

MARINE BIODIVERSITY

Patterns and Processes

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Chapter 1

Marine biodiversity in its global context

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Abstract

How important is marine biodiversity for understanding global biodiversity? This introductory chapter compares and contrasts marine with terrestrial (including freshwater) diversity by looking at the present state of knowledge and our ability to explain diversity patterns and richness.

Diversity is not only species number; phyletic, morphological, ecological and genetic diversity are important concepts, if difficult to measure satisfactorily. In phyletic diversity, marine systems are superior in the metazoa, inferior in green plants and fungi. Ecological diversity is probably the measure most needed, hardest to achieve and, for the moment, impossible to compare between sea and land. In species numbers, weak evidence suggests there are ten times as many multicellular terrestrial as marine species, but our ignorance, even in well-known areas, is great. In patterns, particularly the tropical–polar gradient, and in richness, terrestrial studies suggest that the nature of energy input, heterogeneity and specificity are all strongly involved. The detailed balance of different factors is undoubtedly different in different groups, and many factors are involved. The importance of heterogeneity and specificity in the sea is rightly a subject of active research.

In knowledge and in ignorance, marine studies are on a par with terrestrial. In academic activity and repute, marine studies are not given sufficient weight. The relatively low level of productivity of the sea and the differences in the scaling of heterogeneity may be important in the contrast with terrestrial systems. Further comparisons of marine and terrestrial diversity should improve our understanding of both.

1.1 Introduction

Most of the world's surface is sea, but most general works on biodiversity concentrate on the land. Is that because land organisms are more diverse or just better known? How important is marine biodiversity for understanding global biodiversity? What do studies of global biodiversity tell us about what should or could be studied with marine organisms?

In this review, I discuss some of the points that may be important and concentrate on four questions. Firstly, what do we know about biodiversity in general, and the status of marine organisms in particular? Secondly, can major patterns in biodiversity be explained? The pattern that is relevant here is the contrast between marine and terrestrial diversity, taking terrestrial to include (almost always) freshwater diversity. I will approach this contrast by looking at the intensively studied latitudinal gradient. Thirdly, can richness be explained? Finally, what do the answers to these questions say about the present status, in a global context, of marine biodiversity studies?

1.2 What do we know about diversity?

Although most studies on biodiversity discuss the number of species, other aspects are at least as important. To mention four, there is cladistic or phylogenetic diversity, morphological diversity, ecological diversity and genetic diversity. All four are harder to study, and to quantify, than species diversity, and all are independent of it.

With phylogenetic diversity, we are familiar with diagrammatic trees indicating the relationship of cellular organisms and showing three main branches for eubacteria, archaeobacteria and eucaryotes (e.g. Embry *et al.*, 1994 or Schlegel, 1994). Viruses do not appear. In such diagrams, the higher plants, animals and fungi occupy three small, closely related branches. At a molecular level, multicellular organisms may be very uniform, but such diagrams are a reminder that any one measure of biodiversity is insufficient. Animals (metazoa), are of course primarily marine; all phyla appear to have started in the sea (even the Onychophora, now purely terrestrial, but marine in the Cambrian). However, multicellular plants and fungi are primarily terrestrial; it is the marine forms that are derived. How many of the unicellular groups are primarily marine is unknown, as are most other aspects of their diversity (Margulis *et al.*, 1989; Hawksworth & Colwell, 1992).

Morphological and ecological diversity are perhaps more relevant to

the preservation of biodiversity, but it is far from clear how either should be measured. Claims that the morphological disparity of Cambrian arthropods is about the same (Briggs *et al.*, 1992a,b) or greater (Foote & Gould, 1992) than that of modern arthropods seem highly dependent on the characters chosen. If it were to be measured just by variation in wing structure then clearly modern disparity would be greater, but uninformative about anything except insects. It is not clear that the use of characters in these Cambrian studies is appreciably less arbitrary than using just wings, or just 16 S RNA. Wilson (1992), from a more holistic standpoint, also doubts the claims for great Cambrian morphological (and ecological) diversity.

