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# Latitudinal diversity relationships of fiddler crabs: biogeographic differences united by temperature

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## ABSTRACT

**Aim** To investigate whether latitudinal diversity gradients differ among biogeographic realms for members of a closely related clade and to examine whether differences can be explained by environmental differences such as the temperature gradient.

**Location** Indo-Pacific, eastern Pacific and western Atlantic temperate to tropical coastal intertidal.

**Methods** We digitized the ranges of fiddler crabs (Decapoda, Ocypodidae, genus *Uca*) and calculated standing diversity as a function of latitude in the Indo-west-Pacific, eastern-Pacific Americas and western Atlantic regions. We examined correlations between diversity and summer sea surface temperature, water column primary productivity, and also investigated the contribution of spatial autocorrelation.

**Results** There was a latitudinal diversity gradient with a peak in the tropics or subtropics, but richness as a function of latitude differed by region. The western Atlantic had a broad zone of equal diversity with a peak that corresponds to the Gulf of Mexico–Caribbean Basin. The eastern Pacific had a distinct peak of diversity at about 10° N latitude corresponding to Panama. The Indo-west-Pacific had a broad relatively flat upper level of diversity, reaching a peak at about 20° S latitude corresponding to the north coast of Australia. In both the eastern Pacific and western Atlantic, Northern Hemisphere diversity was greater than Southern Hemisphere. Species richness of the three regions was positively and strongly correlated with air and sea surface temperature at the start of summer. In contrast, diversities were weakly and inconsistently correlated with productivity.

**Main conclusions** This paper shows that a physical factor is more important in explaining latitude distributions than regional cladal structure or presumed dispersal patterns. While observed diversity–latitude functions are region specific, the feature seen across regions to most strongly explaining the pattern is temperature.

## Keywords

Biogeography, diversity, fiddler crabs, latitude, productivity, temperature, *Uca*.

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## INTRODUCTION

The latitudinal diversity gradient is one of the most widespread biogeographic relationships, having been observed in many groups at several taxonomic levels (Stehli *et al.*, 1967; Hillebrand, 2004). In ‘prosobranch’ gastropods, the latitudinal gradient along the east and west coast of the Americas is strikingly similar, and diversity appears related generally to tempera-

ture (Roy *et al.*, 1998). Considering different groups of Crustacea in the Americas, species diversity reaches a peak in the tropics, in the Panamic zoogeographic province in the Pacific and in the Caribbean province in the Atlantic (Boschi, 2000). But in other cases, distinct differences have been found. Benthic diversity, for example, is strikingly more peaked at low latitude on the eastern, relative to the western, side of the Atlantic (MacPherson, 2002). Such regional variation extends to

morphology such as shell size in bivalves (Berke *et al.*, 2012). For pelagic taxa, homogeneity of high species diversity (broad plateaus) is the rule at lower latitudes; however, variance in latitudinal diversity gradients among taxa is great, requiring explanation (MacPherson, 2002). Examples of marine reverse latitudinal species diversity gradients have been noted but are relatively uncommon (Kiel & Nielsen, 2010).

Explanations for the latitudinal correlation with species richness are still elusive (Mittelbach *et al.*, 2007), with debate centring on the whether major oceanic barriers or latitudinal factors (insolation, productivity, habitat area and environmental stability) effectively predict species richness (Roy *et al.*, 1998). Kiel & Nielsen (2010) have related a high-latitude peak in the palaeodiversity of Pacific molluscs to adaptive radiations in interglacial recolonization. Many studies have related diversity to sea surface temperature or to inputs of solar energy (Rohde, 1992; Roy *et al.*, 1998). The actual mechanism(s) promoting rapid diversification at lower latitudes, though, are not so clear. Solar energy input might be related to productivity, which might drive population growth and diversification (Roy *et al.*, 1998; Vermeij, 2004). High temperature itself might foster shorter generation times, greater selection intensity and greater mutation rates (Rohde, 1992), but the connection has not been well specified. The temperature peak may favour a redistribution of species from elsewhere combined with lower extinction rates in the tropics. This explanation is especially attractive in marine coastal clades with high dispersal distances. Temperature has been related to a total input of kinetic energy, either in terms of general tolerance of species of higher temperatures or simply higher metabolic rates (Tittensor *et al.*, 2010).

A basic constraint on distributions might strongly influence the nature of a latitudinal species diversity relationship. If a group is conservative in its thermal niche (Wiens & Graham, 2005), then speciation might occur in warm low-latitude regions, but dispersal and further diversification into higher latitudes might be dampened. Suggesting geographic origin as cause, evidence suggests that species in mollusc lineages may first appear in the tropics before dispersing to higher latitudes (Jablonski *et al.*, 2006). An alternative historical model for birds (Hawkins *et al.*, 2007) posits higher diversification in the tropics, with derived lineages spreading to cooler climates at tropical high altitudes and higher latitudes. But recent deterioration of climate at higher latitudes has resulted in extinction of ancestral lineages at higher latitudes, leaving only less diverse derived and cool-adapted lineages at higher latitudes, creating a current strong latitudinal diversity gradient (Hawkins *et al.*, 2007). In fact, there is general evidence in several taxonomic groups for higher-latitude groups being nested in derived positions on a tree, relative to more ancestral tropical members of the same clade (Mittelbach *et al.*, 2007), which would emphasize the more ancient origin of groups within the tropics.

While most models consider evolutionary history as causally related to climate, a null model, 'the mid-domain effect' (Colwell & Lees, 2000), has been suggested, recognizing the fact that random shuffling of species ranges within the continental domains could alone result in a peak in diversity around the

equator, which is generally the central area. Models using differing dispersal can cause quite different diversity curves (Connolly, 2009), especially when considering species with smaller ranges, and the resulting pattern gained by shuffling appears now to be strongly affected by species with large geographic ranges (Colwell *et al.*, 2009). Yet, a study of Nearctic birds found no difference among species with different sized ranges and poor conformance to the null model (Hawkins & Diniz-Filho, 2002).

