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Higher Taxa in Biodiversity Studies: Patterns from Eastern Pacific Marine Molluscs

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Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs

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SUMMARY

Several recent studies have proposed the use of higher taxa as a proxy for species–level biodiversity patterns. Here this premise is evaluated by using a large database of benthic marine molluscs from the eastern Pacific. In this assemblage, diversity patterns at the genus and family level are significantly correlated with those at the species level. However, the choice of taxonomic rank depends on the resolution required to address a given problem. Although familial data are very robust to sampling and adequately reflect the general species–level patterns (for example, the presence and sign of diversity gradients), they cannot adequately resolve regional variations such as stepped diversity trends. Genera are useful even at regional scales, but species-frequency distributions within higher taxa vary with diversity (and biogeography). Hence, for regional studies, calibration based on a few well-sampled local assemblages is recommended to increase the effectiveness of genera as proxies for species–level patterns. Information contained within the taxonomic hierarchy can also provide insights into other macroecological patterns that are not evident from a simple tabulation of species, such as estimates of the latitudinal deployment of biodisparity.

1. INTRODUCTION

It is generally agreed that the need to quantify global biodiversity patterns is urgent. However, the sheer magnitude of this task, involving as it does unprecedented sampling problems, has forced ecologists to consider indirect methods for estimating species–level biodiversity (see, for example, Colwell & Coddington 1994; Williams & Gaston 1994). One such approach is to extrapolate species richness estimates from counts of higher taxa (Gaston & Williams 1993; Williams & Gaston 1994; Williams et al. 1994*a*). Several factors suggest that such an approach might be practicable (see Gaston & Williams 1993; Harper & Hawksworth 1994; Williams & Gaston 1994). These include: (i) the existence of a relation between diversity at various taxonomic levels is intuitively reasonable; (ii) studies of Phanerozoic diversity patterns have demonstrated empirically that such relations exist over geological time (see, for example, Valentine 1970; Raup 1976; Sepkoski *et al.* 1981; Sepkoski 1984, 1992, 1994); and (iii) the pattern also exists for some extant taxa (see, for example,Taylor & Taylor 1977; Gaston & Williams 1993; Williams & Gaston 1994). In fact, higher taxa have proven to be useful in environmental monitoring and impact studies (Beattie & Oliver 1994 and references therein; Somerfield & Clarke 1995). However, for some extant faunas or regions, higher taxa appear to be poor predictors of species richness and hence the usefulness of this approach has been questioned (Prance 1994; Andersen 1995).

Here the effectiveness of the higher-taxon approach is evaluated using a large data set for eastern Pacific marine molluscs. In particular, the latitudinal diversity gradient and the biogeographic structure of this fauna are compared at three different taxonomic levels (species, genus and family); the implications of this approach for understanding species deployment at various latitudes are discussed.

2. PATTERNS OF HIGHER TAXA AS SURROGATES FOR SPECIES–LEVEL PATTERNS

The uses of higher taxa in palaeobiology have been debated; some of these discussions are briefly evaluated before using higher taxa in evaluations of present-day species diversity patterns. The incomplete nature of the fossil record, coupled with the difficulties of applying the biological species concept to extinct organisms, has long forced palaeobiologists to use supraspecific taxa to infer species–level patterns over a wide range of situations (Raup 1979; Sepkoski 1992 for review). The more inclusive genus- or family-level categories are less subject to the vagaries of sampling and preservation, and thus have been held to reflect large-scale biological patterns more accurately. This approach has been criticized, however, primarily on the grounds that higher taxa tend to be artificial constructs with varying significance from group to group, making them inappropriate surrogates for species (Patterson & Smith 1987, 1989; Smith 1994).

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Two points can be made in defence of the higher taxon approach in the fossil record. First, the use of higher taxa as a proxy for species–level patterns can be viewed simply as a sampling strategy: given sufficiently large samples even arbitrary groupings of entities can reflect the underlying patterns quite well (see Sepkoski 1984, 1992; Sepkoski & Kendrick 1993 for an important simulation study using model phylogenies). Thus, higher taxa can be used simply as statistical generalizations without necessarily implying that they are real evolutionary units (Sepkoski 1984, 1992). In fact, neither the criterion of strict monophyly nor equivalent evolutionary divergence between higher taxa is required for using them to estimate species richness (Sepkoski 1992; Williams & Gaston 1994).

