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Spatial patterns of morphological diversity across the Indo-Pacific: analyses using strombid gastropods

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Biological diversity can be measured using various metrics, but existing knowledge of spatial patterns of diversity is largely based on species counts. There is increasing evidence that trends in species richness might not match trends in other biodiversity metrics, such as morphological diversity. Here, we use data from a large group of Indo-Pacific gastropods (family Strombidae) to show that the species richness of a region is a poor predictor of the morphological diversity present there. Areas with only a few species can harbour an impressive array of morphologies and, conversely, morphological diversity in the most species-rich regions is no higher than in regions with half their taxonomic diversity. Biological diversity in the Pacific is highly threatened by human activity and our results indicate that, in addition to species richness, morphological diversity metrics need to be incorporated into conservation decisions.

Keywords: morphological diversity; Indo-Pacific; Strombidae; Gastropoda

1. INTRODUCTION

Biological diversity can be quantified using various metrics that range from species counts to ecological and phylogenetic diversity, each of which highlights a different aspect of biodiversity (Harper & Hawksworth 1994; Williams & Humphries 1996; Purvis & Hector 2000). Existing knowledge about spatial patterns of biodiversity is based almost exclusively on taxonomic richness, i.e. numbers of species or higher taxa (Groombridge 1992; Gaston 2000). Although species richness usually correlates with other metrics of biodiversity (Magurran 1988), the strengths of such correlations vary between different groups of organisms and different regions (e.g. Gaston 1996). Morphological diversity is arguably one of the most intuitive measures of biological variety (Williams *et al.* 1994; Williams & Humphries 1996), and palaeontological studies have shown that temporal trends in morphological diversity are often poor predictors of taxonomic richness trends (Roy & Foote 1997; Foote 1997). However, for most groups of living organisms very little data exist on how spatial patterns of species richness relate to similar trends in morphological diversity.

For marine organisms, the area around the Philippines, Malay Peninsula and New Guinea has long been known to harbour the greatest number of species, with species richness declining outwards from this region (Ekman 1953; Connell 1978; Levinton *et al.* 1996; Briggs 1974, 1999*b*). The ecological and evolutionary processes that underlie this prominent species richness gradient in the Pacific remain a subject of intense debate (McCoy & Heck 1976; Vermeij 1987; Rosen 1988; Pandolfi 1992; McMillan & Palumbi 1995; Levinton *et al.* 1996; Palumbi 1997; Briggs 1999*a,b*), but the ecological and morphological changes associated with this gradient have not been well studied. Gastropods of the family Strombidae are among the groups for which species-level distributional patterns are best known (Abbott 1960, 1961; Walls

1980), and they are commonly cited as a classic example of the Indo-Pacific species-richness gradient (e.g. Briggs 1974, 1999*b*; Vermeij 1987). This monophyletic clade of gastropods (M.E.H. and K.R., unpublished DNA sequence data) also provides an ideal system for quantifying spatial patterns of morphological diversity, as they show a wide spectrum of shell shapes that results in high overall morphological diversity (Roy 1996) and well over an order of magnitude variation in body size (Abbott 1960, 1961). In addition, shell growth in strombids is determinate (Abbott 1960, 1961; Vermeij & Signor 1992), which allows unambiguous identification of adult specimens. Here, we compare and contrast spatial patterns of species richness and morphological diversity across the Indo-Pacific in 82 species and named subspecies of strombid gastropods.

2. METHODS

We compiled a database of occurrences of strombid taxa throughout the Pacific using published range maps (e.g. Abbott 1960, 1961; Walls 1980). Spatial trends in species richness and morphological diversity were quantified using a 20° latitude × 20° longitude grid. Although distributional patterns of strombid gastropods are better known than those of most groups of tropical marine invertebrates, the Indo-Pacific remains seriously under-sampled and published range maps for any given species are based on interpolations between known occurrences (e.g. Abbott 1960, 1961). To minimize the error due to such interpolations, we only used the known occurrences of species, rather than the postulated extent of the range. Thus, our species richness value for any given grid cell represents a minimum estimate of the true richness, and these values will certainly change with better sampling of the Indo-Pacific region and more detailed taxonomic studies in the future. However, our aim here is to explore the relationship between two different diversity metrics, and hence we are interested in relative changes rather than in true richness. Thus, our sampling scheme is appropriate for the question.