Measuring ecological diversity is even harder, but probably nearer what is needed for conservation decisions. Harper & Hawksworth (1994) make the same point. As different ecological characters are incommensurable, any single index is more or less arbitrary. Ecological comparisons among similar organisms are conceivable; comparing the ecological diversity of marine and non-marine scarcely so. Genetic diversity has the merit of being measurable in nucleotide differences, but would only be informative if the relative importance of changes in different parts of the genome were weighted.

So it is not surprising that quantitative studies of biodiversity have, apart from a nod to phyletic diversity, been based almost entirely on species counts. It is well-known that most species have not been described. Counts of those that have been and estimates of those to come (or to become extinct before they are described) can be found, for example, in Groombridge (1992) and Wilson (1992). It is less well-known that the numbers can be changed appreciably by changes in the definition of a species. In 1899, R.B. Sharpe, using a definition comparable to that of most modern botanists, counted 18 939 species of birds (see Bock & Farrand, 1980). Modern estimates are about 9000 (9021 in Bock & Farrand, 1980, and over 9200 in Howard & Moore, 1991) and the variations are primarily due to differences of opinions between splitters and lumpers. New bird species are still being described, but only at a rate of about three or four a year (May, 1994). The number can be expected to increase as it is usually easier, for various reasons, to push for the conservation of a species than of a subspecies.

Birds are exceptionally well-known. In most groups the true number of species is not known to an order of magnitude. There has been much discussion of the number of insect species, as this is widely believed to be the group with the most species. It is certainly the group with the

most described species, Wilson's (1992) figure being 751 000. Estimates for all insects are now in the range of from 3 to 10–30 million, the lower part of this range being more likely (Gaston, 1991; Groombridge, 1992). Estimates for deep-sea invertebrates range from 200 000 to 1–10 million (Grassle & Maciolek, 1992; May, 1992), so they could be either more or less speciose than insects. Estimates for the number of fungal species, mostly terrestrial, are comparable to those of deep-sea invertebrates, 0.2 to 1–1.6 million (May, 1991, 1994; Groombridge, 1992). No other set of multicellular taxa is thought to have as many as a million species, so it is likely, despite the wide extent of the oceans, that most multicellular species are terrestrial. The numbers of species of viruses, procaryotes and protists can not yet sensibly be estimated (Giovannoni *et al.*, 1990; Groombridge, 1992; Fauquet, 1994).

Estimates of the world number of species usually depend on extrapolating from more or less accurate estimates for a small patch. It is possible to compare the number of recorded species of British insects with those of British marine crustacea (Fig. 1.1), both very well-known by global standards. There are about ten times as many insects as Crustacea, 22 056 compared with 2240. A difference of this size is robust against the obvious problems of taxonomy, area and recording. But Fig. 1.1 shows this comes from the richness of the four major insect orders: Hymenoptera, Diptera, Coleoptera and Lepidoptera. The distribution in the number of recorded species in the other insect orders is very much like the distribution of numbers in the Crustacea.

In a fashion common to papers on biodiversity, I shall extrapolate wildly to say that there are globally about ten times as many terrestrial and freshwater species as there marine species of eucaryotes. In support, this figure matches the published guesses (Wilson, 1992) for photosynthetic plants, about 250 000 *versus* 25 000, where again the difference is due to one particular taxon, the angiosperms. Briggs (1994) thinks the ratio of terrestrial to marine is nearer 60:1, but his total for all marine invertebrates is less than May's (1992, 1994) minimum estimate for the deep sea alone.

The ratio of species in different groups is probably a more reliable statistic than the total number, but it too is subject to change. Among British insects, the Coleoptera and Lepidoptera have always been much more popular than Diptera or Hymenoptera. Gaston (1991) showed that the rate of discovery in the first two orders flattened off in the mid-nineteenth century, while in the other two the number of species recorded continues to increase at a steady rate. (Gaston's figures are based on