A second but perhaps more important point for ecological studies is that higher taxa are not arbitrary ecological or functional units; species within them tend, on average, to be more similar ecologically than any random species pair (see. for example, Elton 1946; Williams 1964; Simberloff 1970, 1978; Sepkoski 1984; Valentine 1973, 1990; Vermeij 1994). This view also suggests that, given their position in the hierarchy, higher taxa should be useful for identifying emergent patterns that cannot exist at the species level (see, for example, Ricklefs 1987; Valentine 1990). These extrapolations have their limits, however; palaeobiological data indicate that the concordance of patterns between species and higher taxa begins to break down at about the ordinal level (Bambach 1985; Erwin *et al.* 1987; Jablonski & Bottjer 1990, 1991) and increasingly diverges at still higher levels. The authors cited suggest that this discordance is biologically meaningful, and is not due to some failure of the Linnaean hierarchy.

This second rationale for the utility of higher taxa draws on their genealogical or phylogenetic basis. A number of authors would go much further in this direction; for example, a number of useful biodiversity indices make use of the cladistic topology (see, for example, Vane-Wright *et al.* 1991; Nixon & Wheeler 1992; Faith 1992*a*, *b*, 1994*a*, *b*; see Williams *et al.* 1994*b*for discussion). However, a drawback of phylogenetic metrics is their requirement of detailed cladistic analyses, currently unavailable for most groups. Further, consistency indices decline and the number of alternative or slightly less parsimonious topologies increases with the number of taxa analysed, so that subgroups can potentially change their conservation status with alternative interpretations of character-state distributions or with alternative tree topologies that differ slightly from the most parsimonious one. Genealogy is extremely important for understanding biodiversity, but it cannot be the only basis for weighing biological 'quality' against 'quantity'. Alternative approaches need to be considered; as discussed here, using the information available in the taxonomic hierarchy may be one such approach. Such methods gain additional support with recent work showing that traditional Linnaean taxa, even when commonly paraphyletic, adequately capture temporal dynamics of monophyletic clades (Sepkoski & Kendrick 1993; Wagner 1995).

3. THE DATABASE

The database for this study contains the latitudinal ranges of 2884 species of shelled gastropods and bivalves living in eastern Pacific waters shallower than 200 m from Peru to the Arctic Ocean. The data were compiled through an extensive search of the primary literature as well as from major museum collections (see Jablonski & Valentine 1990; Roy *et al.* 1994). Generic and familial assignments reflect the most recent systematic revisions (see, for example, Keen 1971; Radwin & D'Attilio 1976; McLean 1978; Bernard 1983; Ponder 1985; Hickman & McLean 1990; Finet 1994). As the distinction between molluscan genera and subgenera is often arbitrary, they have been assigned equal rank (genus) for the analyses presented here.

4. DIVERSITY PATTERNS AMONG TAXONOMIC LEVELS

Eastern Pacific molluscan species exhibit a strong latitudinal diversity gradient (figure 1*a*) (Roy *et al.* 1994). This gradient has a stepped appearance, most of the major changes in diversity being concentrated at provincial boundaries. Essentially the same pattern is seen with generic data, although, as expected, the

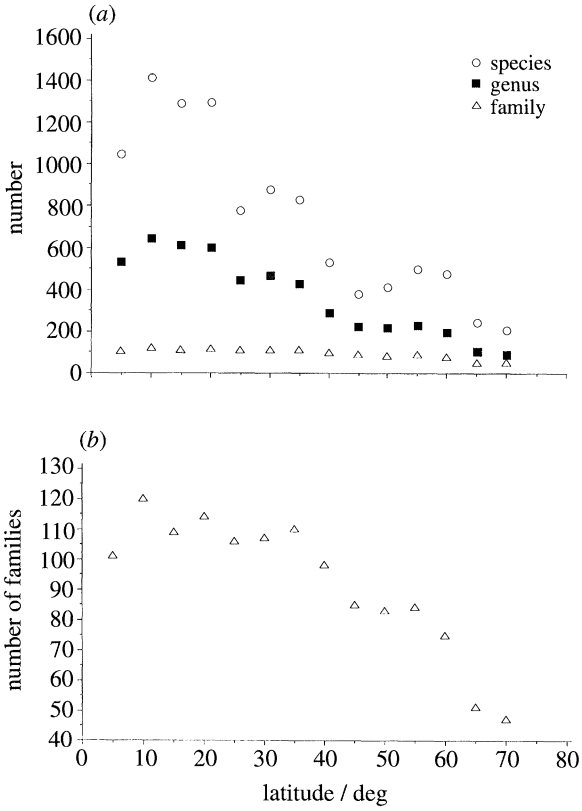

Figure 1. Latitudinal diversity gradient of eastern Pacific benthic molluscs at different taxonomic levels. (*a*) Number of species (open circles), genera (filled squares) and families (open triangles) present in each 5 deg latitudinal band. The value for each latitudinal band is plotted at its end. (*b*) Number of families present per 5 deg latitudinal band plotted on an appropriate scale. Note that at this scale families also show the same general trend as species and genera.

