

Scale and species numbers

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One of the main tasks confronting community ecologists is to explain why a particular site harbours a certain number of species. The site might range from a drop of water to the whole Earth, and the species might be drawn from a very restricted taxon or include all living organisms. The common problem, however, is to understand the relative importance of speciation and extinction and, more locally, of immigration and loss. Speciation is the ultimate motor driving biodiversity and ecologists need to know the factors influencing rates of speciation, and whether there is a feedback, positive or negative, between species numbers and the generation of new taxa. However, the relative importance of speciation and other factors determining species numbers varies crucially across different scales of enquiry. Here, we explore some of these issues as we move from a macro- to microscale perspective, focusing on a limited number of studies that we believe make important advances in the field.

The number of organisms in a particular area is determined by speciation and extinction, and by immigration and local loss. The relative importance of these processes depends upon the scale of the investigation. We discuss a series of recent studies that have made important contributions to disentangling these issues at the global, regional and local scales. Ecological processes are, of course, crucial to many theories of SPECIATION (see Glossary) itself, a topic discussed by Schluter in this issue¹.

At a global scale

Consider first the largest scale: what determines the number of species on Earth? At this scale, the immigration rate is zero (although some cosmologists and the Men in Black would disagree), local loss of species does not apply, and the total species count is determined by the history of speciation and extinction events. It is possible that species numbers are at a dynamic equilibrium at which the rates of extinction and speciation precisely balance each other and that many suitable niches are unoccupied, or it could be that the number of species increases until all niches are filled up.

For some taxa, the fossil record is good enough to investigate these issues directly (see Benton and Pearson², this issue). We know that the history of life on Earth is punctuated by episodes of mass extinction after which diversity recovers. However, what is less certain, and what depends crucially on issues such as the quality of the fossil record and the TAXONOMIC level at which the analysis is conducted, is whether the recovery is best explained by an exponential or a logistic model. The significance of a logistic relationship is that the asymptote might reflect a ceiling or equilibrium for global biodiversity at any particular level of complexity^{3–6}.

At global scales, speciation and extinction have generated several obvious patterns in species richness. One of the most striking is the relationship

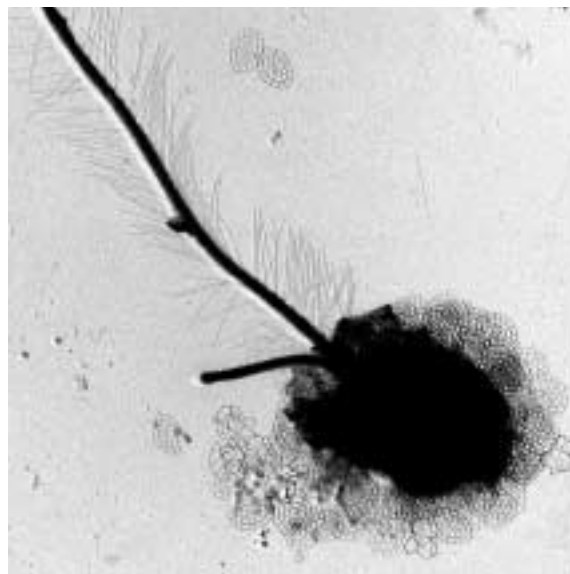
between body size and species diversity⁷: the number of described species in logarithmic size classes first increases as one moves from larger to smaller organisms, but then begins to decline again when a threshold of ~1 mm is reached. This pattern is still not fully understood, but clearly involves changes in the balance between speciation and extinction rates as a function of body size, modulated by resource availability as perceived by species of different sizes⁸. Interpretation of the body size–diversity relationship is made harder by the fact that we tend to know less about the biology and systematics of organisms as their size decreases.