In this paper we focus on diversity gradients of a group of closely related species, fiddler crabs (Decapoda, Ocypodidae, genus *Uca*) from three biogeographically distinct domains. This study has the advantage of considering a closely related clade whose species live in a relatively narrow range of intertidal soft-shore habitats, namely sandy and muddy sediments (Crane, 1975). Most species live in open marine salinities or in estuaries; co-existing species usually have some degree of variation of regulation (Thurman, 2002), but only a small number can tolerate very low salinity (Crane, 1975; Barnwell & Thurman, 1984). The narrowness of habitat occurrence strongly reduces potential sources of environmental variation that might affect diversity. We ask whether there is a latitudinal diversity gradient and whether the patterns in these three realms differ. Finally, we try to relate diversity from the three realms to unifying single variables, such as latitude itself, sea surface temperature and water column primary productivity. Reflecting recognition of species complexes occupying different ocean domains, and observation of ecological effects in different, independent replicate communities provides a means of broad inference. As community members, *Uca* are well suited to study as systematically relevant replicates. For example, the Indo-Pacific constitutes an independent clade relative to the Americas (Sturmbauer *et al.*, 1996).

Fiddler crabs are principally a tropical group and striking cases of co-existence of a number of species have been noted, in some instances six or seven species in a few square metres (Crane, 1975; Barnes, 2010). Although a number of species are endemic to basin regions, such as the Gulf of Mexico (Barnwell & Thurman, 1984), endemism at a small scale of 100 km of coast is uncommon. An understanding of the pattern of diversity would be useful in understanding factors that cause diversity changes with latitude and in identifying priorities for conserving areas of biological interest.

## METHODS

The total geographic range of the genus *Uca* was divided into four biogeographic realms:

- (1) Eastern Atlantic (EATL) including the one species living on the eastern Atlantic shore from Portugal to along much of the Atlantic coast of Africa. Only one species lives in this region (Crane, 1975), so it was excluded from further analysis.
- (2) Gulf of Mexico–western Atlantic (WATL), including all species living along the Atlantic coast of North America, the Gulf of Mexico and the Caribbean Basin, and the Atlantic shore of South America.

(3) Eastern Pacific (EPAC), including all species living along the Pacific and adjacent estuarine shores of the Americas.

(4) Indo-west-Pacific (IWP), which includes all species occurring in the Indian Ocean and Pacific Oceans, not including those species living along the Pacific coast of the Americas.

We used data on the digitized ranges of 88 taxa, close to the total number (97, Rosenberg, 2001; but see Landstorfer & Schubart, 2010) of species of *Uca*, to accumulate latitudinal species richness curves by each degree of latitude. ARCMAP v. 9.1 (ESRI Corporation, Redlands, CA, USA) was used to trace ranges along coastlines. Lines were converted into chains of cells 50 km × 50 km on a cylindrical equidistant global projection. Usually ranges were continuous, but we also found a disjunct range for one species (*Uca leptodactyla*). For the combined global species data we calculated a random distribution of ranges for comparison (Colwell & Lees, 2000; Colwell *et al.*, 2004). We used a series of pseudo-random numbers to select random and northern and southern extremes of ranges for species on a relative range scale of [0,1]. We used 10,000 random ranges to generate a diversity curve on 100 'latitudes' over the range scale. The resultant curve was scaled to the data by fitting the maximum species richness of the actual data to the peak of the random data set and the zero points of the random data set to the northern and southern latitudes where species richness reaches zero in the *Uca* data set.

We acquired data on summer sea surface temperature (SSST) and winter sea surface temperature (WSST) by each degree of latitude for 20 June in the Northern Hemisphere and 20 December in the Southern Hemisphere from the NOASS/NESDIC 50-km resolution maps ([http://www.ospo.noaa.gov/Products/ocean/sst/50km\\_night/index.html](http://www.ospo.noaa.gov/Products/ocean/sst/50km_night/index.html)) for summer and the reverse scheme for winter. For the WATL and EPAC regions we used temperatures at the coastline to the nearest degree centigrade. For the IWP, which has a vast longitudinal range, we arbitrarily used a temperature determined at the coast that intersected nearest to 120° longitude. Surface air temperature data for summer (SSAT) and winter (WSAT), to the nearest 0.1 °C, was collected using the WorldClim database (Hijmans *et al.*, 2005) at every degree of latitude. Summer air temperature was considered as the June average in the Northern Hemisphere and the December average in the Southern Hemisphere, with the reverse for winter. Temperature from this database was an average for 1951–2000. We used averaged calculated primary productivity from satellite-derived chlorophyll data, taken from annual average SEAWIFS satellite data (Behrenfeld & Falkowski, 1997). We compared the relative explanatory power of the four measures of temperature by comparing values of  $R^2$  and the Akaike information criterion (AIC) for the individual temperature measures and measures taken in combination. These were calculated using stepwise regression of temperature parameters against species number, using JMP v. 7.0 (SAS Institute Inc., Cary, NC, USA). We used productivity data only for the WATL and EPAC realms, which was taken along the continental coasts on the Atlantic and Pacific sides of the Americas. The IWP covers a far too large two-dimensional area for such an analysis to be very useful.

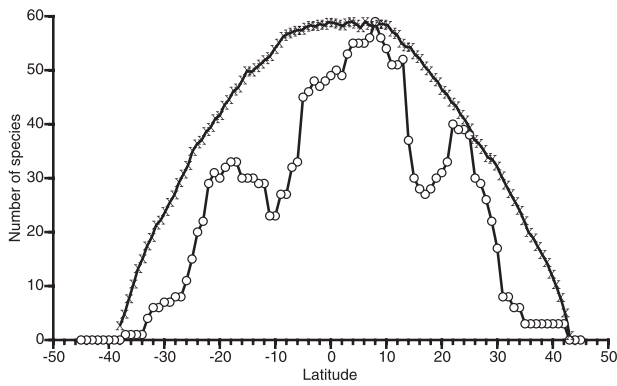
We used two measures of effect size to estimate the latitudinal gradient and its relation to temperature and primary production, following Hillebrand (2004). The strength of the latitude–diversity relationship as measured by  $r^2$ , the percentage of variance explained, and the steepness, as measured by a linear approximation of the trend of species richness as a function of latitude. It is not clear that the measures we used of species number, temperature or primary productivity were normally distributed. Moreover, geographically adjacent latitudes consist of a number of species that are present at both sites. Accordingly, for bivariate correlations we calculated nonparametric correlations based upon Spearman's rho. For tests involving comparisons among regions we used a nonparametric method based upon ranks to make comparisons of trends, by analysis of covariance, according to the method suggested by Conover & Iman (1981). Statistical tests and power analysis were performed using JMP v. 7.0.

