RESEARCH PAPER

Latitudinal gradient in niche breadth of brachyuran crabs

Katherine J. Papacostas[1,2]* and Amy L. Freestone[1,3]

[1]*Department of Biology, Temple University, Philadelphia, PA 19122, USA,* [2]*Moore Center for Science and Oceans, Conservation International, Arlington, VA 22202, USA,* [3]*Smithsonian Tropical Research Institute, Apartado 0843-03092 Balboa, Ancon, Panama*

ABSTRACT

Aim Niche breadth has long been hypothesized to decrease at low latitudes and contribute to global patterns of species diversity. Range size, phylogenetic relatedness and body size also have hypothesized relationships with both latitude and niche breadth, which may further affect niche breadth patterns. Existing terrestrial data are inconclusive and few data exist on latitudinal gradients in niche breadth in the marine realm. We tested the latitude–niche breadth relationship in a marine system while exploring the correlations of both variables with range size, and accounting for relatedness and body size.

Location Global.

Methods We compiled a global dataset on the dietary niche breadth of 39 brachyuran crab species from existing studies and additional analyses on species collected in Connecticut and Florida, USA and Bocas del Toro, Panama. Estimates of latitude, range size, clade and body size were obtained for each species. We then tested for correlations among focal variables and examined the strength of their relationships with diet breadth.

Results Latitude was the strongest predictor of niche breadth in temperate species, and the latitude–niche breadth relationship was stronger in larger-bodied species. The strongest predictor of the niche breadth of tropical species was clade, with the newest clade having the narrowest diet. Niche breadth was related to range size for both temperate and tropical species. Tropical species had larger ranges on average than temperate species.

Main conclusions We found an interesting division in the niche breadth relationships of temperate and tropical species; diets of temperate species were positively correlated with latitude, range size and body size, and diets of tropical species were related to range size and clade. Therefore, only temperate species demonstrated the predicted positive relationship between niche breadth and latitude, while evolutionary history was a stronger predictor of niche breadth in tropical species.

Keywords

Body size, brachyuran crab, diet, gut content analysis, latitude, niche breadth, phylogenetic relatedness, range size.

*Correspondence: Katherine J. Papacostas, Department of Biology, Temple University, Philadelphia, PA 19122, USA. E-mail: kpapacostas@temple.edu

INTRODUCTION

Niche breadth is defined as the range of environmental conditions and resources that a species can utilize (MacArthur, 1968), and can range from very broad (i.e. generalist species) to very narrow (i.e. specialist species). Species interaction strength, such as competition, may determine niche breadth according to classic ecological theory; weaker species interactions should allow for species to evolve a broader niche (Bolnick *et al.*, 2010) while strong interactions should, over time, drive species to

utilize fewer resources and show greater specialization, which in turn should reduce interspecific competition (Bolnick *et al.*, 2010).

It has long been hypothesized that niche breadth varies with latitude (MacArthur, 1972). Species diversity peaks in the tropics (Hillebrand, 2004b) and studies have shown that species interaction strength varies spatially, being strongest at lower latitudes (Schemske *et al.*, 2009; Freestone *et al.*, 2011). These strong species interactions could drive a higher prevalence of specialist species at lower latitudes, which is a proposed mechanism contributing to the coexistence of tropical species (Schemske *et al.*, 2009). Despite this, research on the relationship between niche breadth and latitude remains inconclusive. Terrestrial studies have shown mixed results (Vazquez & Stevens, 2004), with approximately half of existing studies supporting a latitudinal gradient in niche breadth [e.g. Krasnov *et al.* (2008) and Belmaker *et al.* (2012), who specifically examined richness–specialization patterns] and half refuting it (e.g. Fiedler, 1998; Slove & Janz, 2010). In the marine realm, examination of latitudinal gradients in specialization are rare (but see Rohde, 1978; Sunday *et al.*, 2011) and it is unclear how niche breadth relates to latitude in marine species.

Other factors may also be related to niche breadth, either alone or in conjunction with latitude. For instance, the range of resources a species is able to utilize can influence geographical range size (Slatyer *et al.*, 2013), with generalist species having larger ranges and specialist species having narrower ranges. However, range size may also be correlated with latitude; Rapoport's rule predicts that species at higher latitudes have larger ranges on average than species restricted to lower latitudes (Stevens, 1989), potentially due to the increased seasonal variability at higher latitudes selecting for broader climatic tolerances (i.e. broader environmental niches; Fernandez & Vrba, 2005). Both latitude and range size thus have a hypothesized relationship with niche breadth, but may also be related and could interactively influence interpretations of patterns of niche breadth. For instance, recent research suggests that a narrow dietary niche breadth at lower latitudes may be related to the smaller range size of low-latitude species rather than having a direct relationship with latitude (Slove & Janz, 2010).

Phylogenetic relatedness may also affect niche breadth (Barnagaud *et al.*, 2014). Specifically, very closely related species are expected to be more ecologically similar due to niche conservatism (Kerkhoff *et al.*, 2014), thus the niche breadth of such species may also be similar. Conflicting hypotheses exist for the distribution of related clades across latitude. The 'out of the tropics' model suggests that more species originate in the tropics and then spread towards the poles (Jablonski *et al.*, 2006), in which case newer clades should be more prevalent in the tropics. In contrast, the 'tropical niche conservatism' hypothesis posits that older, more basal, clades remain closer to the tropics, and newer derived clades that have overcome the cold winter temperature barrier are more prevalent at higher latitudes (Hawkins & DeVries, 2009).

Finally, body size has also been proposed to contribute to diet breadth; large species have been suggested to be more generalist,

and able to utilize a wider variety of prey resources, than smaller species (Ashmole, 1968; Novotny & Basset, 1999). Support for this hypothesis is mixed, however, and other more recent studies of vertebrate and invertebrate taxa suggest that larger-bodied animals may target larger more energetically profitable prey and thus may be more specialized (e.g. Costa *et al.*, 2008). Body size is also predicted by Bergmann's rule to increase with latitude (Bergmann, 1848), with lower average temperatures being a hypothesized driver of greater cell growth (van Voorhies, 1996), resulting in another potentially confounding factor in the niche breadth–latitude relationship.