Although new bird and mammal species continue to be discovered, and the application of molecular techniques will throw up surprises such as the recent demonstration that there are at least eight species of mouse lemurs (*Microcebus* spp.) in Madagascar⁹, we essentially know how many large animal and plant species there are on Earth. For medium-sized terrestrial animals, such as insects, there is far greater uncertainty, although alarming estimates that there might be 100 million species of arthropod¹⁰ are now generally thought to be too high, with most entomologists arguing for figures in the range 2–8 million¹¹. Uncertainty increases as the organism gets smaller, or the habitat is less well explored, such as the marine or subterranean environments. In a forest in south-central Cameroon, the proportion of animal species that expert taxonomists could assign to known (named) species was inversely related to the log of the geometric mean body length of each taxon, from 0% for birds and 1% for butterflies, through to 30–80% for beetles, ants and termites in various forest strata, to over 90% for soil nematodes¹². Free-living nematodes, with body sizes spanning the crucial 1-mm length class, could be one of the most speciose animal taxa on Earth, but also one of the most poorly known.

Crossing the 1-mm threshold, we encounter true microbes and the number of described species begins to fall. It is possible that this dip reflects a lack of study, because the tools to investigate systematically microbial diversity have only been developed in recent decades. Indeed, the frontiers of life are continually being pushed back as new communities of archaea and bacteria using non-solar sources of energy are discovered underground or on the sea floor (see, for example, the recent report¹³ of symbiotic consortia of archaea and bacteria anaerobically oxidising methane in submarine sediments). Moreover, tallying the described species of prokaryotes using a eukaryote species concept might not make sense for organisms that often share DNA

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Fig. 1. The flagellated protozoon *Paraphysomonas butcheri*. The body of the cell (which is ~0.004 mm in diameter) is covered with siliceous scales having a species-specific pattern. The long flagellum beats to create water currents that bring bacteria and other particles close to the anterior of the cell. These particles are then ingested with the help of the short flagellum. Flagellated protozoa as a group are the most abundant group of phagotrophs in the biosphere. Photograph by Ken Clarke, CEH Windermere, courtesy of Bland Finlay.



promiscuously and have reticulate rather than tree-like patterns of evolution¹⁴.

Organisms <1 mm in size differ from larger creatures in more than just their genetics. As has previously been emphasized^{15,16}, they are small enough to be dispersed passively in the atmosphere and sufficiently abundant that populations of at least free-living species could be relatively homogeneous on a global scale. Such pervasive gene flow might lower speciation rates, leading to a true drop in the global diversity of the smallest organisms. Recent work, not with bacteria but with protists, supports the 'bugs are everywhere' hypothesis. Ciliated protozoa have a rich microstructure that allows traditional MORPHOLOGICAL SPECIES CONCEPTS to be applied successfully. Using various enrichment techniques, 85 different species of ciliates were isolated from a sample from a volcanic crater lake in Victoria, Australia¹⁷. The number in itself is not significant, because larger samples and different enrichment cultures would doubtless have increased the figure. But what was amazing is that none of the species from this little-explored site was new, and the type localities of all but one of the species were in Northern Europe (the exception being known only from tropical Africa). A similar exercise with breeding birds (ignoring human introductions) might at most yield three to four species in common between Northern Europe and Victoria. Neither is there something odd about ciliates. Chrysomonad flagellate species in the genus *Paraphysomonas* (Fig. 1) can be identified by their structure (they have siliceous scales that are preserved after death) and morphological and genetic species concepts agree. Globally, there are 50 described species and 32 of them were found in Priest Pot, a 1-ha pond in the Lake District, UK¹⁸. More significantly, the relative abundance of species in Priest Pot was highly correlated with their world-wide commonness as derived from a compendium of surveys of the genus. In these very small organisms, local and global distributions appear tightly linked.

At a regional scale

One of the major discoveries of the heroic age of explorer–naturalists was that biodiversity was not constant throughout the Earth, but tended to peak at or near the equator and to decline towards the poles. This pattern occurs in most, but not all, terrestrial taxa¹⁹, and is also found in some marine groups, although the overall picture there is far less clear. Tremendous effort has gone into explaining this pattern, and the problem if anything is now a surfeit of hypotheses, with perhaps 30 competing ideas, although not all of these are independent²⁰.