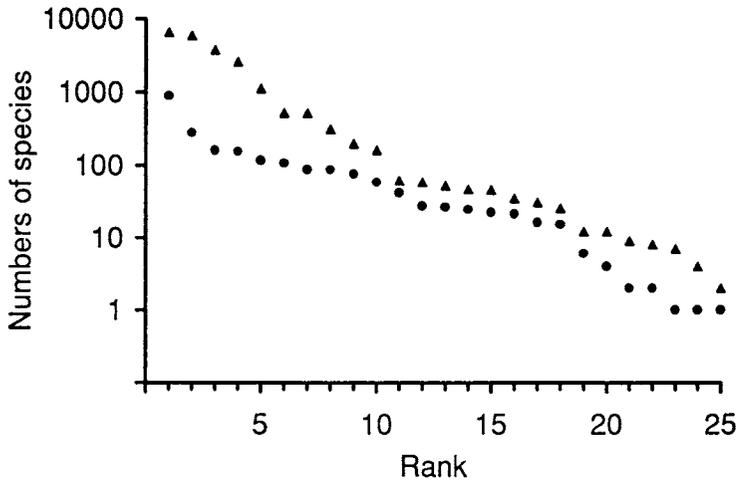


Fig. 1.1. A scree graph comparison of species diversity in British insects (▲) and British marine Crustacea (●). The ordinate is the logarithm of the number of species, the abscissa the rank order of those numbers. Data from Kloet & Hincks (1964–78), Emmet (1991) and Crothers (1997, with one datum from Dr M. Angel). The insect orders are, in rank order: Hymenoptera, Diptera, Coleoptera (including Strepsiptera), Lepidoptera, Homoptera, Heteroptera, Mallophaga, Collembola, Trichoptera, Thysanoptera, Neuroptera, Siphonaptera, Psocoptera, Ephemeroptera, Odonata, Plecoptera, Orthoptera, Anoplura, Diplura, Protura, Thysanura, Dictyoptera, Dermaptera, Mecoptera and Phasmida. The crustacean orders are, in rank order: Harpacticoidea, Amphipoda, Siphonostomatoidea, Decapoda, Podocopida, Poecilostomatoidea, Myodocopida, Isopoda, Mysidacea, Cyclopoida, Cumacea, Tanaidacea, Monstrilloidea, Calanoidea, Thoracica, Rhizocephala, Euphausiacea, Platycopeida, Cladocera, Leptostraca, Mormonilloidea, Stomatopoda, Acrothoracica, Platycopeioida and Misophrioida.

year of description rather than year of discovery in Britain). The numbers of both Hymenoptera and Diptera known in Britain have been increasing at a rate of about 30 species a year since the time of Linnaeus. Consequently, although equal numbers of Diptera and Coleoptera were known about a century ago (about 3500), there are now 60% more Diptera listed (about 6000 *versus* about 3800). However, even the Coleoptera and Lepidoptera are still adding species each decade that match the numbers of species in middlingly common orders. The recorded British Lepidoptera went up from 2357 in 1972 (Kloet & Hincks, 1964–78) to 2595 (Emmet, 1991) in 1991, averaging 125 per decade. It would be rash to draw conclusions from any differences less than times two when comparing distantly related groups. For instance, it is probably safe to say that there are about as many British Homoptera (1111 species in

Fig. 1.1, the fifth commonest order of insects) as there are British Harpacticoida (900 species, the commonest Crustacea).

Although the numbers and ratios are so uncertain, they seem no more uncertain, on a logarithmic scale, in the sea than on land. They are also changing, due to improved collecting, improved taxonomy and natural causes. Both evolution and extinction are happening at rates as fast as ever before in the history of the planet. But the time scales are quite different. With extinction, the concern is with effects on scales of tens to thousands of years. With evolution, the scales are hundreds of thousands to tens of millions of years, four orders of magnitude slower. Wilson (1992) and Benton (1995) give graphs for the recorded history of both marine animals and terrestrial plants, which show the present (last 10 million years) high rate of increase, and the considerable variation in rate of change in the past. Both graphs show periods of around 200 million years when diversity was more or less static. The time series as a whole are certainly not stationary. Diversity has a strong historical component, and has apparently not been in equilibrium between origination and extinction in the Neogene and Quaternary, even without the effects of the current extinction crisis.

1.3 Can major patterns be explained?

The historical component no doubt figures largely in the differences between marine and terrestrial biodiversity; most lineages have been largely confined to one biome or the other for hundreds of millions of years. The differences arise from the action of ecological factors on species origination and extinction rates. Species can to some extent, and during the Pleistocene they were compelled to, migrate to find to an appropriate ecological environment. So it makes sense to consider whether and to what extent other major patterns in biodiversity (Brown, 1988) can be understood in terms of contemporary environmental factors.