We therefore examined latitudinal trends in niche breadth using brachyuran crabs as a model system and diet as a measure of niche breadth, while accounting for variation in phylogenetic relatedness and body size. We further explored the bivariate relationships of range size with niche breadth and latitude to aid in interpreting findings. Due to limited phylogenetic variation in the brachyuran crab group, and to mixed support for body size as an important predictor of niche breadth, we hypothesized that these covariates would have limited importance in understanding niche breadth–latitude relationships in brachyuran crabs. We therefore predicted that dietary niche breadth would increase with latitude and that species range sizes would be positively correlated with both dietary niche breadth and latitude.

METHODS

We conducted a global analysis of brachyuran crab diets by compiling published data ($n = 30$ species) and completing diet analyses on temperate, subtropical and tropical crabs ($n = 10$ species; one species whose diet had been analysed in numerous other studies and nine species whose diets had not been previously analysed). We searched ISI Web of Science for relevant studies using the broad search string 'crab' AND 'marine' AND 'diet'. We then included data from studies that conducted gut content analyses on a population of crabs of one or more species in their native range, and reported the average diet composition of those species as either volumetric proportion (%V) data or frequency of occurrence (%O) data (a full list of studies included and species examined can be found in Appendices S1 and S2 in the Supporting Information). Volumetric proportion (%V) is defined as the estimated volume per prey item in an individual's gut, averaged across all the analysed guts of that species (total $n = 100\%$). Frequency of occurrence (%O) is defined as the number of times a prey item is found in an individual's stomach (N_i; for i = category 1 to n), divided by the total number of guts analysed, multiplied by 100 (total $n > 100\%$).

To supplement the data obtained from the literature, gut content analyses were conducted on animals collected from Connecticut and Florida, USA (41.320° N, 72.057° W; $n = 2$ native crab species) and Bocas del Toro, Panama (9.352° N, 82.258° W; $n = 8$ native crab species). Specimens in each region were gathered at the same time of day (morning), and during the late summer/autumn. Specimens were preserved within 2 h

of collection. For each crab we noted the sex and size, measuring the carapace width to the nearest millimetre. We then removed the carapace, extracted the stomach with forceps and measured the width of the cardiac stomach (posterior ventral edge) to the nearest millimetre (Griffen & Mosblack, 2011). Using a dissection microscope, we visually identified gut contents for individuals of each species (4–16 individuals per species, $N = 88$) to the lowest possible taxonomic level (Appendix S3). Gut contents were separated by food type into grid cells on a Petri dish. We determined the proportional contribution of each food type from the number of grid cells (or portions of grid cells) that each occupied. This method provided an estimate of the percentage of each food type in the diet (Griffen & Mosblack, 2011). We used these data to calculate both %V and %O of prey items for each species.

In order to standardize the dataset (total $n = 100\%$), we converted frequency of occurrence to relative frequency (%F) of prey items (Safi & Kerth, 2004) using the following equation:

$$\%F = (\%O_i) \Big/ \sum_{i=1}^{n} (\%O_i).$$

We then calculated Levins' standardized measure of niche breadth (Hurlbert, 1978) using %V and %F data for each species ($n = 39$) as follows:

$$B_A = (B - 1) / (n - 1),$$

where B_A is Levins' standardized niche breadth, B is Levins' measure of niche breadth and n is a constant that reflects the total number of prey resources used across all species. Levins' measure of niche breadth (Levins' B) (Safi & Kerth, 2004) was calculated as

$$B = 1 \Big/ \sum_{i=1}^{n} (\%F_i^2) \quad \text{or} \quad B = 1 \Big/ \sum_{i=1}^{n} (\%V_i^2).$$

Standardizing Levins' B puts the measure of niche breadth on a scale from zero to one. Those species with a Levins' B closer to zero have a narrower diet and are more specialized, and those with a Levins' B closer to one have a broader diet and are more generalist. When multiple studies examined the same crab species, we calculated a standardized Levins' B from the average %V or %F of prey items across the studies examining that particular species in order to obtain one value for Levins' B per crab species. Most studies had unidentifiable prey items (usually labelled 'detritus' or 'unidentifiable remains'), which were excluded from analyses. Additionally, the way in which %V and %F are inferred from stomach contents differs fundamentally, so we tested for a relationship between standardized Levins' B values calculated from both %V and %F, using our own data. Calculations of standardized Levins' B values using %V and %F data had a strong linear relationship ($r^2 = 0.86$, $N = 10$, $P < 0.0001$), and Levins' B values using %F data were converted to Levins' B values using %V data using the following equation prior to other analyses:

$$B_{A(\text{from }\%V\text{ data})} = 0.5944 \times B_{A(\text{from }\%F\text{ data})} - 0.0044.$$

Our estimates of diet breadth are conservative: brachyuran crabs are considered a generalist taxon (Griffen & Mosblack, 2011) and the taxonomic resolution of prey items reported in the literature is coarse (generally phylum, class or order) due to the feeding mode of crabs (McGaw & Reiber, 2000). However, visual gut content analysis was the most commonly used method for examining crab diet and provides a useful estimate of diet breadth. Also, prey availability, a factor that can influence diet breadth (Petraitis, 1979), was unavailable in this dataset. Given our coarse taxonomic resolution of prey items, however, it is highly likely that these broad prey categories were available as food items in all locations (e.g. Gosling, 2003; Horton et al., 2013), ensuring a conservative and comparable estimate of diet breadth for all focal species.