Computation of morphological diversity requires the establishment of a morphospace, each axis of which represents some

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quantifiable trait. Because organisms present an indefinitely large number of quantifiable traits, morphological diversity can only be measured with respect to a selected set of traits (Roy & Foote 1997). Here, we use shell shape and shell size to quantify morphological diversity patterns. Shell shape has been shown to correlate with many aspects of species ecologies and functional biology in gastropods (Vermeij 1978, 1987; Savazzi 1991). Similarly, body size is generally considered to be one of the single most important attributes of an organism as it correlates strongly with many physiological, ecological and life-history traits (Peters 1983; Blackburn & Gaston 1994; Brown 1995; West *et al.* 1997).

Many different techniques are available for quantifying shapes of biological objects, some of which are based on homologous landmarks, whereas others use outline data (Rohlf & Bookstein 1990). Given the wide variety of shell shapes in the family Strombidae, identification of homologous landmarks is difficult so we generated a shape morphospace for the strombid species using an elliptical Fourier analysis (EFA; Kuhl & Giardina 1982; Rohlf & Archie 1984; Rohlf 1990) of outlines and a principal components analysis (PCA) of the resulting coefficients. Published photographs of each species (e.g. Abbott 1960, 1961; Walls 1980) were digitized in a standard orientation using a video imaging system (Image Pro Plus) and these co-ordinates were used to compute 10 harmonics for each specimen using available EFA software (Rohlf & Ferson 1992; Isaev 1995; Isaev & Denisova 1995). The number of harmonics was chosen by visually inspecting the fit between the original and reconstructed outlines. All specimens were standardized with respect to size and orientation. Because the focus of this study is on interspecific trends, we have ignored intraspecific variation in both shape and size. A PCA of the EFA coefficients using a covariance matrix was used to define the shape morphospace (Ricklefs & Miles 1994).

For the body size analyses, we used the maximum reported lengths of each species as the size metric. Shell length is a generally accepted measure of size in marine gastropods (e.g. Rex *et al.* 1999) and correlates well with other measures of size, such as body mass (K.R. and D. Jablonski, unpublished data).

Two types of metric are commonly used to quantify morphological diversity: (i) measures of the extent of morphospace occupation, and (ii) measures that focus on dispersion among taxa (Roy & Foote 1997). The latter set of metrics is often referred to as disparity (e.g. Wills *et al.* 1994). We used the geometric mean of the ranges of scores on each PCA axis as a measure of the volume of morphospace occupation (Foote 1997). The geometric mean of the variance of scores on each axis was used to measure dispersion among forms (Foote 1997). For the body size data we used variance as a measure of morphological disparity.

3. RESULTS AND DISCUSSION

The family Strombidae is characterized by a large variety of shell shapes, and the distribution of individual species in an empirically defined morphospace is shown in figure 1. Our data on spatial patterns of species richness of strombid gastropods are consistent with the previously documented pattern of highest richness around the Philippines and New Guinea, with a general decline outwards from that region (figure 2*a*). However, the relationship between morphological diversity and species richness is highly nonlinear (figure 3). Similarly, variation

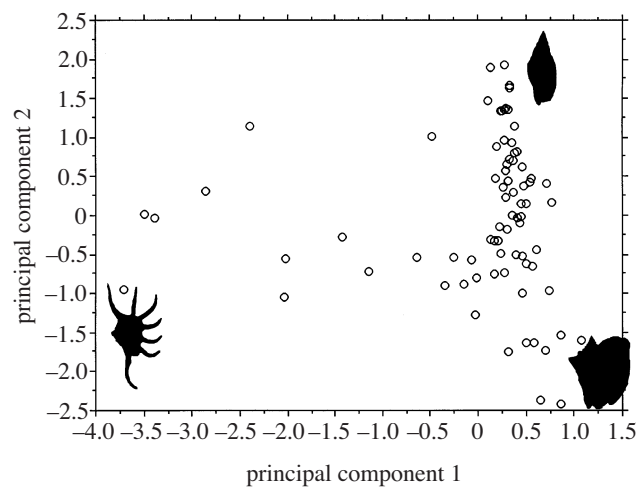


Figure 1. The distribution of individual strombid species along the first two axes of the empirically defined shape morphospace. These two axes explain 61.4% of the total variance. Shell shapes that characterize different parts of the morphospace are shown in silhouette.

in body size of strombid species also shows surprisingly little relationship with species richness (figure 4). Thus, overall, the correspondence between spatial patterns of species richness and morphological diversity in this group is remarkably poor (figure 2). In general, areas with high species richness tend to have high morphological diversity, but many regions of low-to-moderate species richness also show surprisingly high morphological diversity (figures 2 and 3).