The major pattern I shall consider is the well-known polar–tropical gradient in biodiversity, partly because it is shown in both marine and terrestrial systems. Other chapters in this book deal with this pattern in various marine systems. This pattern is remarkable for its pervasiveness, its lack of a generally agreed explanation, and for the plethora of explanations put forward. There are even those who dispute there is such a gradient. So I start with three empirical points and shall then turn to explanations. Firstly, there is such a gradient in diversity as a whole.

Secondly, many groups do not show this gradient, but they are more than compensated for by those that do. Thirdly, in detail the gradient is different in different groups and frequently not a uniform monotonic gradient. Understanding those points makes it easier to understand what is typical and what is unusual about marine biodiversity in a global context.

Fig. 1.2, which is a plot of trees/hectare in nearly equal sized plots, shows the major differences between temperate and tropical systems. Tropical communities are both richer and more even in their species diversity; the total number of species is greater, the scree plot of log number of individuals against log rank is flatter. Note that the total number of individuals is not significantly different in the two systems, a consequence of using a single life-form. The differences in diversity are reflected in all the species, not just in, say, the common or the rare ones.

There are many maps in the literature based on species in equal areas that show the polar–tropical gradient and its standard variations. On land, Africa usually has fewer species per unit area than South America or South-East Asia. So, when it is the richest, as in termites (Eggleton *et al.*, 1994), historical explanations are sought, but these are used to modify the primary explanation based on productivity or other contemporary factors. Similarly, in the oceans, it is normal for equal areas of the Indo-Pacific to be generally richer than the Atlantic, as for instance in Euphausiids (McGowan & Walker, 1993), often explained in terms of history (and total area). The same gradient is shown, albeit weakly and with much variance, in the deep-sea benthos (Rex *et al.*, 1993; and see Chapter 5). The importance of comparing like with like in diversity studies is evident in Brey *et al.* (1994).

Nevertheless, there are many groups that do not show a uniform gradient, i.e. that are not most diverse in the tropics. Penguins, being both marine and terrestrial, are a convenient and well-known example (Williamson, 1973). Birds as a whole are undoubtedly more diverse in the tropics than in temperate and arctic regions, though seabirds may not be. Various groups of insects are most diverse outside the tropics. A pattern with an extra-tropical maximum is shown in some parts of both the Hymenoptera and the Homoptera. In the Hymenoptera these are some (but not all) sections of the enormous parasitoid family Ichneumonidae, the herbivorous Symphyta (sawflies) and the Apoidea (bees) (Noyes, 1989). In the Homoptera, it is the Aphids and Psyllids (Dixon, 1985) that show this pattern.