In an attempt to reduce this mass of ideas, several authors have explored models of species diversity that incorporate a minimum number of biological processes. For example, global biota was constructed by randomly choosing the latitudinal midpoints and ranges of a set of simulated distributions, subject to the constraint that there is a hard latitudinal limit to the placement of ranges^{21,22}. Species with midpoints near the equator can have greater latitudinal range than those towards the poles, and this is sufficient to generate higher species diversity at the equator. However, variants of the null model, where midpoints are distributed uniformly across latitude, tend to predict smaller ranges towards the poles, at variance with the common (but not universal) empirical pattern known as the 'Rapoport effect' (real range-sizes increase towards the poles). It would be remarkable if such simple null models reproduced all the details of global patterns in species richness, and that is not their point. Rather, they serve to identify features of the patterns that require biological, rather than statistical, explanations.

One of the few universal rules in ecology is that more species are found in larger areas and the idea has been championed^{23,24} that area might explain latitudinal patterns in species diversity. Tropical areas are larger than Polar Regions because the Earth is a sphere, because the north and south tropics abut and because climate changes more slowly with latitude at the equator. The greater area of the Tropics generates the tropical–polar decrease in species richness^{23,24}, by the same mechanisms that generate other continental-scale species–area relationships. A recent review²⁵ of the area hypothesis concluded that although area almost certainly has a role in determining the latitudinal gradient in species numbers, it is unlikely to be whole story. In particular, some of the assumptions about how climate affects species ranges and how the probability of ALLOPATRIC SPECIATION varies with range size might affect the predictions of the hypothesis.

Another idea with a long pedigree is that biodiversity is correlated with energy flow into the environment, for example, with net primary productivity or some related variable^{26,27}. At more local levels, diversity tends to peak at intermediate levels of productivity, although at the regional level, the relationship is usually linear. More refined recent

Box 1. Species diversity and scale

Consider the relationship between species diversity and scale. Traditionally^a, ecologists have partitioned diversity into local diversity (α) and regional diversity (γ), with the two linked by the extent to which species composition varies over space (β). The relationship between the three quantities has been described as multiplicative^a (γ depends on $\beta\bar{\alpha}$, where the bar indicates a mean), but more recently, an additive approach, $\gamma = \bar{\alpha} + \beta$, has been borrowed from genetics^{b,c}. Such a partitioning has several desirable statistical properties and lends itself to a hierarchical extension in which diversity is partitioned into α and β components at successively larger geographical scales.

The relationship between local and regional diversity can now be seen as a problem of how diversity is partitioned between the α and β components, which depends crucially on scale^b. At the smallest scale, that of individuals, a Type II saturating response can occur as a habitat fills up, because it is impossible for two individuals to occupy the same patch of ground. However, as the local area approaches the regional, a Type I response must occur. It is very difficult to predict the type of pattern to be expected in between these two scales. In the absence of species interactions, limitations on the number of habitats found in a local area can give rise to scale-dependent Type II responses^{d,e}.

Alternatively, highly structured communities can give Type I responses. A hypothetical example^b contains a landscape of n species, each of which does best in one of n different patch types where it excludes all other competitors. If the scale at which diversity is measured is that of the patch then $\alpha = 1$, $\beta = n - 1$ and $\gamma = n$ and in comparisons across regions that vary in n a Type II relationship is expected. However, merely increasing dispersal can lead to all species being present in all patches, although niche differences continue to maintain community diversity: now, $\alpha = n$, $\beta = 0$ and $\gamma = n$, and Type I relationships are expected. A general point is that most models of resource competition predict saturation relative to a certain species pool rather than absolute levels of saturation.

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analyses have found that composite environmental measures are better correlated with diversity. Just two explanatory variables, energy and rainfall, were able to explain approximately 80% of woody plant diversity in 25 000 km²-grid squares in southern Africa²⁸ (although the fit is exaggerated by spatially correlated error terms). The mechanism postulated to underlie these relationships is that high-energy input allows a greater biomass to be supported and this, in turn, allows more species to coexist in a given area, primarily through a reduction in the risk of extinction. But the chain of causation is probably complex, especially as one moves away from plants to secondary and tertiary consumers of energy. Do available resources in plants influence herbivore

diversity in the same way as ambient solar energy influences plant diversity, or do the complex trophic interactions that constitute natural food webs magnify or diminish these processes²⁹? To answer these questions we need to move from simply comparing species diversities in different regions to looking at how the structure of food webs is influenced by factors such as diversity, productivity and other environmental variables^{30,31}.