Latitudinal correlations between variables are complicated by spatial autocorrelation, where the correlation between two variables (e.g. species number and temperature) is influenced by the spatial distance between sites. In the case of one-dimensional gradients, this is especially difficult because a monotonic change of temperature, as would be expected with a change of latitude, will inevitably have spatial autocorrelation. We evaluated the influence of spatial autocorrelation using two approaches, when relating species number to sea surface temperature. First we evaluated the correlation between SSST and species richness, but then evaluated a correlation corrected for spatial autocorrelation, using a modified *t*-test (Clifford *et al.*, 1989). These tests were implemented using the spatial analysis software PASSAGE 2.0 (Rosenberg & Anderson, 2011). Interlatitude distance classes were combined to 10 classes. This analysis was done by region and for all regions combined. Distances were measured in terms of units of latitude. Waller & Gotway (2004) suggest that a complementary approach would consider the spatial autocorrelation of residuals from a regression plot of environmental variables. We therefore used our previous calculations of regression relationships of temperature and latitude and examined the spatial autocorrelation of the residuals to see if spatial autocorrelation existed beyond that explained by species–temperature predictions. We calculated Moran's *I* to inspect for changes of correlations of the residuals with distance for the combined three biogeographic regions. This graph was produced by use of PASSAGE 2.0 (Rosenberg & Anderson, 2011).

## RESULTS

### Latitude and hemisphere variation

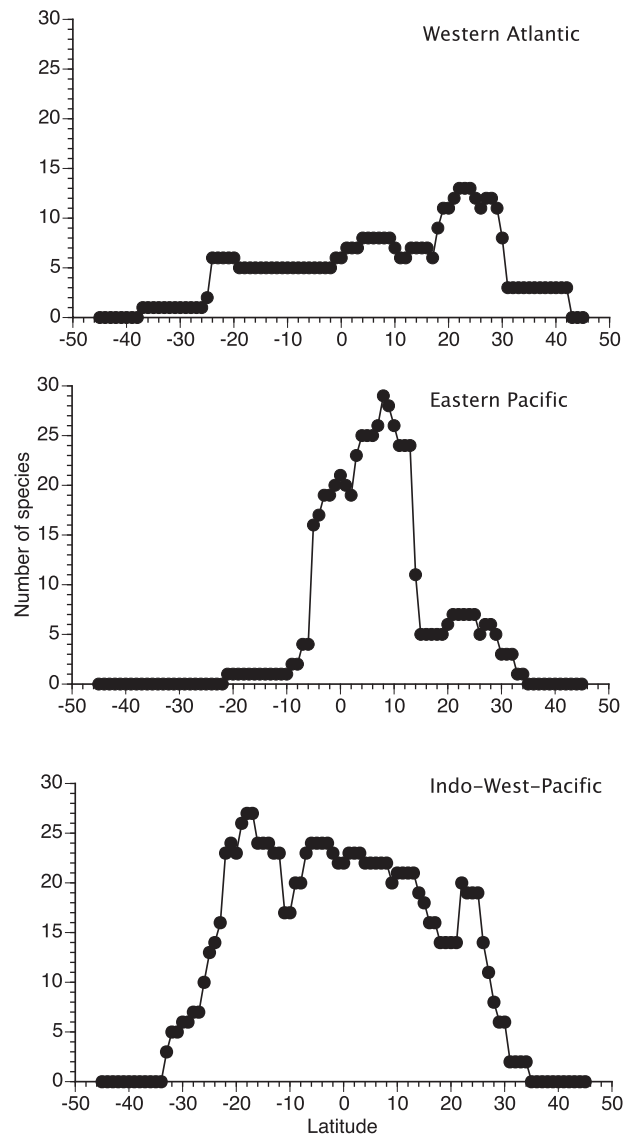
Figure 1 shows species richness as a function of latitude for *Uca* species in the combined IWP, EPAC and WATL realms. Diversity reaches a peak at about 10° N latitude and declines to two symmetrical shoulders at around 10 to 20° S latitude and 16 to 26° N latitude. The drop-off from the peak is far greater at both the north and south of the equator than would be predicted from the raw random distribution.



**Figure 1** Species numbers of *Uca* as a function of latitude in the combined WATL (western Atlantic), EPAC (eastern Pacific) and IWP (Indo-west-Pacific) regions. (open circles). Diversity is compared with a random expectation (x).

Figure 2 shows species richness as a function of latitude for the three individual biogeographic regions. The shapes of the distributions differ considerably, and the locations of diversity maxima also differ. The WATL region shows overall lower diversity than the other two regions and a level value of diversity from 20° S to 20° N, with a peak at approximately 25° N latitude, which corresponds to the Gulf of Mexico and Caribbean Basin. The diversity of the EPAC region reaches a sharp peak at about 10° N latitude with a strong drop-off northward and southward. The IWP region has a broad and level distribution from 18° N to 15° S latitude, with a slight drop and then a peak at 20° S latitude, corresponding to northern Australia. Table 1 shows Kolmogorov–Smirnov two-sample comparisons for all regions and the total distribution. Even when taking into account the higher stringency of probability for multiple comparisons (via Bonferroni correction, a significant difference at the 0.05 level corresponds with multiple comparisons to  $P < 0.008$ ), it is clear that all regional distributions differ significantly from each other as do all from the total *Uca* latitudinal diversity–latitude relationship) with  $P < 0.001$  probability level). This suggests that factors other than simple latitude and its correlates control the diversity gradients of the three biogeographic realms. Comparing the three regions, length of the coastal zone occupied by fiddler crab ranges clearly is not related to overall diversity differences (J.L. and J.M., unpublished). For example, much of the diversity of the EPAC region is crowded in a narrow coastline including a region centred in Panama, but is the most diverse of the three regions.