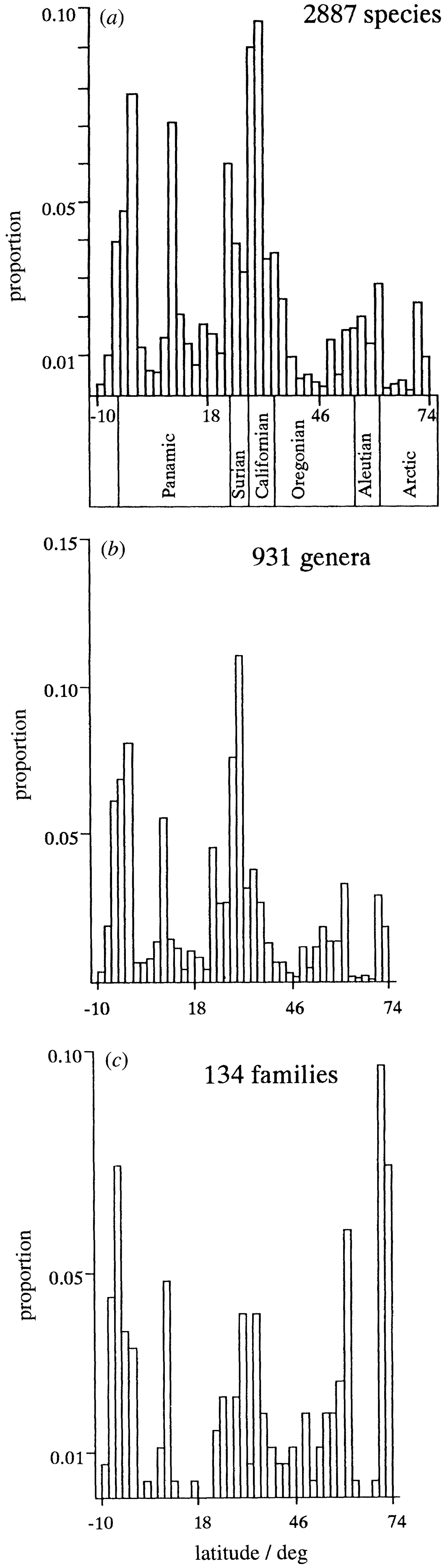

Figure 2. Latitudinal distribution of range endpoints of species (*a*), genera (*b*) and families (*c*) of eastern Pacific benthic molluscs. Each bar represents 2 deg latitude. For both species- and genus-level data, the major provincial boundaries are marked by clusters of range endpoints. However, for familial data, the boundaries are not as clearly demarcated. Note that a high proportion of range endpoints occur between latitudes 8 °N and 10 °N, away from any major provincial boundary. The cause of this anomaly is not clear at present, but may be partly driven by much greater sampling intensity around Panama compared with Colombia and Ecuador.

diversity steps are somewhat damped. The correlation between species- and genus-level diversities for 5 deg latitudinal bands from the equator to northern Alaska is highly significant (figure 1*a*; $p = 0.0004$, Spearman's rank correlation). The overall latitudinal gradient is also quite evident in the familial data, but the families do not reflect the stepped structure of the species diversity pattern very closely (figure 1*b*). Spearman's rank correlation between familial and species–level diversity is still quite significant ($p = 0.001$) although the relation is less linear than the species–genus one.

The distributions of eastern Pacific Mollusca, together with those of some other benthic marine groups, permit the recognition of a number of well-defined provinces, the boundaries of which are marked by clusters of endpoints of species' ranges (Valentine 1966; Hayden & Dolan 1976; Murray & Littler 1981; Maluf 1988; Roy *et al.* 1994). Campbell & Valentine (1977) analyzed the distinctiveness of such provinces at different taxonomic levels by using faunal similarity indices. They found that similarity metrics that take into account differences in diversity can distinguish even contiguous provinces at both genus and family level. A comparison of the latitudinal distribution of range endpoints tallied here shows that the proportions of range endpoints present per 2 degree band are highly correlated at species, genus, and family levels (Spearman's rank correlation for species–genus data, $p < 0.0001$; for species–family data $p = 0.0001$). All of the major provincial boundaries identified at the species level are marked by clusters of generic range endpoints (figure 2*a*, *b*). In fact, the only boundary that is not well demarcated by the species range endpoints, between the Oregonian and Aleutian provinces, shows up more prominently at the generic level. At the family level, however, some of the major boundaries are not as clearly distinguishable (such as the ones between the Panamic and Surian provinces or between the Surian and Californian provinces) although others are still distinct (such as the southern boundary of the Panamic province,the boundary of the Californian and Oregonian provinces and that of the Oregonian and Aleutian provinces) (figure 2*c*). The wider scatter at the family level is not surprising given that families will, on average, have more species and hence broader latitudinal ranges than genera (figure 3).