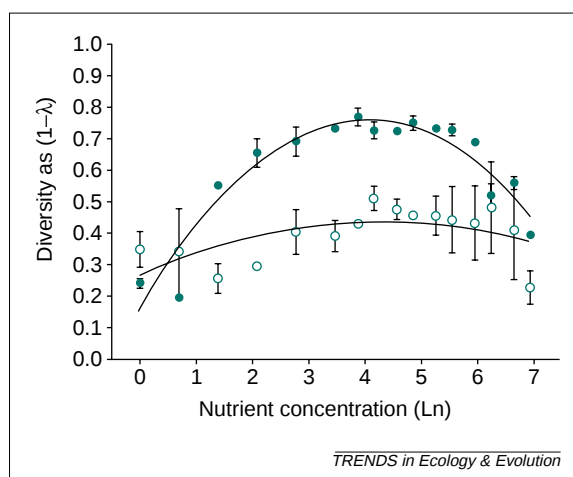
At the local level

To what extent are local communities simply haphazard sub-samples of the regional species pool, as opposed to non-random assemblages of species determined by competition, predation and other ecological processes? As several authors have recently stressed³² the answer depends on scale; that is, on exactly what is meant by 'local'.

A simple way to explore this issue is to plot local versus regional species richness for sites of similar size and structure^{33,34}. If local richness is determined by statistical sampling processes, a linear (Type I) relationship is predicted, whereas non-linear (Type II) saturating relationships might indicate other processes at work. The exact nature of these other processes is elusive but several workers have argued that ecological mechanisms, in particular resource competition, should generate Type II local–regional relationships. However, the majority of workers have found Type I relationships, linear or with little evidence of saturation³². Does this imply that competition, predation and other ecological processes are of minor importance in structuring communities? The difficulties of deducing process from pattern using this type of plot have recently been reviewed³⁵. Using a hierarchical decomposition of species diversity (Box 1), it has been argued that the relationship between local and regional species diversity is crucially dependent on scale, and that both statistical and biological processes can generate the two types of local–regional diversity plots. Thus, although this approach has been important in demonstrating the role of regional diversity in influencing local species patterns, local–regional diversity plots are probably a relatively coarse tool for investigating the processes underlying community structure^{32,35–37}.

So how might one understand the processes determining species diversity at more local levels? Much of current community and population ecology is devoted to this issue and there have been several interesting recent developments, for example in exploring diversity and species area effects using forest inventories^{38–40}. However, we concentrate here on one particular problem, the relationship between local productivity and diversity. Recall that at regional scales, diversity tends to increase monotonically with productivity. At local levels, there is a marked tendency for diversity to peak at intermediate levels of productivity, although a recent

Fig. 2. The diversity of microbial *Pseudomonas fluorescens* morphotypes (expressed as one minus Simpson's index) as a function of nutrient concentration for stirred (open) and unstirred (closed) cultures. Results from a second base population were similar. Reproduced, with permission, from Ref. 47.



meta-analysis of diversity–productivity patterns suggests a much more varied range of relationships⁴¹. However, the pattern is certainly widespread and hypotheses involving both competition and predation have been put forward to explain unimodal patterns⁴². It has been suggested that low and high productivity environments are characterized by intense competition for different resources and the plant species that best competes for the appropriate limiting resource becomes dominant⁴³. At intermediate resource levels, no single resource is universally limiting, and this allows a greater diversity of plants to persist. Alternative explanations involve the roles of higher trophic levels in maintaining diversity^{44,45}. Since the classic experiments on removing a keystone predator⁴⁶, we have known that higher trophic levels can promote ecological diversity. Possibly, in low productivity environments, insufficient energy is available to higher trophic levels to maintain diversity, whereas in very high productivity environments, predators are so abundant that they reduce diversity by driving extinct all but the prey species most able to survive their onslaughts. Of course, these and other processes could combine, possibly idiosyncratically, to determine local diversity/productivity patterns.