There are notable differences in the latitudinal diversity gradient between the Northern and Southern hemispheres (Fig. 2). In the WATL region, there is a maximum diversity in the Northern Hemisphere at latitudes 20–30° N, corresponding to the Gulf of Mexico–Caribbean Basin. A general excess of species richness is found in the Northern Hemisphere of the EPAC region, relative to corresponding values of latitude in the Southern Hemisphere. But species richness is maximal in the IWP region in the vicinity of 20° S latitude, owing to the local presence of members of the subgenus *Australuca* along with other species on the northern coast of Australia.



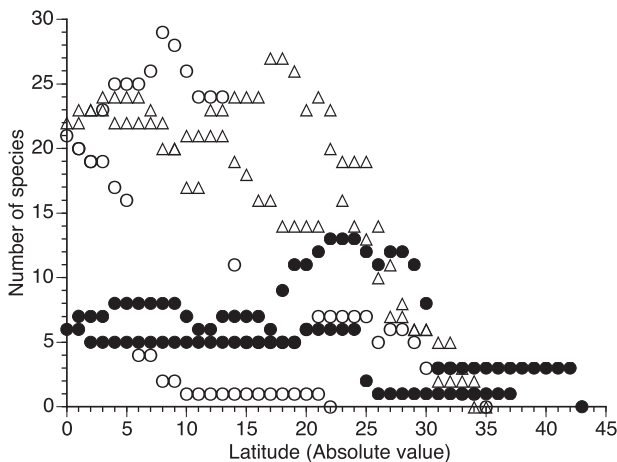
**Figure 2** Species richness of *Uca* as a function of latitude for the three biogeographic regions.

Figure 3 shows a plot of species richness versus the absolute value of latitude, as a function of biogeographic region. The WATL is distinct in its lower value of species richness and lower slope of species richness as a function of latitude, but the IWP also appears to be shifted to the right of the EPAC, though the slopes are not apparently significantly different. Table 2 shows our two measures of effect size,  $r^2$  and slope, of diversity with latitude. The slope of species versus latitude for both EPAC and IWP are much greater than for the WATL, and the same relationship holds for the percentage of variance explained by the relationship. The ANCOVA analysis based on ranks (Conover & Iman, 1981) demonstrates a significant heterogeneity of slope ( $F = 29.35$ , d.f. = 2,  $P < 0.001$ ); residuals from the regressions are approximately normally distributed. The slope heterogeneity is consistent with the visual differences among biogeographic

**Table 1** Comparison of latitudinal diversity curves for the three biogeographic realms. Kolmogorov-Smirnov two-sample comparisons (Kolmogorov-Smirnov values above the diagonal; probabilities below the diagonal).

	WATL	EPAC	IWP	Total
WATL	–	0.325	0.614	0.675
EPAC	$< 3.4 \times 10^{-4}$	–	0.421	0.554
IWP	$10^{-7}$	$10^{-6}$	–	0.554
Total	$10^{-7}$	$10^{-7}$	$10^{-7}$	–

EPAC, eastern Pacific; IWP, Indo-west-Pacific; WATL, Gulf of Mexico–western Atlantic.



**Figure 3** Species number versus absolute value of latitude for WATL (western Atlantic) (closed circles), EPAC (eastern Pacific) (open circles), and IWP (Indo-west-Pacific) (triangles) biogeographic realms.

**Table 2** Values of proportion of variance explained ( $r^2$ ) and slope of relationship of ranked number species as a function of ranked absolute value of latitude for the WATL, EPAC and IWP regions.

Region	$r^2$	Slope	$P$ for Spearman's rho
WATL	0.15	–0.11	$< 10^{-4}$
EPAC	0.40	–0.63	$< 10^{-4}$
IWP	0.68	–0.63	$< 10^{-4}$
Total	0.64	–0.44	$8 \times 10^{-4}$

EPAC, eastern Pacific; IWP, Indo-west-Pacific; WATL, Gulf of Mexico–western Atlantic.

regions that are observable in Fig. 3 and shown in Table 2, with the WATL having a lower slope of species richness on latitude.

### Temperature relationships

Table 3 shows a comparison of the success of the four measures of temperature in relation to species number. Using  $r^2$  and the

**Table 3** Success of different temperature parameter estimates, using the  $r^2$  and Akaike information criteria (AIC). A higher value of  $r^2$  and lower value of AIC, respectively, indicate better fits.

Parameter	$r^2$	AIC
Summer air temperature	0.42	776.4
Winter air temperature	0.32	810.4
Summer water temperature	0.36	796.8
Winter water temperature	0.25	829.7
Combined variables	0.46	768.0

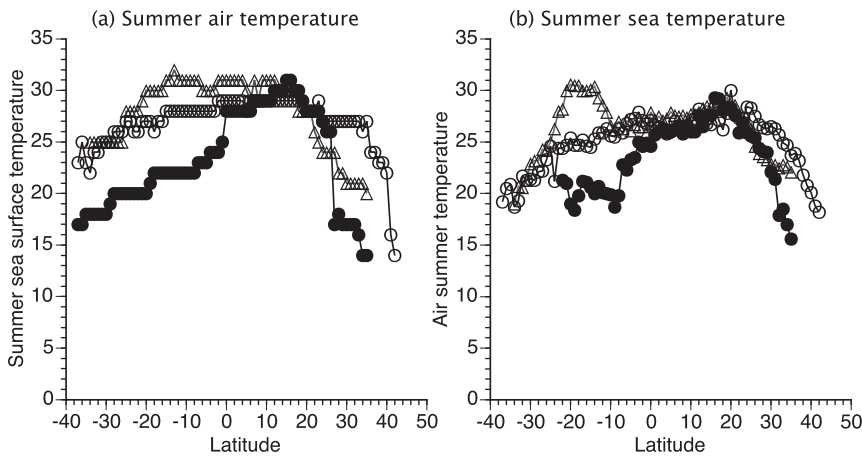
AIC criterion, SSAT and SSST best explain temperature relations with species richness. As a consequence we present analyses below using these parameters. Fit was improved with a more complex model; all four parameters combined have a maximum value for  $r^2$  and a minimum (best) value for AIC.