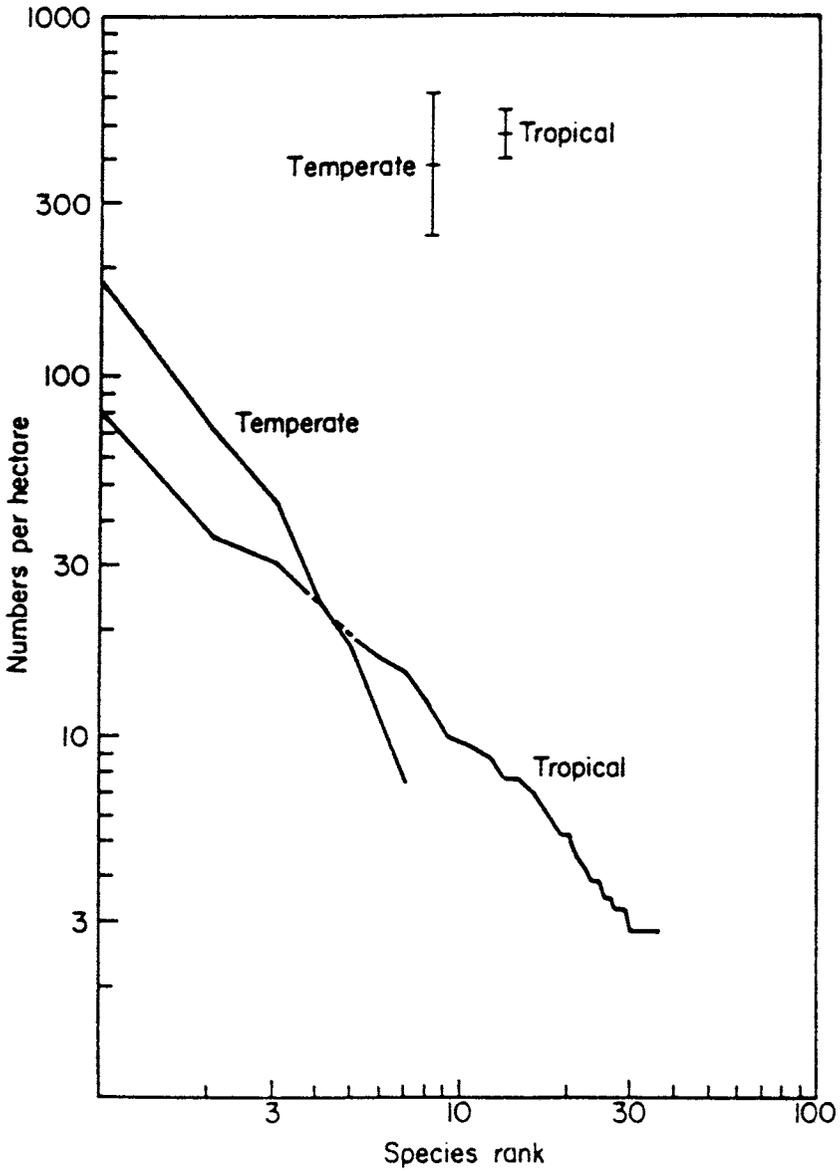


Fig. 1.2. A scree graph of the number of stems 10 cm (4 inches) in diameter in each species of tree in forests in Wisconsin and Brazil, on plots varying from 0.4–3 hectares. Numbers are plotted as log number per hectare, rank is also on a logarithmic scale. From Williamson (1973).

These patterns may just be marked examples of a general phenomenon. Rosenzweig & Abramsky (1993) argue that almost all tropical–polar clines, and for that matter clines in altitude, up mountains and into the deep sea, show a hump. The maximum diversity is not at the end of the cline, but at an intermediate point often much closer to the rich end. They give marine and terrestrial examples, and the phenomenon is well-known in the deep sea (Angel, 1993 and see Chapter 3; Gage & Tyler, 1991). As far as I am aware, none of the numerous general explanations of the polar–tropical gradient predicts this pattern. If humpiness is as common as Rosenzweig & Abramsky argue, then some new models are needed. Entomologists have made a start with possible explanations for the diversity of patterns seen in the Ichneumonidae (Gauld *et al.*, 1992) based on the balance of advantage of different life-histories in relation to the diversity of other groups.

Another point not addressed by most explanations, is that the north–south pattern of the gradient is notably different in different groups. This is also evident, if not systematically documented, for marine groups. On land, equal area diversity plots are available for more groups in North America than anywhere else. North of Mexico, trees are most diverse in the east, in the southern Appalachians (Currie & Paquin, 1987); tiger beetles (Cicindelidae) in the centre of the continent, in Kansas (Pearson & Cassola, 1992; Pearson & Juliano, 1993); and birds in the western mountains (Cook, 1969; Williamson, 1981; Cotgreave & Harvey, 1994). The tiger beetles may show a hump in the USA, as there are fewer species in Texas, which is south of Kansas. In the Indian subcontinent they show two peaks, one, as expected, at the south of India and in Sri Lanka, the other in the Himalayas, in Nepal and Bhutan, and so there is a trough in central India (Pearson & Cassola, 1992).

The North American birds show the importance of both origination patterns and the detailed ecology of the group in explaining details of the geographical distribution of diversity. Although birds as a whole are richest in the west, individual families show different patterns (Cook, 1969). The Parulidae (wood warblers), are found throughout the continent up to the tree line but show a maximal diversity in the mid-eastern states, with a lesser centre of diversity in Mexico (Cook, 1969; Williamson, 1981). For birds as a whole, there is an interesting tongue of high species density stretching east–west across the contact zone of deciduous and coniferous forests (Williamson, 1981). Presumably this particular type and scale of habitat heterogeneity favours bird diversity in particular.