Out of all the morphological diversity metrics used here, the geometric mean of the range of PCA scores shows the best fit to the species richness data (figure 3*a*). This implies that the volume of morphospace occupied increases with increasing diversity, and that as taxonomic richness increases, species tend to be preferentially added to the margins of the morphospace (Ricklefs & O'Rourke 1975; Ricklefs & Miles 1994; Roy & Foote 1997). A positive relationship between morphospace volume and species richness has also been documented in some terrestrial groups, including certain groups of birds, bats, lizards and fishes (see Ricklefs & Miles 1994). However, for strombid gastropods this relationship is nonlinear, and little change in the volume of morphospace is seen once regional species richness exceeds moderate levels (figure 3*a*). The relationship between morphological disparity and species richness in strombid gastropod assemblages is similar to that for morphospace volume, albeit with higher scatter (figure 3*b*). Thus, as regional species richness changes, species are not only added to the periphery of the morphospace, but the internal packing of the space also changes. Such a positive relationship between changes in morphospace volume and disparity has been shown to characterize the evolutionary radiations of some Palaeozoic clades (e.g. Foote 1997), but has rarely been documented for modern assemblages (see Ricklefs & Miles 1994).

The presence of high morphological diversity in areas with low or moderate species richness raises interesting questions about the origin of such patterns. At the level of local communities, ecological processes such as competition can influence morphology and hence determine