While SSST obviously declines with increasing latitude, there are interesting differences among biogeographic realms (Fig. 4a). For example, the WATL summer temperature is greater than the other two regions at latitudes 30–45° N. The EPAC was notably cooler than the other two realms from c. 0–25° S latitude and 28–36° N latitude, and its thermal gradient had a more pronounced low-latitude peak than the other two realms. There also are notable differences among latitude–temperature relations with regard to SSAT (Fig. 4b). Most notable is a dramatic fall-off of SSAT at 10–20° S latitude for the EPAC region, but a rather dramatic increase of temperature in the IWP at these same latitudes. A smaller IWP excess at 10–20° S latitude can also be seen for SSST.

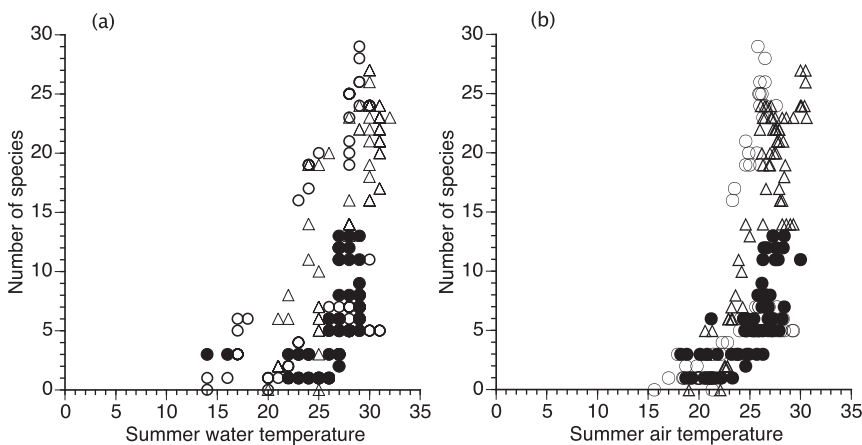
Figure 5 shows a strong similarity between temperature and species richness among regions – much stronger than the relationship of species richness to latitude. Using the ranks approach, we investigated possible differences among biogeographic realms in the relationship of ranked species richness relative to temperature range. In all regions, there is a significant relationship between summer air or summer water temperature and species richness ( $P < 0.0001$ , Spearman's rho correlation). Considering ranked species number and ranked temperature, there appears to be no difference in slopes of summer sea temperature relations for different biogeographic realms (ANCOVA analysis of homogeneity of summer temperature slope differences: for sea,  $F = 1.58$ ,  $P = 0.21$ , d.f. = 2; for air,  $F = 0.39$ ,  $P = 0.69$ , d.f. = 2). However, as is also apparent in the plot (Fig. 5a,b), while the slopes are homogeneous, the WATL region is displaced downward for both SSST and SSAT (sea,  $F = 37.12$ , d.f. = 2  $P < 0.0001$ ; air,  $F = 6.90$ , d.f. = 2  $P \sim 0.001$ ). Thus while observed species diversity is relatively lower, the trend does not change.

Table 4 shows our analysis of the correlation between SSST and species number, corrected for spatial autocorrelation. With the correction, the WATL relationship is still significant, but the relation for the other two regions is not. When data from the three regions are pooled, the temperature–diversity relationship is still significant with the correction for spatial autocorrelation.

As mentioned above, the difficulty with this analysis is the direct correspondence between latitude and temperature



**Figure 4** Temperature near the beginning of summer (June for Northern Hemisphere, January for Southern Hemisphere) for (a) summer air temperature and (b) summer sea surface temperature for the three biogeographic realms as a function of latitude. Open circles, WATL (western Atlantic); closed circles, EPAC (eastern Pacific); triangles, IWP (Indo-west-Pacific).



**Figure 5** Species richness as a function of (a) summer sea surface temperature and (b) summer air temperature for the three regions: WATL (western Atlantic) (closed circles); EPAC (eastern Pacific) (open circles); IWP (Indo-west-Pacific) (open triangles).

**Table 4** Correlations of summer sea surface temperature and species richness for the three regions and combined regions calculated directly and with a correction for spatial autocorrelation.

Region	Correlation	Conventional <i>P</i>	Corrected <i>P</i>
WATL	0.397	$2.5 \times 10^{-4}$	0.044
EPAC	0.515	$4 \times 10^{-5}$	0.128
IWP	0.467	$5 \times 10^{-5}$	0.235
Combined	0.594	$< 10^{-5}$	0.053

EPAC, eastern Pacific; IWP, Indo-west-Pacific; WATL, Gulf of Mexico–western Atlantic.

change, which makes it unclear what it means to correct for spatial autocorrelation. Figure 6 shows a correlogram plot of Moran’s *I* for spatial autocorrelation of residuals from a temperature–species number regression of ranked species on SSST for the combined three biogeographic regions. The values of *I* hover around zero and the residuals show no apparent patterns of spatial autocorrelation, which suggests that for the combined data set, temperature is a sufficient explanatory variable for species number, even though temperature is clearly a spatially autocorrelated parameter.

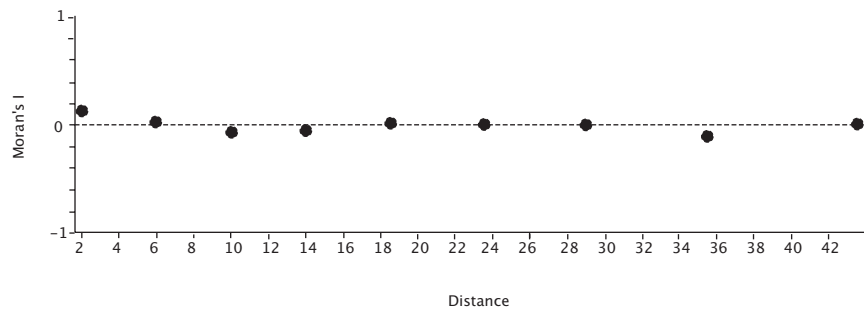
### Primary productivity

Using a linear regression approach, a negative relationship was found (Fig. 7) between primary productivity and latitude for the WATL ( $r^2 = 0.18$ ,  $P < 0.0001$ ,  $n = 81$ ) and similar results are obtained for the ranks of these parameters. However, for the EPAC, there was no relationship between primary productivity and species number ( $r^2 = 0.01$ ,  $P = 0.41$ ). Despite the significance in the WATL relationship, the values of  $r^2$  for both WATL and EPAC were considerably lower than for comparisons of either latitude or temperature with number of species. Further, a combination of the two regions shows no significant relationship between species number and productivity ( $r^2 = -0.01$ ,  $P = 0.32$ ). ANCOVA of the ranked species and productivity relationships demonstrates a significant difference in the slope of species on productivity in the WATL and EPAC ( $F = 7.91$ ,  $P = 0.006$ ) – this is apparently reflective of the negative slope of the WATL species–primary productivity relationship.