There are many explanations in the literature. Pianka (1994, and earlier editions) gives a well-known list of 10, which has been expanded to 14 in papers in the *American Naturalist* (Huston, 1979; Terborgh, 1985; Stevens, 1989; Pagel *et al.*, 1991), with a further explanation in Rohde (1992), who also gives a comprehensive list. Brown (1988) has a somewhat different, but largely overlapping, list of six factors. The comparison emphasises that many factors are correlated, and that it is difficult to decide what should be considered a distinct factor. Wilson (1992) favours energy, stability and area. Colwell & Hurtt (1994) put forward a null model. History, including origination rates, energy, constancy and heterogeneity are, I think, the factors most generally and enthusiastically championed, and there is a steady stream of papers debunking particular explanations in particular areas. For instance, Hoffman *et al.* (1994) show that in a zone covering 6 deg. of latitude, energy is negatively related, either by itself or in a multiple regression, to higher plant species richness. In the multiple regression, area and precipitation have significant positive coefficients. This negative relationship with energy, which has been seen in several studies (Huston, 1979) may fit with Rosenzweig & Abramsky's (1993) claim that there is in general a humped relationship between productivity and diversity.

It is obvious that no single explanation can be universally applicable, and it is likely that all the explanations have some validity in some circumstances. Rohde (1992) dismisses most explanations because they are inadequate on their own, but that is throwing out the baby with the bath water. Marine studies, particularly of deep-sea benthos, are likely to be important in teasing out the variation of the strength of different factors in different circumstances. We are some way from a sophisticated global model for any major group, let alone life as a whole. Nevertheless, there are some pointers to the factors that allow some groups to show remarkable richness in the tropics, though how these factors translate through population dynamics to co-existence is far from clear.

1.4 Can richness be explained?

If the variation in richness could be explained, it is possible that an understanding of the polar-tropical gradient, humpiness, the elevational gradient, and other major patterns would follow. In particular, the study of terrestrial richness might indicate why most marine systems are much less rich, if they are, or equally rich, if that turns out to be true.

There have now been sufficient quantitative studies on biodiversity

that a start can be made on meta-analysis, seeing how concordant different studies are, and the extent to which combining weak conclusions leads to a stronger one. Rosenzweig & Abramsky (1993) tried to determine the relationship of biodiversity to productivity. In contrast, Wright *et al.* (1993) studied what factors have been implicated in variations in diversity. The weakness of their study is a weakness inherent in much modern ecology: most studies concentrate on a single hypothesis. Yet we all should know, from the statistical discipline of the design of experiments, that it is much more efficient and informative to study several factors simultaneously. So the review by Wright *et al.* is more a meta-study of what ecologists have thought important, than of what factors have been found to be important. The studies investigated are also largely terrestrial. In 53 studies I can only identify 5 that are freshwater (excluding marsh plants) and 3 that are marine, and of those 1 is on corals, 1 on mangroves and 1 on subtidal algae; there were no deep-sea or planktonic studies!

From 97 relationships, they found that the 41 relationships with energy-related factors were all statistically significant, as were all of the 4 for seasonality. In contrast, other factors gave mixed results. For instance habitat complexity etc gave nine significant to three not. So although there is a bias to studying energy and stability, there is good evidence that they are usually important. Counter-examples were noted above. The commonsense conclusion that the polar-tropical gradient in some way results from geophysical or astronomical effects on the environment, in seasonality and energy, is confirmed.

The question remains of how such physical effects are translated into variations in biodiversity. On land, the main contributors to richness are the insects and angiosperms, particularly trees, which set the structure of many terrestrial ecosystems. A simple model may encapsulate what happens, a model based on tree layering and two sorts of specificity in insects.

Terborgh (1985) pointed out that the simple geometrical facts of the angle of the sun and its variation through the year could explain the degree of layering seen in vegetation. When the sun is often vertical, as in the tropics, many layers, up to five, can coexist. When the sun is never vertical, and often at a low angle, trees grow as tall and narrow cones, in just one layer, as in the boreal forests. This variation in layering leads to an exponential increase in heterogeneity, as shown for instance by the abundance and variety of epiphytes. Roots are also a significant source of heterogeneity.