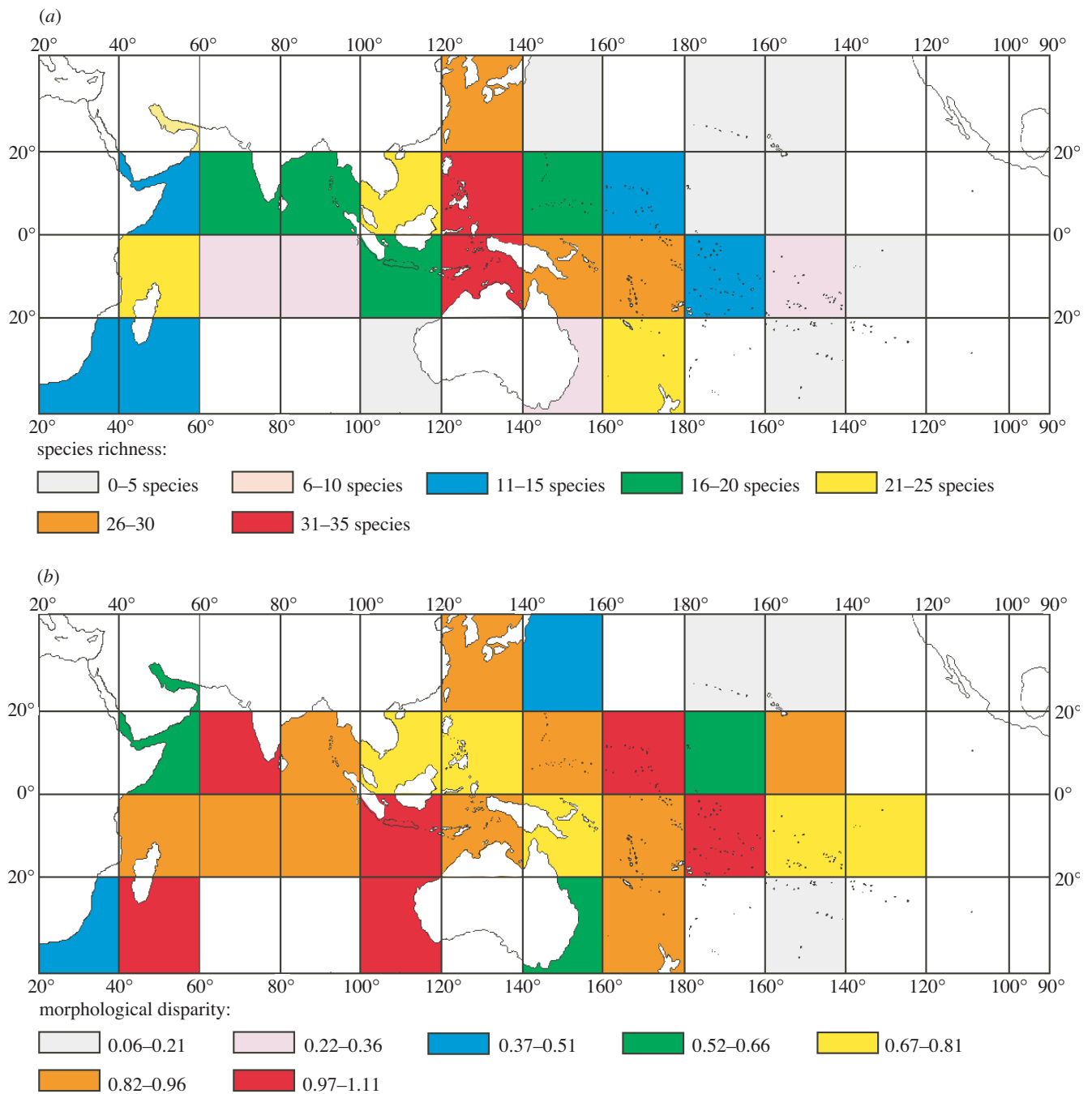


Figure 2. A comparison of spatial patterns of taxonomic and morphological disparity of strombid gastropod species across the Indo-Pacific region reveals a strong discordance between the two trends. (a) Distribution of species richness using a 20° latitude × 20° longitude grid. Colours denote the total richness of each grid. (b) Spatial distribution of morphological disparity along the same grid as in (a). Morphological disparity is defined here as the geometric mean of the variance of scores on six principal component axes (see § 2). These six axes explain 86% of the total variance.

patterns of morphospace occupation (Ricklefs & Miles 1994). However, on a regional scale, such as the one used here, speciation and extinction dynamics have a fundamental role in generating morphological diversity, and distributions of species in morphospace are, at least partially, constrained by their phylogenetic relationships (e.g. Richman & Price 1992; Wagner 1996; Shepard 1998). In general, closely related species tend to be similar both in body size and in morphology (Richman & Price 1992), and the presence of high morphological diversity in a region of low species richness is likely to result from the

presence of a few distantly related lineages there. Phylogenetic relationships of strombid taxa are poorly known at present, but ongoing work on the molecular phylogeny of the group indicates that lineages represented in some species-poor regions are indeed distantly related to each other (M.E.H. and K.R., unpublished data).

An alternative explanation of the relationships between taxonomic and morphological diversity seen here is that they simply represent what would be expected from sample size alone, with each assemblage representing a different random draw of species from an underlying

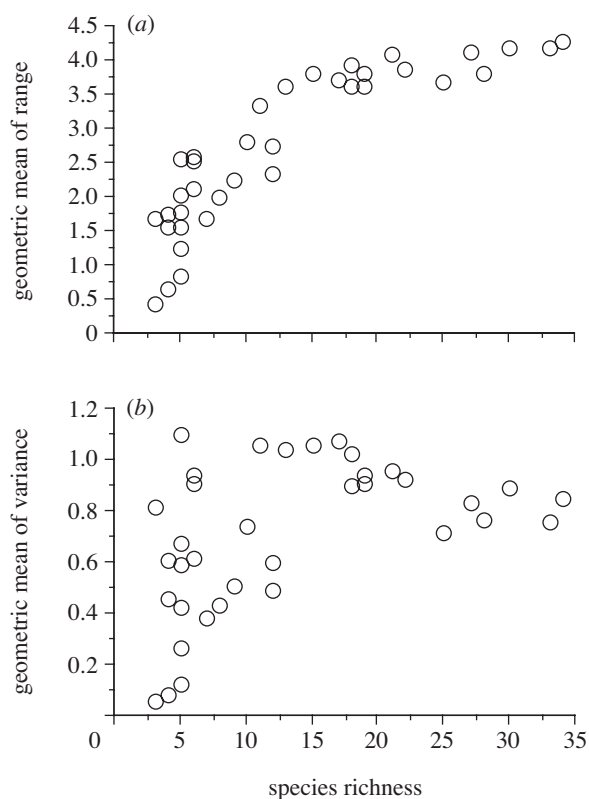


Figure 3. The relationship between species richness and two different metrics of morphological diversity for each 20° latitude–longitude grid cell; (a) geometric mean of the range of scores on the first six principal component axes, representing the volume of morphospace occupied; (b) geometric mean of the variance of score on those six axes, reflecting species packing in the shape morphospace.