These analyses demonstrate the correlation of latitudinal diversity patterns at different taxonomic levels. However, such correlations say little about how the species are distributed within higher taxa across latitude. Insight into these distribution patterns can be

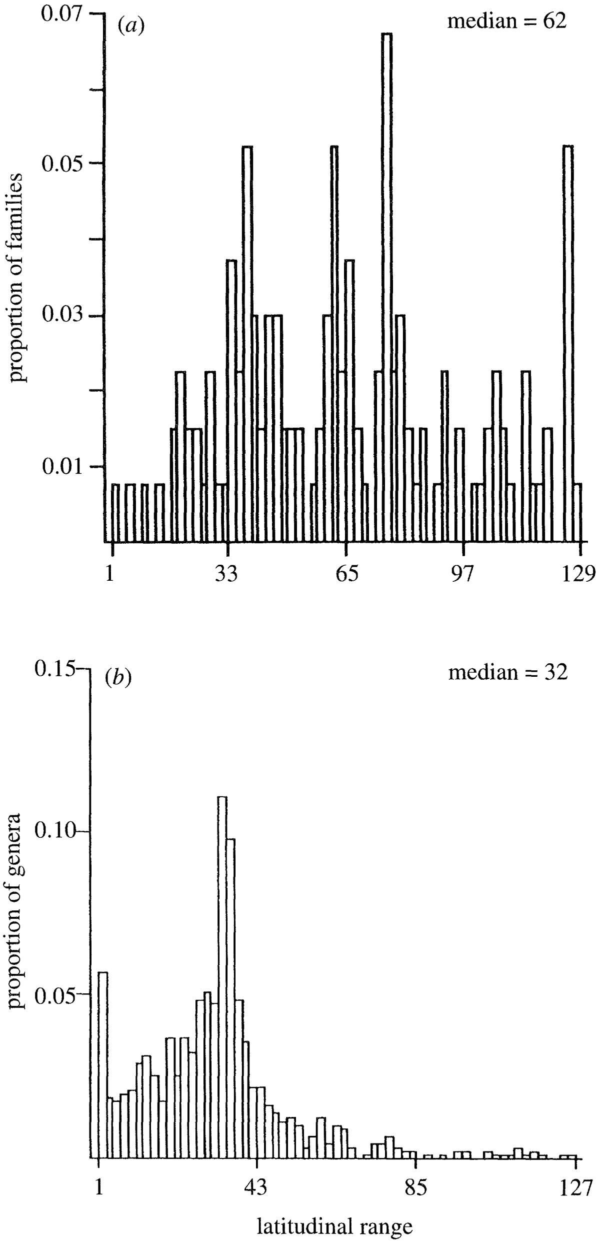

Figure 3. Frequency distributions of latitudinal ranges of eastern Pacific benthic molluscan families and genera. Each bar represents 2 deg latitude. Families tend to have wider latitudinal ranges compared with genera, as shown by the median values.

gained from the latitudinal distribution of species/genus (S/G) and species/family (S/F) ratios. As pointed out by Simberloff (1970, 1978), S/G and S/F are diversity-dependent and under the null expectation should increase monotonically with the number of species (also see Järvinen 1982; Jablonski & Flessa 1986). Thus, if the distribution of species within higher taxa is random with respect to latitude, then latitudes with higher diversity should also have higher S/G and S/F. Figure 4*a* shows the fit of our generic data to this expectation based on random resampling of the entire data set. Each sampling consisted of a random drawing of n species (with replacement) to determine the numbers of higher taxa that were produced. There is a systematic deviation from the mean expectation in that low-diversity assemblages tend to have fewer genera than expected and species-rich assemblages tend to have more. The differences are large enough that the observed values tend to fall outside the 95% confidence interval for the simulations. The same general trend is also true for family-level data (figure 4*b*) although the differences are less significant. In terms of S/G and S/F this result translates into significant deviations from the null expectation at both ends of the diversity spectrum (see, for example, figure 5). Williams & Gaston (1994) noted similar patterns in other groups, including British ferns and North and Central American bats.