After diet breadth had been calculated for each species we obtained estimates for our focal predictor variables. Most crabs in our dataset were coastal species representative of all oceans apart from the Southern, although the majority of temperate studies were conducted in the east and west Atlantic (Appendix S2). For each crab species, latitudinal range size and latitudinal position were estimated primarily through species distribution data and species occurrence maps found on the World Register of Marine Species database (WoRMS Editorial Board 2014). We calculated latitudinal range size (hereafter referred to as range size) by subtracting the degree of latitude of the lowest-latitude observations of the species in its native range from the highest-latitude extent of the species in either the Northern or Southern Hemisphere. If species ranges extended across both hemispheres, the total distribution of the species in degrees latitude was used for this estimate of range size (Appendix S2). We then used these data to determine the midpoint of each species' geographic range (hereafter termed latitude). This midpoint approach is generally accepted for use in biogeographic studies (e.g. Rohde, 1999; Krasnov et al., 2008; Sunday et al., 2012) based on the classical 'abundant centre' hypothesis which posits that species abundances peak in the centre of their ranges (Wulff & Brissenden, 1943; Rohde, 1999; Fenberg & Rivadeneira, 2011; but see Sagarin & Gaines, 2002; Ruggiero & Werenkraut, 2007, for limitations of this method). Only one species lacked distribution information on WoRMS, and for that species we consulted the literature directly to determine its latitudinal distribution (Appendix S2). Each crab species was then categorized by clade; while Brachyura is a monophyletic group, it can be divided into seven clades of increasing distance from the ancestral species (Brosing et al., 2007). The 39 species studied fell into three clades: (1) Majoidea ($n = 10$), (2) Cancridae/Portunidae/Xanthoidea ($n = 17$), and (3) Neobrachyura ($n = 12$); Majoidea are closest to the ancestral species (Brosing et al., 2007). Average body sizes for each species were obtained from the literature (Appendix S2).

We tested for linear relationships between: (1) latitude and range size, as predicted by Rapoport's rule (Stevens, 1989), (2) latitude and clade, and (3) latitude and average body size as predicted by Bergmann's rule (Bergmann, 1848) to detect any potential multicollinearity in the dataset. Approximately half of our data were for tropical species ($n = 18$) and the other half for

Table 1 Results of model selection for tropical species. Comparison of the best fit model and the four other models, listing the corrected Akaike information criterion (AICc), the difference from the 'best fit' model (ΔAICc), the Akaike weight (w_i) and the evidence ratio (w_j/w_i) for each model. Main effects are midpoint of latitudinal range (MLR), clade (C), average body size of crabs sampled (ABS), sample size for each crab species (SS) and body size range of crabs within the sample (BSR).

Model	No. of parameters	Variables included in model	AICc	ΔAICc	w_i	w_j/w_i
M5 (best fit)	1	Main effects: C	−53.30	0.00	0.822	1
M4	2	Main effects: C, ABS	−50.22	3.08	0.177	4.655
M3	3	Main effects: C, ABS, SS	−40.93	12.37	1.70×10^{-3}	4.85×10^{2}
M2	4	Main Effects: MLR, C, ABS, SS Interactions: MLR × C, MLR × ABS	0.18	53.48	2.01×10^{-12}	4.10×10^{11}
M1 (full)	6	Main Effects: MLR, C, SS, BSR Interactions: MLR × C, MLR × ABS	34.91	88.21	5.76×10^{-20}	1.43×10^{19}

Table 2 Results of model selection for temperate species. Comparison of the best fit model and the four other models, listing the corrected Akaike information criterion (AICc), the difference from the 'best fit' model (ΔAICc), the Akaike weight (w_i) and the evidence ratio (w_j/w_i) for each model. Main effects are midpoint of latitudinal range (MLR), clade (C), average body size of crabs sampled (ABS), sample size for each crab species (SS) and body size range of crabs within the sample (BSR).

Model	No. of parameters	Variables included in model	AICc	ΔAICc	w_i	w_j/w_i
M5 (best fit)	4	Main effects: MLR	−61.96	0	0.575	1.00
M4	2	Main effects: MLR, ABS Interactions: MLR × ABS	−60.93	1.03	0.343	1.67
M3	5	Main effects: MLR, ABS, SS Interactions: MLR × ABS	−58.06	3.9	8.18×10^{-2}	7.03
M2	6	Main Effects: MLR, C, ABS, SS Interactions: MLR × C, MLR × ABS	−35.33	26.63	9.48×10^{-7}	6.06×10^{5}
M1 (full)	7	Main Effects: MLR, RS, C, SS, BSR Interactions: MLR × C, MLR × ABS	−24.93	37.03	5.23×10^{-9}	1.10×10^{8}

temperate species ($n = 21$), and in these preliminary analyses we found an interesting division in latitude–range size relationships between tropical and temperate species (see Appendix S4 and Results). Tropical species were defined as those whose latitudinal midpoints fell between 23.5° N and 23.5° S, and temperate species as those whose latitudinal midpoints fell between 23.5 and 90° N or S. To ensure that this division was not driven intrinsically by the way latitudinal range size and midpoint were calculated (since temperate species with large ranges could by default have a higher latitudinal midpoint, while tropical species spanning both hemispheres would not), we conducted a randomization test to compare the slope (i.e. the strength) of our latitude–range size relationship for temperate species with the slope that would be observed for the relationship purely by chance. We generated 10,000 random datasets consisting of 21 high-latitude range limits and 21 low-latitude range limits between 0° and 90°, including a condition that random range limits would continue to be generated until all the midpoints of those ranges were above 23.5° (R 3.2.1; R Core Team, 2014). From these range limits we calculated the latitudinal range sizes and latitudinal midpoints for each dataset. We then calculated the slope of the latitude–range size relationship for each of the datasets, as well as the 95% confidence interval of these slopes, to compare with the slope of our own dataset; our observed slope

of 0.535 was well outside the 95% confidence interval (−0.103, −0.097) of the randomized dataset, supporting that the relationship observed in our dataset was much stronger than expected by chance. We therefore proceeded to analyse tropical and temperate species separately.