distribution. Under such a scenario, the range and volume of morphospace is expected to increase with increasing species richness (Foote 1992, 1997; Wills *et al.* 1994). Similarly, the variance should show higher fluctuations at low sample sizes and stabilize as species richness increases. To test the relevance of such a statistical explanation, we generated random assemblages with different levels of species richness by subsampling (without replacement) the empirical body size distribution. For each level of sampling, we generated 1000 replicates and computed the variance in body size for each of these assemblages. As shown in figure 4, the empirical pattern of size variance does fall within the 95% confidence interval of what would be expected from such sample size effects. Thus, although we consider it to be unlikely that the regional assemblages of strombids simply represent random assemblages of species, at present we cannot reject such a statistical explanation for the observed patterns.

Depending on their nature, past extinctions also have the potential for influencing both the volume of morphospace and morphological disparity (Jablonski 1995; Roy & Foote 1997; Smith 2000). Given the climatic and tectonic history of the Indo-Pacific region, local and regional extinctions are likely to have been important in shaping the present-day distributions of species and higher taxa (Ladd 1960; Pandolfi 1992). Phylogenetic and

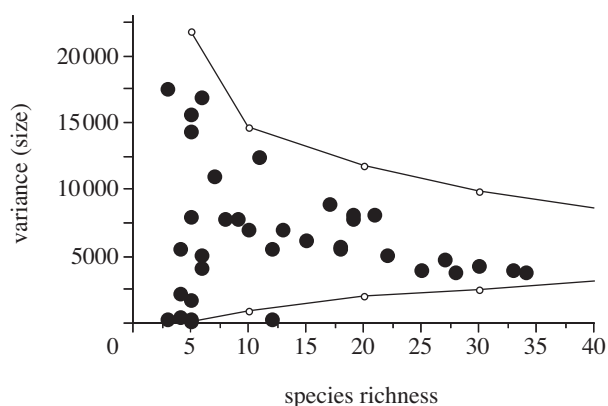


Figure 4. Relationship between variance in body size and species richness of strombid gastropod species for individual 20° grid cells. The filled circles represent empirical observations. The two lines represent the 95% confidence interval around the expected variances in size for random assemblages of species. The expectation was calculated by randomly subsampling (without replacement) the entire size distribution for strombids. The subsampling was done in increments of 10 species and the confidence interval for each level of sampling was calculated using 1000 replicates. Note that for both empirical data and the random assemblages, variance in body size shows large fluctuations at low sample sizes but stabilizes as species richness increases. This trend could simply reflect sample size effects or alternatively reflect increased internal packing of the body size space as more species are added.

palaeontological work on the evolution of diversity in the Indo-Pacific has largely focused on the origins of species richness (e.g. Pandolfi 1992; McMillan & Palumbi 1995; Levinton *et al.* 1996; Palumbi 1997). The poor correspondence between patterns of taxonomic and morphological diversity documented here underscores the need for a better understanding of the morphological evolution of this fauna.

Causality aside, our analyses show that the spatial pattern of biological diversity in the tropical Indo-Pacific that emerges when morphology is used as a diversity metric is different from the traditional view based on species richness. Parts of the Pacific that might not be as rich in species diversity as the Indo-Malayan region nonetheless harbour an impressive variety of morphologies that sometimes even exceeds that of more species-rich regions. Indo-Pacific marine biodiversity is highly threatened by human activities and previous studies have highlighted the need for conserving the high species richness present there (e.g. Maragos *et al.* 1996). In practical terms, our results underscore the need for incorporating metrics other than taxonomic richness (such as morphological diversity) into conservation efforts. In particular, increased attention needs to be focused on those areas of the Indo-Pacific that might have anomalously high morphological diversity given their species richness. The loss of even a few species in these areas can lead to a disproportionately high loss of morphological variety and potential regional extinction of distantly related evolutionary lineages. Alternatively, preserving these areas could conserve a large segment of the strombid morphospace. The regional pattern shown here provides a template

for identification of such areas at a finer spatial scale. Finally, whether the patterns for strombid gastropods represent a general trend is unknown at present; similar analyses using data for other groups of organisms are sorely needed.

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