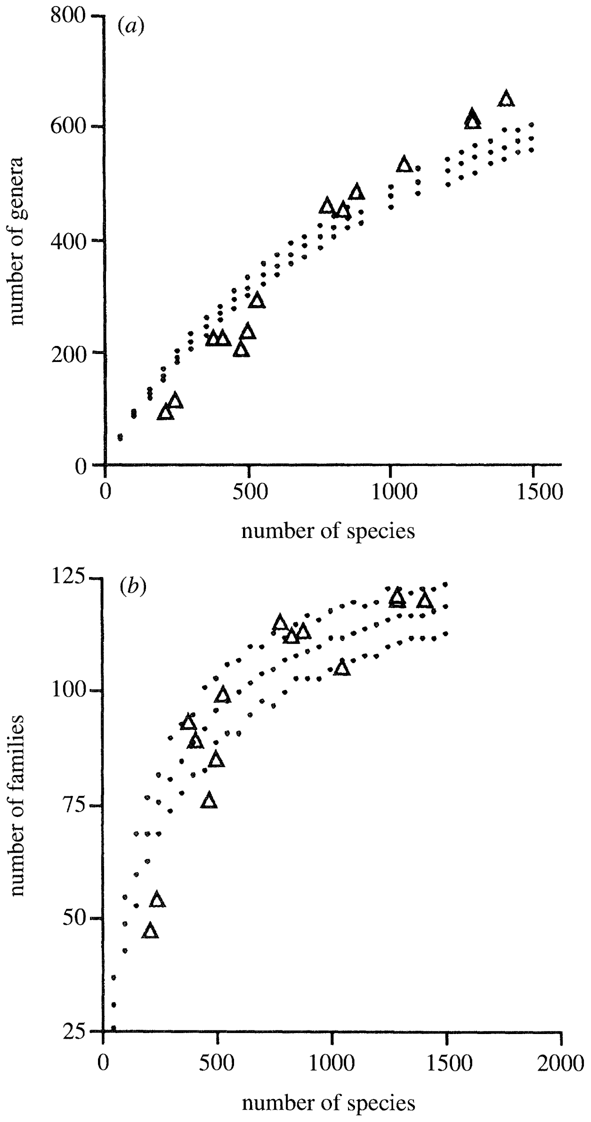

Figure 4. Relation of species richness to generic richness (*a*) and familial richness (*b*) for eastern Pacific benthic molluscs. The dotted lines represent the mean expectation with 95% confidence interval produced by a random resampling (with replacement) of our entire data set. The resampling was done in increments of 50 species; 100 iterations were run for each sampling level. The triangles represent observed values. For both genera and families, high-diversity assemblages tend to have more higher taxa than expected whereas low-diversity ones have fewer higher taxa than expected (see also text).

The observed deviations from the null expectation can be partly explained by the relation between species richness and range size in higher taxa, and the distribution of species within higher taxa (also see

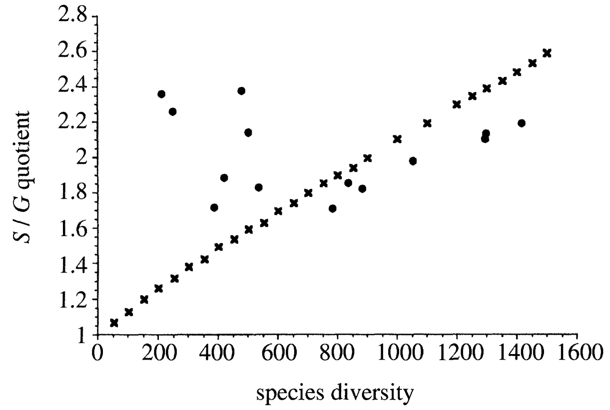

Figure 5. Species/genus (S/G) ratios for eastern Pacific molluscs as a function of species diversity. The crosses show the mean expectation resulting from randomly resampling the entire data set (see figure 4); the circles represent observed values.

