolerance, and the underpinnings of rarity and commonness in nature. We suggest several directions for future research:

- (1) Additional studies that directly test both the niche position–range size and niche breadth–range size hypotheses are needed to determine the extent to which these patterns are both true and interrelated.
- (2) Experimental comparisons of niche breadth among close relatives will help to determine whether rarity is driven primarily by lack of physiological capacity or genetic variation to tolerate changing conditions. These would ideally be conducted under field conditions where biotic and abiotic factors interact.
- (3) Investigations of the niche breadth–range size relationship in a phylogenetic framework that allows incorporation of life-history traits and dispersal ability are needed.
- (4) Tests of niche breadth in narrow and widespread species that incorporate species-, population- and individual-level variation would allow partitioning of overall niche breadth between genetic variation and phenotypic plasticity and are crucial to uncovering the causal links between local processes and geographical distribution.

Besides uncovering general, predictive patterns, we should consider how species' distributions could inform us about ecological and evolutionary theory. In this regard, species that are exceptions to the general pattern present opportunities for understanding a wide variety of important effects on distribution.

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## AUTHORSHIP

RAS, MH and JPS designed the study; RAS and JPS extracted the data; RAS performed the meta-analysis; all authors contributed to writing the manuscript.

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