We examined our focal predictors of diet breadth for both temperate and tropical species by conducting backward stepwise (Neter *et al.*, 1996) model selection using the corrected Akaike information criterion (AICc), which is the AIC adjusted for small sample size (Burnham & Anderson, 2002). We further calculated Akaike weights (w_i) and evidence ratios (w_j/w_i) for each model for comparison purposes. The predictor variables included in the two full models were as follows: latitude, clade, average body size, body size range of individuals dissected (to control for sample bias in the dataset), sample size for each species (to control for sample bias in the dataset), and interactions between latitude and our focal covariates (see Tables 1 & 2). To complement the model selection we also ran linear regressions to assess the relationship between all continuous predictor variables and diet breadth as well as an ANOVA for the effect of clade on niche breadth. Range size was not included in the model selection and the bivariate relationship between diet breadth and range size was analysed separately since the expected direction of causality of this relationship is the oppo-

Figure 1 Comparison of the relationships between latitude, range size and diet breadth in tropical and temperate brachyuran crab species. Linear regressions were used to analyse relationships between latitude (midpoint of latitudinal range) and range size (degrees of latitude) for (a) tropical species and (b) temperate species, as well as diet breadth and range size for (c) tropical species and (d) temperate species. Both linear regressions and model selection were used to test the strength of latitude and diet breadth relationships for (e) tropical species and (f) temperate species. Each point is a brachyuran crab species. Diet breadth was calculated from the published literature and from our diet analyses on crab species collected in Connecticut, Florida and Panama ($n = 21$ temperate species, and 17 tropical species). Positive relationships were found between latitude and range size for temperate species only (panel b). Positive relationships between diet breadth (as represented by standardized Levins' B values) and range size were found for both temperate and tropical species (panels c and d). Latitude was related to diet breadth for temperate species but was not retained in the best fit model for tropical species (panels e and f).
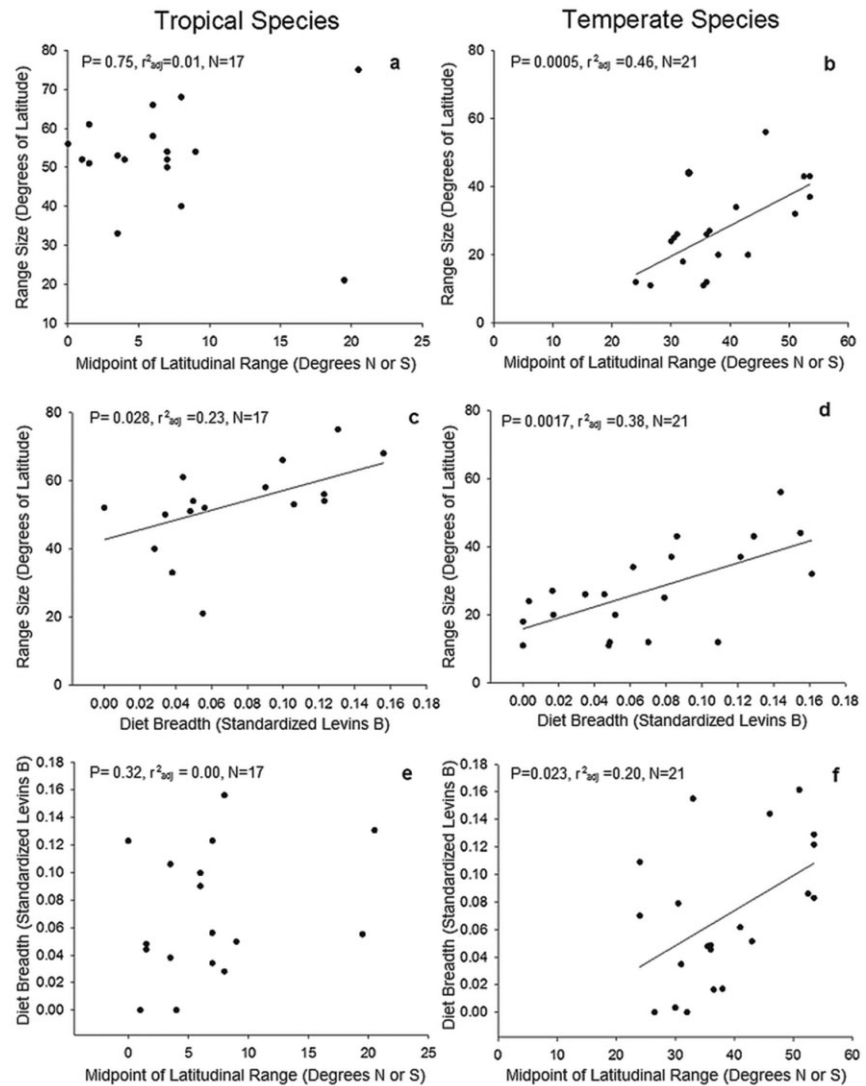
site of the other factors of interest (Ashmole, 1968; MacArthur, 1972; Krasnov *et al.*, 2008; Slatyer *et al.*, 2013). One outlier was identified in the dataset *Callinectes sapidus* (average body size of 12.2 cm, size range 0.1–24 cm and sample size of 4117 individuals which were 4, 8 and 40 times greater than those values for all other crabs, respectively; Appendix S2) and was removed prior to analyses.

RESULTS

Overall, brachyuran crabs have broad diets characteristic of generalist species, using prey resources from 25 taxonomic categories (Appendix S5). Most crabs were found to utilize both plant and animal resources, with crustaceans and molluscs being the dominant animal food groups (Appendix S5). Plant and algal matter were the dominant food items used across species, with over 70% of the individuals examined consuming some type of vascular plant and over 60% consuming algal material (Appendix S5).

Our hypothesis of a positive latitude–range size relationship was only supported by temperate species, while a positive relationship between range size and diet breadth was supported across the dataset. First, the relationship between latitude and range size differed significantly for tropical and temperate species (Fig. 1a, b, Appendix S4). We found that tropical species had large ranges on average that had no relationship with latitude ($P = 0.75$, $r^2_{adj} = 0.007$, $N = 17$; Fig. 1a, Appendix S4), while temperate species had range sizes that increased with latitude as expected ($P = 0.0005$, $r^2_{adj} = 0.46$, $N = 21$; Fig. 1b, Appendix S4). Range size was positively correlated with diet breadth in both tropical (Fig. 1c, linear regression: $P = 0.028$, $r^2_{adj} = 0.23$, $N = 17$) and temperate species (Fig. 1d, linear regression: $P = 0.0017$, $r^2_{adj} = 0.38$, $N = 21$).