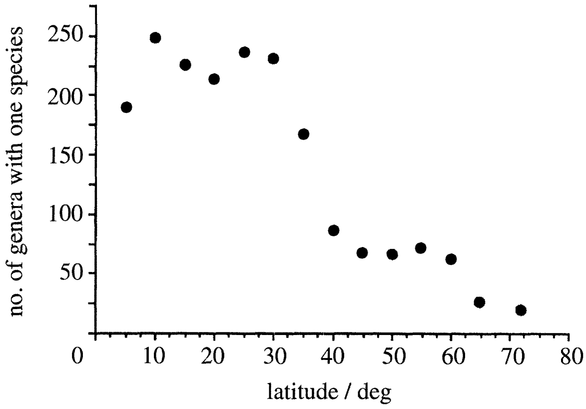

Figure 7. Latitudinal distribution of genera with only one eastern Pacific species. Each points represents the number of such genera present in a 5 deg latitudinal band.

Williams & Gaston 1994). In our data set the frequency distribution of species within higher taxa forms the classic 'hollow curve distribution' at all diversity levels (figure 6) (see Willis 1922; Anderson 1974; Flessa & Thomas 1985; Dial & Marzluff 1989; Williams & Gaston 1994 and references therein). The proportion of genera that have only a single species along the eastern Pacific coast is high (45.6%); these genera show a strong latitudinal gradient (figure 7). Combined with a significant correlation between species richness and latitudinal range ($p < 0.0001$ for genera and families; Spearman's rank correlation), these features would account for much of the observed deviations. In other words, the trends in S/G and S/F reflect, in a crude but convenient way, the distribution patterns of species within higher taxa.

The primary controls on the shape of such 'hollow curve' distributions remain poorly understood. As pointed out by a number of authors, such distributions are unlikely to be simple artefacts of taxonomy (see Anderson & Anderson 1975; Glazier 1987; Dial & Marzluff 1989; Williams & Gaston 1994). Variations in species richness among higher taxa can be attributed to many biotic factors, such as various life-history traits (see, for example, Bush 1975; Dial & Marzluff 1988, 1989; Farrell & Mitter 1993) as well to abiotic variables such as the availability of nutrients. The regional variations shown here, such as the presence of

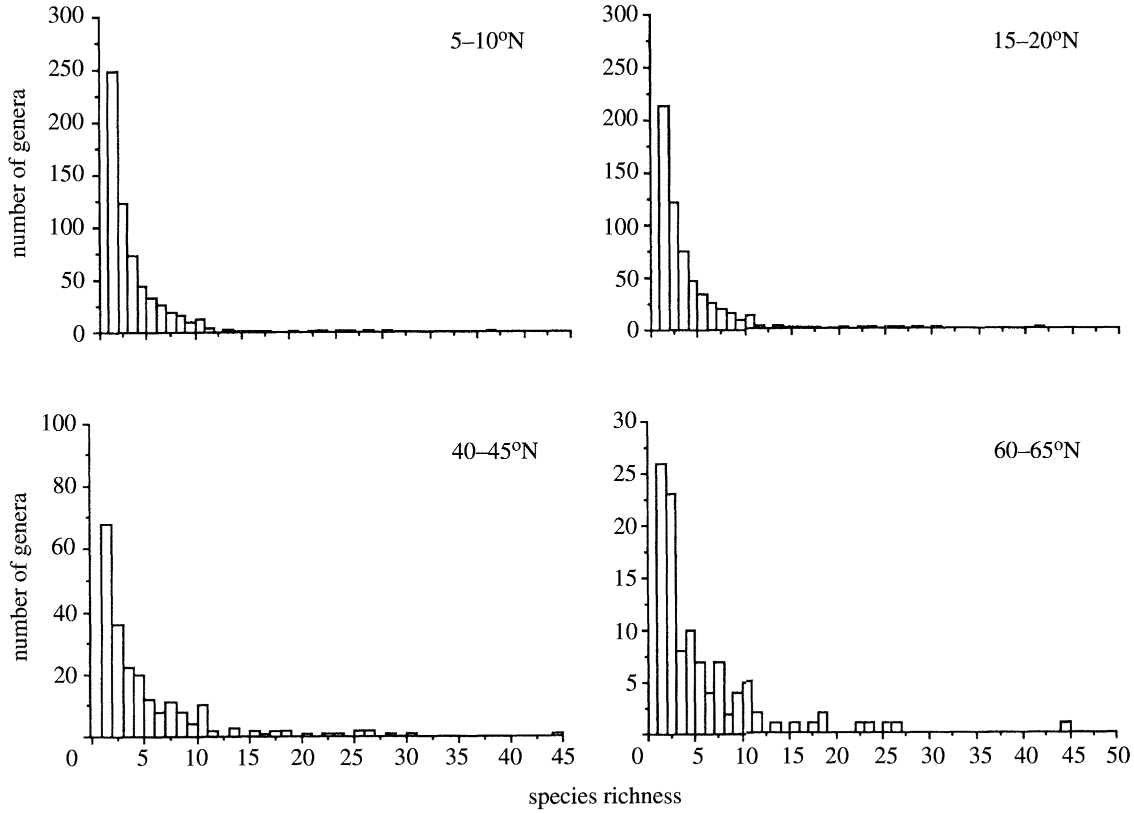

Figure 6. Frequency distributions of species within genera of eastern Pacific molluscs at tropical and temperate latitudes. Note that the 'hollow curve' distributions persist at all latitudes (see also text).