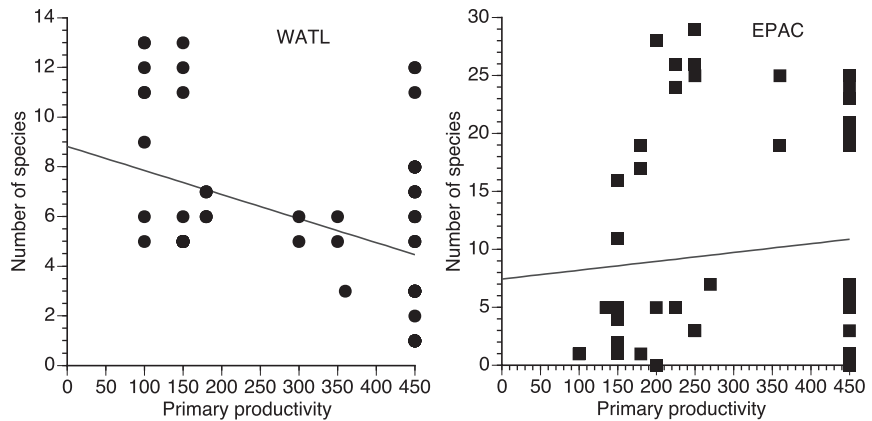
### Relation of primary productivity to temperature

Because both primary productivity and temperature are related to species richness it is of interest to determine if primary productivity and temperature are themselves related and whether

**Figure 6** Spatial autocorrelation of residuals from a temperature–species number regression, as a function of latitudinal distance, for the combined three biogeographic regions between summer sea surface temperature and species number, as visualized by Moran's  $I$ .



**Figure 7** Primary productivity versus species richness: WATL (western Atlantic) (closed circles); EPAC (eastern Pacific) (closed squares).



the relationship is similar within the EPAC and WATL regions. We performed an ANCOVA with primary productivity as the dependent variable, temperature the independent variable, and region the covariate. The results are the same using raw values of temperature and primary productivity or ranks. For raw values, there is a significant overall negative relationship between temperature and primary productivity in the WATL ( $F = 13.93$ ,  $P = 0.0004$ ) but not in the EPAC ( $F = 1.26$ ,  $P = 0.27$ ). But there is a difference in slope between regions ( $F = 5.59$ ,  $P = 0.02$ ), with a more negative slope for the WATL (Fig. 7).

We conducted a power analysis for the effect of temperature and primary productivity on rank species occurrence, using a GLM model in JMP, considering the rank number of species as the dependent variable and rank temperature and rank primary productivity as the independent variables. For temperature, power = 1.0, but for primary productivity, power = 0.09. Given this much lower power (consistent also with low  $r^2$  values observed) we would probably fail to see a relationship for primary productivity if one existed. The high statistical power found for temperature is also consistent with the high  $r^2$  obtained for temperature–species relationships within regions.

## DISCUSSION

The genus *Uca* is distributed throughout the tropics along soft shores. The three diverse regions have rather different coastal distributions. The EPAC species occur along a sinuous coast over a linear latitudinal range. By contrast, the WATL species have a central broad region in the Gulf of Mexico and Caribbean

Basin. The Indo-Pacific distributions occur over a large longitudinal range, from the east coast of Africa to islands somewhat east of Australia, and also occur over a larger coastline range than the other two biogeographic regions (J.L. *et al.*, in preparation). Thus it may not be very surprising that the latitudinal diversity gradients and their respective low-latitude peaks of richness are distinct from each other, even if they all show a general increase of species richness toward the tropics. Coastline length alone fails to explain differences because the EPAC is the most diverse but has the shortest coastline of the three regions (J.L. *et al.*, in preparation).

The genus *Uca*, which includes a small number of sister species pairs on either side of the Isthmus of Panama, has a complex geographic distribution of clades across different ocean basins (Sturmbauer *et al.*, 1996). Overall, the *Uca* species complex considered in terms of phylogenetic (morphological character derived) distance (Rosenberg, 2001) was shown to have low correlation of genetic distance and spatial dispersion, with taxa being widely dispersed except at the global level (Nabout *et al.*, 2010). This analysis found that while there was weak phylogenetic spatial autocorrelation overall, phylogenetic spatial correlation was strong along the axis of longitudinal position, which may be partially explained by phylogenetic differences occurring *between* whole ocean basins (particularly the IWP and the Americas).

Assessed from morphological phylogenetic and mitochondrial gene (*16S*) data, the Indo-Pacific group *Uca* complex is phylogenetically distinct from the EPAC and WATL regions (Sturmbauer *et al.*, 1996; Rosenberg, 2001). But there is no geo-

graphic relationship within the IWP between geographic distance and phylogenetic distance between species in this clade (Nabouk *et al.*, 2010). Apparently dispersal has been sufficient to cause strong overlap and mixing that has erased much of the spatial context of speciation history.