Terborgh's scheme is not enough by itself to explain the great richness of tropical rain forests. There are also non-forest terrestrial ecosystems, such as the South African fynbos (Cowling, 1992), which are remarkable for their plant diversity. (Fynbos is a small shrub heathland, with over 8500 plant species in less than 90 000 km², and surprisingly invisable by trees and shrubs.) The specificity of insects may add the necessary other factor. There are two common views on why insects, and in particular the Coleoptera, Diptera, Hymenoptera and Lepidoptera, are so diverse. These are that their metamorphic life-histories allow them to be either very specific plant herbivores, limited to just one tissue of a species, or to be very specific parasitoids (Wiegmann *et al.*, 1993). The Lepidoptera exemplify the first, the Hymenoptera Parasitica the second. The Coleoptera, Diptera and the remaining Hymenoptera are more heterogeneous, but are still remarkable for their specialisations, particularly in the more species-rich sections.

A recent study in Costa Rica (Memmott *et al.*, 1994) illustrates the point. This was a study of leaf-miners and their parasites, of insects that spend their larval lives in the thickness of a single leaf. Of 88 plant species, larval mines were found in 56. These plants supported 96 species of herbivore, which in turn supported 93 species of parasitoid. The parasitoids with one exception were Hymenoptera; the herbivores were a mixture of Lepidoptera, Coleoptera and Diptera. Any given species of miner occurred in only one host plant, although host plants could have between 1 and 12 species of miners. Similarly, 57 parasitoids were recorded as specific to a particular host, the others were recorded in from 2 to more than 20 hosts. This appearance of specificity is perhaps misleading, in that in large samples of over 100 mines, no parasitoid attacked fewer than four species, and there is a significant positive relationship of log sample size to log number of parasitoid species. Even so, specificity is clearly much higher than is normally found in larger, external, herbivores and predators.

All this leads to a model in which constancy and type of energy input lead to heterogeneity and a system in which many ecologically specific organisms can coexist. For this model to be worked out, the evolution of specificity should be included as well as the way specificity leads to co-existence. History, energy, constancy and heterogeneity are all essential components. How do these ideas impinge on marine studies? How can marine studies be used to clarify and modify these ideas?

These rich terrestrial groups suggest that the importance of heterogeneity and specificity have been undervalued, although the former, at

least, appears in most lists of explanations. There is a contrast with the early views of the deep-sea benthos, which appeared to be unspecialised and living in a rather homogeneous habitat (Gage & May, 1993). However, the nature and scales of heterogeneity in the deep sea are now a subject of great interest (Gage & Tyler, 1991). In shallower waters the importance of specialisation, if not specificity, has been averred (Knowlton & Jackson, 1994).

1.5 Discussion: Where is marine diversity in a global context?

There are three aspects I want to end with; the general state of knowledge, the general academic regard for marine studies, and our understanding of the differences in marine and terrestrial systems.

In knowledge, or ignorance, I am impressed both by how much we know and how little we know. Well over a million species have been described, but that is perhaps 10% or less than those that await description. Even in the best-known phyla new species are still found at a significant rate, although there are a few orders that are apparently completely known. Genetic studies are turning up sibling species in many groups, and the problem of the definition of species remains. In all these respects, marine studies seem not appreciably different from terrestrial ones. The species to be discovered will always be, on average, smaller (Pine, 1994), harder to find, and with poorer diagnostic characters than those already known. There is still a great deal to be learnt of the distribution and abundance of species in all groups. Studies of phylogenetic diversity are making rapid progress thanks to new techniques. The more basic studies on ecological diversity await a satisfactory methodology.

In academic studies, and in the general perception of biodiversity, marine studies are doing poorly. This book may help to redress the balance. The crisis of extinction is more immediate and more obvious in terrestrial systems, so the political impetus for studying biodiversity is concentrated there. Perhaps as a result, academic papers on biodiversity ignore much that is relevant and useful in the sea. The review by Wright *et al.* (1993) mentioned above, which includes only 3 marine out of 53 studies is an example. The splendid volume of Ricklefs & Schluter (1993), of which Wright *et al.* is a part, has only 4 chapters out of 30 on marine topics. It could be argued that if, as I have suggested above, only about 10% of multicellular species are marine, these proportions are about right. That would be to ignore the importance of