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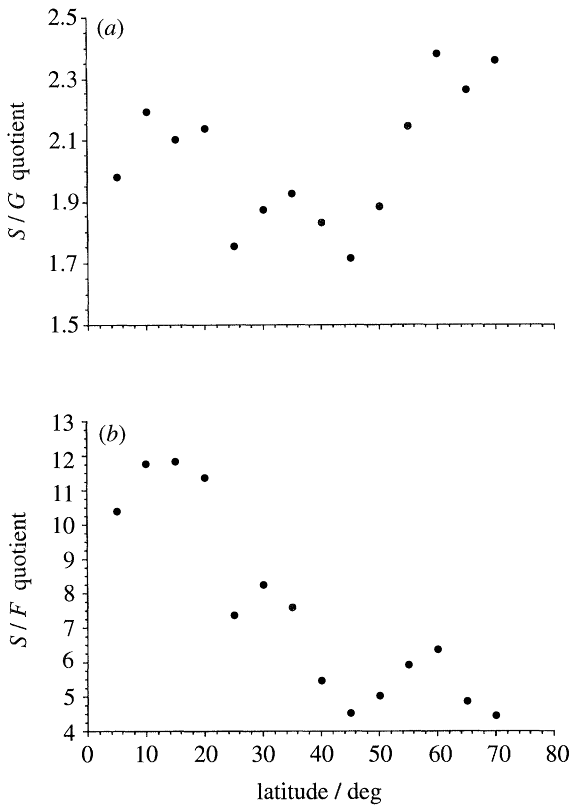

Figure 8. Species/genus (*a*) and species/family ratios (*b*) as a function of latitude for eastern Pacific molluscs. Each point represents a 5 deg latitudinal band. The clusters of *S*/*G* and *S*/*F* values, in general, represent different eastern Pacific provinces (see text).

a large number of monotypic genera and species-poor families in lower latitudes, might also reflect an evolutionary dynamic, with young and species-poor taxa concentrated in the tropics (Stehli *et al.* 1969; Stehli & Wells 1971; Rosen 1988; Jablonski 1993; Judd *et al.* 1994). Alternatively, relict, formerly species-rich taxa, or even geologically persistent species-poor taxa, might underlie this distribution. More phylogenetic and palaeobiological work is needed to test these alternatives.

For eastern Pacific molluscs, biogeography also plays an important role in determining the latitudinal distribution of *S*/*G* and *S*/*F* ratios. Because the latitudinal ranges of species and genera are controlled largely by the spatial distribution of the provincial boundaries, *S*/*G* tends to vary between individual provinces (figure 8*a*). In fact, biogeographical controls are reflected more strongly in the *S*/*F* ratios, in which a strong decline from tropical to polar latitudes is superimposed on the clustering of provincial values (figure 8*b*). This decline is, of course, the expectation, given that the latitudinal gradient in species diversity is much stronger than that of families (see figure 1).

The large-scale trends in *S*/*G* and *S*/*F* documented here are also consistent with the hypothesis that tropical assemblages are characterized by greater specialization and narrower ranges of resource preferences of the species, thus permitting denser species packing. For example, feeding preferences appear to be narrower among tropical than among temperate or polar shallow-marine species (see, for example, Kohn 1970; Miller 1970; Taylor 1976; Taylor & Taylor 1977; Vermeij 1978; Valentine 1983); a single temperate species of the gastropod family Conidae displays a range of diets that is wider than that of all tropical *Conus* species combined (see Kohn 1966). However, exceptions to these trends also exist. For example, niche width in marine parasites does not appear to change significantly with latitude (see Rohde 1981, 1989). By this interpretation, we would take these ratios to mean that low-latitude species, with their specialized morphologies, tend to be distinctive and to the eye of a Linnaean systematist merit taxonomic separation from their allies. Such features lead to the recognition of many subgenera, genera and families to express the distinctiveness, and is also likely to be accompanied by the acquisition of unique derived characters that will lead to greater internodal distances, often used as a cladistic metric of biodiversity (see, for example, Faith 1992*a*, *b*; Williams *et al.* 1994*b*). However, *S*/*G* and *S*/*F* ratios can only serve as consistency arguments and not as direct tests of hypotheses on latitudinal changes in resource partitioning and species packing.