Our hypothesis that diet breadth would decrease with increasing latitude was only supported for temperate species. Latitude was not a strong predictor of diet breadth in tropical species ($P = 0.32$; Table 1, Fig. 1e), but was a strong predictor of diet breadth in temperate species ($P = 0.023$, $r^2_{adj} = 0.20$, $N = 21$;

Table 1), being retained in the top two best-fit models in the temperate analysis (Table 2, Fig. 1f). Therefore, taken together with the results from bivariate range size relationships, we found that higher-latitude temperate species with large ranges had the broadest diets, while small-ranged, lower-latitude temperate species had narrower diets.

In addition to latitude predicting the diet breadth of temperate species, the second best fitting model of the temperate dataset which also had substantial support ($P = 0.038$, $r^2_{adj} = 0.27$, $N = 21$), retained body size and a body size × latitude interaction term (Table 2, Fig. 2). Latitude had a weak relationship with average body size for temperate species, with slightly larger individuals being found at higher latitudes and smaller individuals being found at lower latitudes (linear regression: $P = 0.04$, $r^2_{adj} = 0.16$, $N = 21$; Fig. 2a). There was not a strong relationship between body size alone and diet breadth ($P = 0.24$; Fig. 2b), but the marginally significant interaction term suggested that the relationship between latitude and diet breadth increased in strength as body size increased ($P = 0.08$; Fig. 2c). Although influential, this interaction may be of lesser importance in predicting diet breadth than latitude, since latitude was significant in the simple regressions and retained in both best-fit models (Table 2).

We found no relationship between clade and latitude in our dataset (ANOVA for temperate species, $r^2_{adj} = 0.11$, $N = 21$, $F_{2/18} = 2.35$, $P = 0.1$; ANOVA for tropical species, $r^2_{adj} = 0.18$, $N = 17$, $F_{2/14} = 2.73$, $P = 0.1$), but we did find a relationship between clade and diet breadth for tropical species. Interestingly, clade was the strongest predictor of diet breadth for tropical species, being the only factor retained in the best-fit model ($P = 0.0042$, $r^2_{adj} = 0.48$, $N = 17$; Table 1). Those tropical species belonging to the most evolutionarily recent clade, Neobrachyura, had considerably narrower diets than the two older brachyuran clades represented in our dataset (Table 1, Fig. 3a), while the older tropical clades had diet breadths that were more comparable to mid/high-latitude temperate species (Fig. 1d, Fig. 3a). While the trend of the temperate data interestingly mirrors these results for tropical species (Fig. 3a, b), clade was not supported as a major predictor of diet in temperate species, as the model containing clade was not significant and had far less strength than the best-fit model ($P = 0.77$; Table 2, Fig. 3b).

DISCUSSION

Temperate brachyuran crabs were found to be more specialized at lower latitudes, but in contrast we found no latitude–niche breadth relationship for tropical species. Body size and latitude further had an interactive effect on diet breadth of temperate species, with larger-bodied species demonstrating a broader diet at higher latitudes than at lower latitudes. In the tropics, the strongest single predictor of diet breadth was clade. Our results suggest that niche breadth patterns may relate to latitudinal gradients in competition strength (Schemske et al., 2009) and species richness (Belmaker et al., 2012), both of which are thought to increase towards lower latitudes. Specialization can
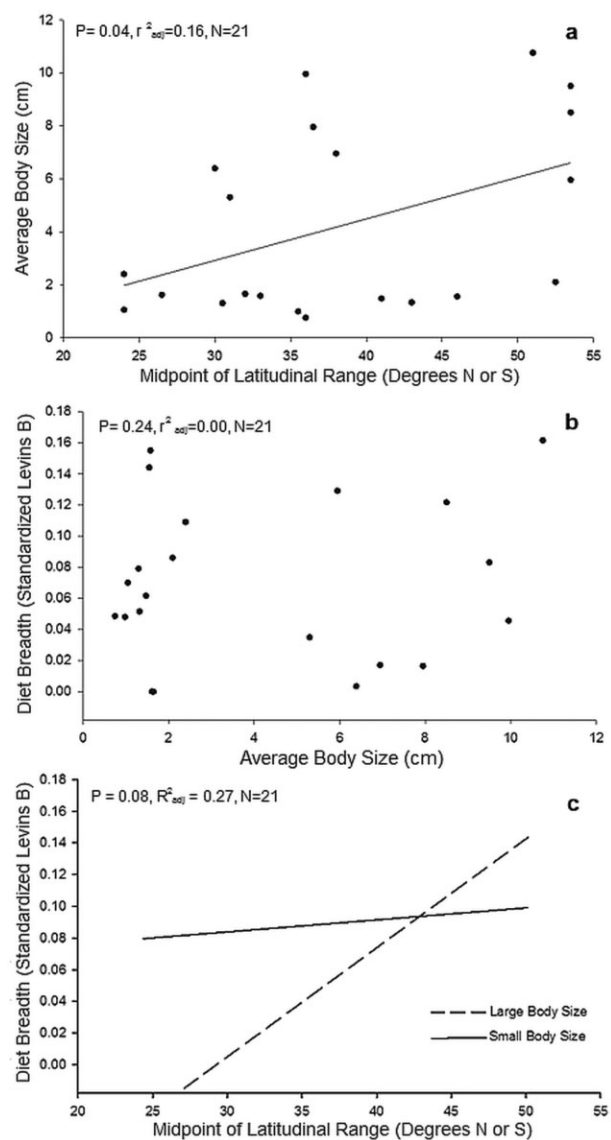

Figure 2 Relationships among body size, latitude and diet breadth for temperate crab species. Linear relationships between (a) average body size and Levins' *B*, (b) latitude (midpoint of latitudinal range) and average body size, with each point representing a brachyuran crab species and (c) a body size × latitude interaction plot demonstrating the predicted strength of the latitude–diet breadth relationship if the smallest body size (0.75 cm) and largest body size (10.5 cm) are held constant across latitude; the plot indicates that the strength of the relationship increases as body size increases. A linear regression was used to analyse the relationship between latitude and average body size, while a regression as well as model selection were used to test the strength of the average body size relationship with diet breadth, and the relationship of the body size × latitude interaction with diet breadth.