The EPAC and WATL fiddler crabs constitute the most complex set of phylogenetic relationships: members of multiple shallower clades occur on both Atlantic and Pacific shores. There is a significant relation between geographic distance and phylogenetic difference for all of the Americas taken together (Nabouk *et al.*, 2010), but not apparently within the EPAC or WATL (J.L. *et al.*, in preparation). One clade identified by Rosenberg (2001) and corresponding largely to the subgenus *Leptuca* (nee *Celuca*, Crane), is confined to the EPAC with one exception that likely preceded the rise of the Isthmus of Panama. Another clade in the subgenus *Leptuca*, consisting of (*batuenta*, *saltitanta*, *tenuipedis*), (*speciosa*, *spinicarpa*) (Rosenberg, 2001) appears to include a trans-isthmian split between Atlantic and Pacific. But members of two subgenera (*Minuca* and *Uca*) have representatives on both sides of the Americas. A newly described species from the Pacific coast of Costa Rica is closely related to the trans-isthmian sister species pair *Uca ecuadoriensis* and *Uca vocator* (Landstorfer & Schubart, 2010). Thus the relationship between evolutionary history, dispersal and latitude within the Americas is complex.

The low-latitude peaks of diversity in the WATL and IWP are associated with possible sites of geographic isolation and local speciation. The Gulf of Mexico corresponds with the low-latitude peak of diversity and six of the total of 21 WATL species are endemic to the gulf (Barnwell and Thurman, 1984, <http://www.fiddlercrab.info>). The IWP low-latitude peak is associated with the occurrence of five species of the subgenus *Australuca* along the north coast of Australia and three species from other subgenera (Crane, 1975). These species are associated with the Sahul shelf and may reflect isolation from the Sunda shelf to the north-west across the Timor Sea (van Andel *et al.*, 1969; Lohman *et al.*, 2011). Otherwise the IWP diversity maximum is spread broadly over a broad range of low latitudes (Fig. 2). The EPAC peak is the most distinct, with a strong maximum along the Pacific coast of Panama (Crane 1975 and Fig. 2). This peak includes species belonging to several subgenera and is congruent with a general peak in brachyuran diversity (Boschi, 2000). We found a more gradual drop in diversity from the WATL peak in the Caribbean province with increasing latitude, an observation also found in viewing multiple brachyurans (Boschi, 2000). Notably, the three low-latitude peaks in diversity of the three biogeographic realms are in widely differing latitudes (Fig. 2).

While intrinsic biogeographic influences are evident, there is a strong unity imposed when summer water or air temperature is plotted against species richness. In fact, the only noticeable difference in species richness as a function of temperature between the three realms is a small shift in intercept, toward generally lower diversity for the WATL realm, relative to the EPAC and IWP. More notable is the strong low-latitude peak in species diversity of the EPAC region (Fig. 2), which corresponds to a low-latitude strong peak of summer temperature (Fig. 4).

By contrast, the WATL and IWP have broader upper bounds of species diversity over a wide range of latitude, and this is reflected in the broad flat peak of summer temperature in the low latitudes (Fig. 4). The IWP latitudinal data are complicated by species occurrence over a broad range of longitudes, ranging from the coast of east Africa to the east Asian coast. Most of the diversity however, is to be found in the Southeast Asian region, where we assayed SSST and surface air temperature. Therefore, while no causative factor can be drawn from this, summer temperature is a good predictor of species diversity and unifies differences in latitudinal patterns among three distinct biogeographic regions. The relationship is instructive, and we stress not comprehensive. The eastern Atlantic has, anomalously, just one species, *Uca tangeri*.

While temperature has a strong explanatory relation to diversity, there does appear to be a signal related to primary productivity, at least in one region, with species diversity being inverse to productivity, (and positively related to summer temperature). Thus productivity itself is not a direct factor driving diversity. In any event, there was a very weak relationship of productivity to diversity. Temperature is clearly a better correlated factor.

Studies of latitudinal marine taxonomic gradients have generally been done at large taxonomic scales, often across widely disparate taxonomic groups (MacPherson, 2002; Tittensor *et al.*, 2010). Roy *et al.* (1998) found very similar latitudinal diversity patterns for 'prosobranch' gastropods on the Atlantic and Pacific coasts of the Americas and related this ultimately to temperature. A global marine analysis demonstrates a strong relationship of diversity to sea surface temperature for a wide range of marine taxonomic groups (Tittensor *et al.*, 2010). Studies such as these have rarely been done at smaller taxonomic scales, such as at the level of a genus. The numbers are not high, but fiddler crabs have the advantage of occurring in three distinct biogeographic realms over broad ranges of latitude. Thus the overall strong unifying correlation of sea surface temperature to diversity is of great interest, and consistent with an energy-speciation hypothesis (Rohde, 1992; Roy *et al.*, 1998; Vermeij, 2004, 2005), perhaps where energy input has indirect effects on competition and other biological factors (Vermeij, 2005). On the other hand the proximate factor of productivity fails to have a strong correlation with diversity, so the relationship cannot be a simple energy-to-diversity linear effect.

We suggest that physiological and behavioural correlates be explored further to examine the strong association of fiddler crab diversity with regional temperature. The role of temperature in regulating latitudinal diversity gradients in the genus *Uca* may have two distinct components. First, the genus *Uca* appears to be largely a tropical taxon. Mating behaviour requires males to spend a great deal of time in air, and activity in these poikilotherms requires input of solar energy. At higher latitudes, reproduction is limited temporally because of lower thermal input and shorter seasons of high temperature. In the tropics a long warm season allows males and females to function efficiently in air for the entire year. High temperatures do cause thermal stress (Allen *et al.*, 2012) but individuals can periodically retreat to moist burrows to gain water and cool down. Other plastic



responses include adjustment of chromatophores, which alter the reflectivity of the carapace in sunlight (Wilkins & Fingerman, 1965). During times of high temperature, males are heat and water stressed, and the major claw acts as a heat sink, allowing dissipation of heat from the carapace (Darnell & Munguia, 2011). In porcelain crabs, there is evidence for the evolution of upper thermal tolerances in accordance with local thermal conditions (Stillman & Somero, 2000). It is therefore possible that higher-latitude fiddler crabs have evolved enhanced activity at lower temperature. But it is equally possible that higher-latitude environmental conditions are inherently limiting to aerial activity and may therefore influence species survival and diversity outside of the tropics.