5. USES OF HIGHER TAXA

These results show that, for eastern Pacific marine molluscs, biodiversity and biogeographic patterns manifested at generic and familial levels are significantly correlated with those at the species level. However, the present analyses also suggest that the usefulness of higher taxa as surrogates for species–level patterns depends on the resolution required to address a given question. For example, although familial data are adequate for identifying the tropical-polar latitudinal diversity gradient for the eastern Pacific, they are not very sensitive to regional changes in diversity, as between climatic zones. As a result, some of the major provincial boundaries are not well demarcated by the familial data. Thus, some *a priori* knowledge of species–level gradients is required before the familial pattern can be fully interpreted. On the other hand, generic data for the eastern Pacific molluscs tend to preserve most of the species–level structure and hence can be used for identifying regional patterns.

The observed distribution of both generic and familial richness suggests that the effectiveness of higher taxa as surrogates for species–level patterns can vary with latitude and biogeography (see also Andersen 1995). This supports the suggestion that for regional studies the method should be checked by computing the *S*/*G* and/or *S*/*F* ratios or, even better, the frequency distribution of species within higher taxa for a few well-sampled local assemblages (see, for example, Gaston & Williams 1993; Williams & Gaston 1994).

The notion that congeneric or confamilial species should, on average, be morphologically more similar than a randomly drawn species pair can be translated into a rough gauge of distinctiveness among taxa, or biodisparity (*sensu* Jablonski 1994, 1995; see Foote

1991 for review). The lower than expected S/G and S/F ratios of tropical eastern Pacific molluscs imply a higher biodisparity in the tropics than predicted from simple species-level diversity; i.e. the species should cover a broader range of morphologies than expected simply from their sheer numbers (see also figure 7 on the variation in the number of monospecific genera with latitude). Such equatorward changes in biodisparity have been documented in a few cases (see, for example, Graus 1974; Ricklefs & O'Rourke 1975; Vermeij 1977; Clark 1978); however, a more rigorous and systematic treatment is needed before applications of this aspect of the taxonomic hierarchy can be made with any confidence.

Here we have emphasized patterns of latitudinal diversity, but another potential use of higher taxa that has received less attention involves identifying diversity 'hot spots' (*sensu* Myers 1990). Genera will be well suited for this task, as they tend to be more restricted geographically than families. Genera can be used in this context not only as proxies for species, but also to compare patterns across taxonomic levels: if areas with high levels of generic endemism can be identified then they presumably should receive higher priority as 'hot spots' than those identified based on species, because generic 'hot spots' will tend to capture a broader array of morphologies and to sample more widely across phylogenies (see Mares 1992 for a similar argument; see also Gaston & David 1994; Gaston *et al.* 1995). Thus, although failure of genus- and family-level diversity to accord with regional species richness can reduce the usefulness of the higher-taxon method as an indirect estimator of species diversity (Prance 1994; Andersen 1995), it still provides a means of pinpointing regions of exceptional interest in terms of biodisparity rather than sheer species numbers. For example, plant diversity in Malesia is less than half that of the Neotropics at the species level (42000 compared with 90000) but Malesia contains more families (310 compared with 292) (data from Prance 1994). Comparative analysis of the Atlantic and western Pacific marine molluscs will almost certainly reveal large-scale trends similar to those seen for the eastern Pacific, but may differ importantly in quantitative details, such as S/G and S/F ratios at a given latitude (as found by Prance 1994 for terrestrial plants). Protocols for such regional comparisons are yet to be standardized; Williams & Gaston (1994) and Williams *et al.* (1994) used family richness per unit area to predict species richness per unit area, whereas other authors (e.g. Prance 1994) compare entire regions of different sizes. These are methodological variations that might explain contradictory conclusions among analyses.

Finally, a point that is often underappreciated is that the diversity patterns of higher taxa can often provide insight into historical influences on contemporary diversity. As noted by Ricklefs (1987, p. 170):

> families have more ancient origins than genera and species, and patterns of familial diversity undoubtedly record the evolutionary, historical, and biogeographical settings of local communities more faithfully than do patterns of generic and, especially, specific diversity.

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