alleviate strong competition by reducing niche overlap, thereby facilitating the coexistence of species as well as higher species richness (Dyer et al., 2007) at low temperate latitudes. Species interactions (Schemske et al., 2009) and associated evolutionary
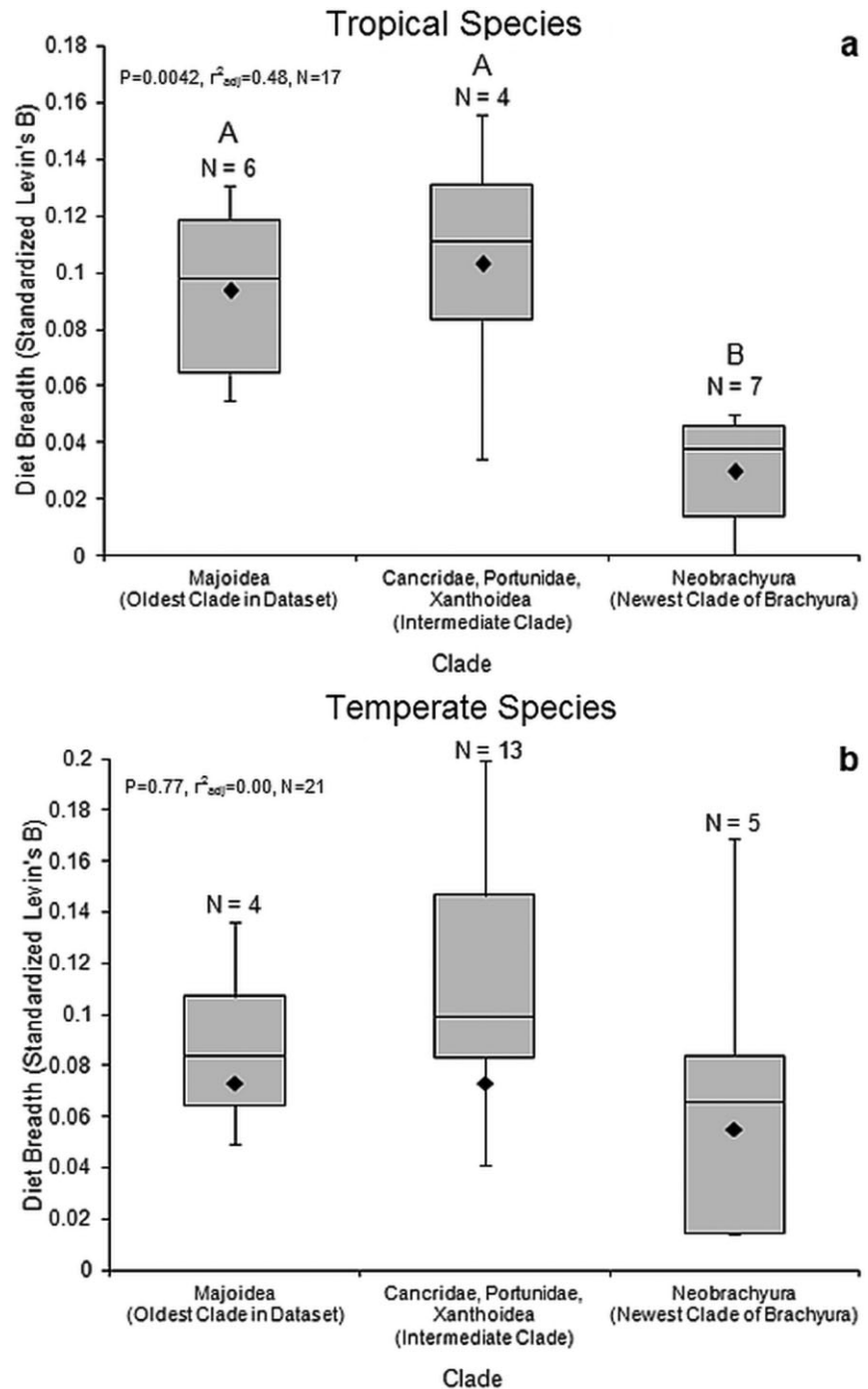
Figure 3 Comparison of the relationship between clade and diet breadth for tropical and temperate species. Majoidea is closest to the ancestral species (the oldest clade represented in the dataset) and Neobrachyura is furthest (the newest clade). Data are presented as box plots for (a) tropical species and (b) temperate species; the lower boundaries of the boxes represent the second quartile, the line within the box represents the median and the upper boundary of the box indicates the third quartile. The bar below the box spans the first quartile, and the bar above the box spans the fourth quartile. The means are indicated with individual data points. Samples sizes for each clade are detailed in the figure. Different letters above boxes indicate significant differences between groups, as determined using Tukey's honestly significant difference test.

selection pressure (Roulin *et al.*, 2009), however, are expected to be strongest in the tropics. Therefore evolutionary history rather than latitude may be more predictive of niche breadth in tropical species.

There is little marine research exploring latitude–niche breadth relationships; one study found mixed results for host specificity in parasites across latitude (Rohde, 1978) while two other studies supported positive relationships between breadth of thermal tolerance and both latitude and range size (Sunday *et al.*, 2011, 2012). In these studies, however, other possible explanatory variables such as body size and phylogenetic relationships were not examined in conjunction with latitude. By examining these other important variables, and also by analysing our temperate and tropical data separately, our results highlight several key mechanisms that may differentially drive large-scale patterns of niche breadth in tropical and temperate species.

The fact that clade is the major factor associated with diet breadth in our tropical dataset suggests that evolutionary history may be a key predictor of niche breadth in tropical species. In the tropics, species diversity has been found to be

greater than at higher latitudes, potentially due to climatic stability, high diversification rates and/or historical factors (Pianka, 1966; Hillebrand, 2004b; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007). New clades in high-diversity systems may therefore evolve as specialists as a mechanism to coexist and increase the efficiency of their resource usage and minimize competition with older, more generalist clades. These results do not necessarily mean that evolutionary history is unimportant at higher latitudes, since temperate clades showed a similar niche breadth pattern to tropical clades (i.e. narrowed niche breadth in the newest clade), although this pattern was not significant. However, our results are consistent with existing hypotheses suggesting that there may be differences in the importance of biotic interactions between temperate and tropical latitudes over evolutionary time-scales (Mittelbach *et al.*, 2007; Roulin *et al.*, 2009).