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## REFERENCES

- Allen, B.J., Rodgers, B., Tuan, Y. & Levinton, J.S. (2012) Size-dependent temperature and desiccation constraints on performance capacity: implications for sexual selection in a fiddler crab. *Journal of Experimental Marine Biology and Ecology*, **438**, 93–99.
- van Andel, T.H., Heath, G.R., Moore, T.C. & McGeary, D.F.R. (1969) Quaternary history, climate, and oceanography of the Timor Sea, northwestern Australia. *American Journal of Science*, **265**, 737–758.
- Barnes, R.S.K. (2010) A remarkable case of fiddler crab (*Uca* spp.) alpha diversity in Wallacea. *Hydrobiologia*, **637**, 249–253.
- Barnwell, F.H. & Thurman, C.L., II (1984) Taxonomy and biogeography of the fiddler crabs (Ocypodidae: Genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. *Zoological Journal of the Linnean Society*, **81**, 23–87.
- Behrenfeld, M.J. & Falkowski, P.G. (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, **42**, 1–20.
- Berke, S.K., Jablonski, D., Krug, A.Z., Roy, K. & Tomašových, A. (2012) Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia worldwide. *Global Ecology and Biogeography*, **22**, 173–183.
- Boschi, E.E. (2000) Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. *Revista de Investigación y Desarrollo Pesquero*, **13**, 1–136.
- Clifford, P., Richardson, S. & Hemon, D. (1989) Assessing the significance of the correlation between two spatial processes. *Biometrics*, **45**, 123–134.
- Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, **15**, 70–76.
- Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, **163**, E1–E23.
- Colwell, R.K., Gotelli, N.J., Rahbek, C., Entsminger, G.L., Farrell, C. & Graves, G.R. (2009) Peaks, plateaus, canyons, and craters: the complex geometry of simple mid-domain effect models. *Evolutionary Ecology Research*, **11**, 355–370.
- Connolly, S. (2009) Macroecological theory and the analysis of species richness gradients. *Marine macroecology* (ed. by J. Witman and K. Roy), pp. 279–309. University of Chicago Press, Chicago, IL.
- Conover, W.J. & Iman, R.L. (1981) Analysis of covariance using the rank transformation. *Biometrics*, **38**, 715–724.
- Crane, J. (1975) *Fiddler crabs of the world*. Princeton University Press, Princeton, NJ.
- Darnell, M.Z. & Munguia, P. (2011) Thermoregulation as an alternate function of the sexually dimorphic fiddler crab claw. *The American Naturalist*, **178**, 419–428.
- Hawkins, B.A. & Diniz-Filho, J.A.F. (2002) The mid-domain effect cannot explain the diversity gradient of Nearctic birds. *Global Ecology and Biogeography*, **11**, 419–426.
- Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007) Niche conservatism, and the global bird diversity gradient. *The American Naturalist*, **170**, S16–S27.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 193–211.
- Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.
- Kiel, S. & Nielsen, S.N. (2010) Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology*, **38**, 955–958.
- Landstorfer, R.B. & Schubart, C.D. (2010) A phylogeny of Pacific fiddler crabs of the subgenus *Minuca* (Crustacea, Brachyura, Ocypodidae: *Uca*) with the description of a new species from a tropical gulf in Pacific Costa Rica. *Journal of Zoological Systematics and Evolutionary Research*, **48**, 213–218.
- Lohman, D.J., De Bruyn, M., Page, T., Von Rintelen, K., Hall, R., Ng, P.K.L., Shih, H.-T., Carvalho, G.R. & Von Rintelen, T. (2011) Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution and Systematics*, **42**, 205–226.
- MacPherson, E. (2002) Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1715–1720.
- 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.

- Nabou, J.C., Terribile, L.C., Bini, L.M. & Diniz-Filho, J.A.F. (2010) Phylogenetic autocorrelation and heritability of geographic range size, shape and position of fiddler crabs, genus *Uca* (Crustacea, Decapoda). *Journal of Zoological Systematics and Evolutionary Research*, **48**, 102–108.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514–527.
- Rosenberg, M.S. (2001) The systematics and taxonomy of fiddler crabs: a phylogeny of the genus *Uca*. *Journal of Crustacean Biology*, **21**, 839–869.
- Rosenberg, M.S. & Anderson, C.D. (2011) Passage: pattern analysis, spatial statistics, and geographic exegesis. Version 2. *Methods in Ecology and Evolution*, **2**, 229–232.
- Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. (1998) Marine latitudinal diversity gradients—tests of causal hypotheses. *Proceedings of the National Academy of Sciences USA*, **95**, 3699–3702.
- Stehli, F.G., McAlester, A.L. & Helsley, C.E. (1967) Taxonomic diversity of recent bivalves and some implications for geology. *Geological Society of America Bulletin*, **78**, 455–466.
- Stillman, J.H. & Somero, G.N. (2000) A comparative analysis of the upper thermal tolerance limits of eastern pacific porcelain crabs, genus *Petrolisthes*: influences of latitude, vertical zonation, acclimation, and phylogeny. *Physiological and Biochemical Zoology*, **73**, 200–208.
- Sturmbauer, C., Levinton, J.S. & Christy, J. (1996) Molecular phylogeny analysis of fiddler crabs: test of the hypothesis of increasing behavioral complexity in evolution. *Proceedings of the National Academy of Sciences USA*, **93**, 10855–10857.
- Thurman, C.L. (2002) Osmoregulation in six sympatric fiddler crabs (genus *Uca*) from the northwestern Gulf of Mexico. *Marine Ecology*, **23**, 269–284.
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature*, **466**, 1098–1101.
- Vermeij, G.J. (2004) *Nature: an economic history*. Princeton University Press, Princeton, NJ.
- Vermeij, G.J. (2005) From phenomenology to first principles: toward a theory of diversity. *Proceedings of the California Academy of Sciences*, **56**, Supplement I, No. 2, 12–23.
- Waller, L.A. & Gotway, C.A. (2004) *Applied spatial statistics for public health data*. Wiley Interscience, Hoboken, NJ.
- Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution and Systematics*, **36**, 519–539.
- Wilkens, J.L. & Fingerman, M. (1965) Heat tolerance and temperature relationships of the fiddler crab, *Uca pugilator*, with reference to body coloration. *Biological Bulletin*, **128**, 133–141.

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