Latitude was the strongest predictor of diet breadth for temperate species, but body size and a latitude–body size interaction were also found to be important. Body size alone did not strongly influence diet breadth, but the positive relationship between latitude and diet breadth was strongest in larger-bodied species. Although it has been suggested that large-bodied species are able to consume prey of a broader size range, and thus a wider diversity of prey, than smaller species (e.g. Diaz, 1994), some studies have demonstrated that larger-bodied species preferentially target fewer, larger, more energy efficient organisms (e.g. Costa *et al.*, 2008). Our results may suggest that large-bodied crabs utilize these alternative foraging strategies depending on latitude; large-bodied species at high latitudes may be able to target a wider range of prey due to lower predator diversity (Paine, 1966; Hillebrand, 2004a,b) and reduced competition (Schemske *et al.*, 2009). As both predator diversity and competition strength are hypothesized to increase at lower latitudes (Paine, 1966; Pianka, 1966; Schemske *et al.*, 2009), specialization may allow more efficient foraging in large-bodied low-temperate/subtropical species.

Although niche breadth was correlated with range size across all latitudes, we observed differential support between temperate and tropical species for Rapoport's rule (predicting a positive relationship between range size and latitude). The ranges of tropical species were very large on average and had no relationship with latitude, but the ranges of temperate species had a significant positive correlation with latitude. Support for Rapoport's rule varies in the literature (Stevens, 1989; Rohde, 1999); strong support has been found in studies conducted in the Northern Hemisphere, but previous global analyses have found weak patterns (see Ruggiero & Werenkraut, 2007). Existing marine studies have found little support for the hypothesis (e.g. Rohde & Heap, 1996; Macpherson, 2003), and it has been suggested that Rapoport's rule may be weaker in marine systems than terrestrial systems (Ruggiero & Werenkraut, 2007), potentially due to variation in propagule dispersal (Byers & Pringle, 2006), larger average scales of connectivity in marine systems (Carr *et al.*, 2003), less temperature variability than terrestrial systems (Sunday *et al.*, 2012) or currents having strong influences on the range sizes of marine species (Gaylord & Gaines,

2000). Our results, however, suggest that large-ranged tropical species could also obscure the pattern.

Variation in tropical and temperate range patterns may be driven by differences in the abiotic and biotic factors to which they are exposed. For instance, the ranges of tropical species are likely to be restricted by cold boundaries (Sunday *et al.*, 2011, 2012). As climate is less spatially and temporally variable at low latitudes (Pianka, 1966), and the tropics span a wide geographical area (47° of latitude), the entire tropics could be within the thermal tolerance range of a tropical species. Indeed, many of our tropical species had ranges that spanned the majority of the tropics (14 out of 17 species had ranges > 45° of latitude) or extended into subtropical areas where temperature extremes are still mild. Therefore, although we found that dietary niche breadth and range size were correlated, breadth of environmental tolerance may also be important in driving these large range sizes of tropical species. Temperate species ranges are also set by cold boundaries, although they experience broader temperature extremes and are likely to have broader thermal tolerances (Sunday *et al.*, 2011, 2012). However, their low-latitude range limits may also be set by biotic boundaries such as competitive exclusion from tropical species; species interactions are also determinants of range size (Briers, 2003; Holt & Barfield, 2009) and low-temperate species may have the smallest ranges, as well as the smallest niches, because they experience these abiotic and biotic limitations on both latitudinal range limits.

Overall, we found a stark division in predictors of diet breadth in temperate and tropical species, with latitude being a strong predictor for temperate species along with a latitude–body size interaction, and evolutionary history as the best predictor for tropical species. We found positive range size relationships with niche breadth for all species, except that tropical species in general had larger ranges and broader niches than expected. The large ranges of tropical species are likely influenced by large geographical areas within their thermal tolerances, and broad tropical niche breadth was shown to be driven by older, more generalist clades. These results suggest that competition may be important to varying degrees across latitude; weak at high latitudes, strong enough at low temperate latitudes to influence niche breadth patterns among species, and strongest in the tropics where it may influence niche breadth patterns among clades. Therefore, ecological mechanisms (e.g. competition strength) may be primarily driving patterns of niche breadth in the temperate zone, while evolutionary mechanisms (e.g. selection due to competition) may be more predictive of niche breadth patterns in tropical, high-diversity areas. These potentially differing mechanisms driving niche breadth may also contribute to large-scale maintenance of diversity in both temperate and tropical systems.

REFERENCES

Ashmole, N.P. (1968) Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Systematic Zoology*, **17**, 292–304.

Barnagaud, J.-Y., Daniel Kissling, W., Sandel, B., Eiserhardt, W.L., Sekercioglu, C.H., Enquist, B.J., Tsirogiannis, C. & Svenning, J.-C. (2014) Ecological traits influence the phylogenetic structure of bird species co-occurrences worldwide. *Ecology Letters*, **17**, 811–820.

Belmaker, J., Sekercioglu, C.H. & Jetz, W. (2012) Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography*, **39**, 193–203.

Bergmann, C. (1848) *Uber die Verhaltnisse der Warmeokonomieder Tiere zu ihrer Grosse*. E. A. Huth, Göttingen.

Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L. & Paull, J.S. (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1789–1797.

Briers, R.A. (2003) Range limits and parasite prevalence in a freshwater snail. *Proceedings of the Royal Society B: Biological Sciences*, **270**, S178–S180.

Brosing, A., Richter, S. & Scholtz, G. (2007) Phylogenetic analysis of the Brachyura (Crustacea, Decapoda) based on characters of the foregut with establishment of a new taxon. *Journal of Zoological Systematics and Evolutionary Research*, **45**, 20–32.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York.

Byers, J.E. & Pringle, J.M. (2006) Going against the flow: retention, range limits and invasions in advective environments. *Marine Ecology Progress Series*, **313**, 27–41.

Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R. & Largier, J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications*, **13**, S90–S107.

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 Ecology and Biogeography*, **17**, 670–677.

Diaz, M. (1994) Variability in seed size selection by granivorous passerines – effects of bird size, bird size variability, and ecological plasticity. *Oecologia*, **99**, 1–6.

Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morais, H.C., Diniz, I.R., Kursar, T.A. & Coley, P.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696–699.

Fenberg, P.B. & Rivadeneira, M.M. (2011) Range limits and geographic patterns of abundance of the rocky intertidal owl limpet, *Lottia gigantea*. *Journal of Biogeography*, **38**, 2286–2298.

Fernandez, M.H. & Vrba, E.S. (2005) Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. *Journal of Biogeography*, **32**, 903–918.

Fiedler, K. (1998) Diet breadth and host plant diversity of tropical- vs. temperate-zone herbivores: South-East Asian and west Palaearctic butterflies as a case study. *Ecological Entomology*, **23**, 285–297.

Freestone, A.L., Osman, R.W., Ruiz, G.M. & Torchin, M.E. (2011) Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology*, **92**, 983–993.

Gaylord, B. & Gaines, S.D. (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *The American Naturalist*, **155**, 769–789.

Gosling, E. (2003) Ecology of bivalves. *Bivalve molluscs: biology, ecology and culture*, pp. 44–78. Wiley-Blackwell, Malden, MA.

Griffen, B.D. & Mosblack, H. (2011) Predicting diet and consumption rate differences between and within species using gut ecomorphology. *Journal of Animal Ecology*, **80**, 854–863.

Hawkins, B.A. & DeVries, P.J. (2009) Tropical niche conservatism and the species richness gradient of North American butterflies. *Journal of Biogeography*, **36**, 1698–1711.

Hillebrand, H. (2004a) Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, **273**, 251–267.

Hillebrand, H. (2004b) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 192–211.

Holt, R.D. & Barfield, M. (2009) Trophic interactions and range limits: the diverse roles of predation. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1435–1442.

Horton, T., Lowry, J. & De Broyer, C. (2013) *World Amphipoda database*. Available at: http://www.marinespecies.org/amphipoda/ (accessed 2 April 2015).

Hurlbert, S.H. (1978) The measurement of niche overlap and some relatives. *Ecology*, **59**, 67–77.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.

Kerkhoff, A.J., Moriarty, P.E. & Weiser, M.D. (2014) The latitudinal species richness gradient in New World woody

angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences USA*, **111**, 8125–8130.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Mouillot, D. & Poulin, R. (2008) Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. *Journal of Biogeography*, **35**, 592–601.

MacArthur, R.H. (1968) The theory of the niche. *Population biology and evolution* (ed. by R.C. Lewontin), pp. 159–176. Syracuse University Press, New York.

MacArthur, R.H. (1972) *Geographical ecology*. Princeton University Press, Princeton, NJ.

McGaw, I.J. & Reiber, C.L. (2000) Integrated physiological responses to feeding in the blue crab *Callinectes sapidus*. *Journal of Experimental Biology*, **203**, 359–368.

Macpherson, E. (2003) Species range size distributions for some marine taxa in the Atlantic Ocean. Effect of latitude and depth. *Biological Journal of the Linnean Society*, **80**, 437–455.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. (1996) *Applied linear statistical models*, 4th edn. McGraw-Hill, Boston, MA.

Novotny, V. & Basset, Y. (1999) Body size and host plant specialization: a relationship from a community of herbivorous insects on *Ficus* from Papua New Guinea. *Journal of Tropical Ecology*, **15**, 315–328.

Paine, R.T. (1966) Food web complexity and species diversity. *The American Naturalist*, **100**, 65–75.

Petraitis, P.S. (1979) Likelihood measures of niche breadth and overlap. *Ecology*, **60**, 703–710.

Pianka, E.R. (1966) Latitudinal gradients in species diversity – a review of concepts. *The American Naturalist*, **100**, 33–46.

R Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/ (accessed 10 March 2015).

Rohde, K. (1978) Latitudinal differences in host-specificity of marine Monogenea and Digenea. *Marine Biology*, **47**, 125–134.

Rohde, K. (1999) Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography*, **22**, 593–613.

Rohde, K. & Heap, M. (1996) Latitudinal ranges of teleost fish in the Atlantic and Indo-Pacific Oceans. *The American Naturalist*, **147**, 659–665.

Roulin, A., Wink, M. & Salamin, N. (2009) Selection on a eumelanic ornament is stronger in the tropics than in temperate zones in worldwide-distributed barn owl. *Journal of Evolutionary Biology*, **22**, 345–354.

Ruggiero, A. & Werenkraut, V. (2007) One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Global Ecology and Biogeography*, **16**, 401–414.

Safi, K. & Kerth, G. (2004) A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology*, **18**, 1293–1303.

Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245–269.

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

Slove, J. & Janz, N. (2010) Phylogenetic analysis of the latitude–niche breadth hypothesis in the butterfly subfamily Nymphalinae. *Ecological Entomology*, **35**, 768–774.

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

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1823–1830.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

van Voorhies, W.A. (1996) Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution*, **50**, 1259–1264.

Vazquez, D.P. & Stevens, R.D. (2004) The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist*, **164**, E1–E19.

WoRMS Editorial Board (2014) World Register of Marine Species. Available at: http://www.marinespecies.org (accessed 20 September 2014).

Wulff, E.V. & Brissenden, E. (1943) *An introduction to historical plant geography* (transl. E. Brissenden, with a foreword by E. D. Merrill). Chronica Botanica Co., Waltham, MA.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 References to data sources.
Appendix S2 Full list of species and data included in analyses.
Appendix S3 Diets of crabs collected in Connecticut, Florida and Panama.
Appendix S4 Relationship between latitude and range size of all species in the dataset.
Appendix S5 Frequency of prey items consumed across all species analysed.

BIOSKETCHES

Katherine Papacostas is interested in both theoretical and applied ecology as well as conservation. Her research examines spatial and temporal variation in marine invasion dynamics, how species interactions change with latitude and global patterns of marine resource usage.

Amy Freestone's research combines community ecology and macroecology. She is primarily interested in the impact of species interactions on community assembly and ecosystem function, and how these processes structure patterns of species diversity across spatial and temporal scales.

Editor: Jonathan Belmaker