While these issues continue to be explored in field experiments, two recent studies using bacterial systems offer novel approaches to this problem. The first⁴⁷ uses the common aerobic bacterium *Pseudomonas fluorescens*. A previous experiment using the same system⁴⁸ had shown that a single genotype of bacterium could give rise, through mutation, to a remarkable range of phenotypically distinguishable forms that in an unstirred culture bottle occupied separate ecological niches (the culture medium body, the vessel surfaces and the culture/air interface). If the culture bottle is shaken, this diversity fails to appear. It thus seems that diversity is maintained through negative frequency-dependent selection in a spatially structured environment. In the more recent experiments, the same bacterial strain was used, but nutrient concentrations were also manipulated by three orders of magnitude. In

unstirred cultures, diversity peaked at intermediate nutrient levels, whereas in stirred cultures, diversity was low and independent of productivity (Fig. 2). Thus, a unimodal diversity–productivity relationship is possible with a single resource and in the absence of higher trophic levels.

Of course pseudomonad phenotypes are not species and their generation and extinction might differ from equivalent processes among true species. Yet, in this system without sex, the parallels between bacterial variants and orthodox species are close. So what ecological process underlies this pattern? This system has been modelled⁴⁷ using a variant of a model of the maintenance of diversity in heterogeneous environments⁴⁹ that incorporates variable productivity. At low productivity, only the variants with the highest absolute fitness are able to maintain themselves; as productivity increases, more variants are viable and the negative frequency dependence identified in the first experiment allows coexistence. But in nutrient-rich culture, the absolute fitness of the best variant in its own niche is so high that it can displace all other variants, even though it does not perform as well in foreign niches.

The demonstration that heterogeneous resources or higher trophic levels are not required for a unimodal diversity–productivity relationship does not mean they are unimportant in the field. Recent experiments with a different microbial system have shown how the relative importance of competition and predation changes with habitat productivity. Although these experiments do not directly show that predation leads to a unimodal diversity–productivity relationship, the results are consistent with models that make this prediction⁴⁵ (see also recent experiments with ciliate communities⁵⁰). Using two strains of *Escherichia coli*, one of which was relatively resistant to the bacteriophage T2, and the other relatively vulnerable a tradeoff between resistance to the phage and efficiency of resource (glucose) utilization has been demonstrated^{51–54}. When the two bacterial strains and phage were cultured at low productivities, the competitively less successful but more resistant strain declined, whereas the reverse occurred at high productivity. Although the qualitative predictions of the theory were confirmed, the precise rates of change of strain densities were not exactly as predicted by a model of the system. One possibility is that spatial heterogeneity in the chemostats influenced the outcome, another is that there were unanticipated nonlinearities in the interaction. A further complicating factor is the appearance of completely resistant *E. coli* strains in high-productivity replicates. This analogue of ‘speciation’ is perhaps peculiar to microbial systems.

Conclusions

Understanding the processes determining species numbers requires the marshalling of all the tools and approaches available to ecologists. At global and

regional scales, consideration of some questions is hindered by taxonomic ignorance and lack of information. Two factors that might help mitigate this are: (1) the increasing adoption of molecular methods; and (2) the revolution in information dissemination brought about by the Internet and related technologies. Acting against these is the difficulty in funding and recruiting systematists. Macroecological approaches will continue to be invaluable in revealing patterns to be explained and teasing apart competing explanations. A greater integration of statistical methodologies will assist this, but as some of the examples we have discussed illustrate, it will often be difficult or impossible to distinguish between competing explanations or identify the direction of

causation. In particular, many microecological processes might explain the same macroecological pattern equally well. Experimental work is required to cut through this Gordian knot. One promising approach is to use experimental communities of microorganisms, in which community ecological and even evolutionary processes occur at a rate amenable to investigation in the laboratory. Another approach is large-scale field manipulation experiments, often involving teams of scientists of a size more familiar to physicists than to ecologists. At a time when the numbers of species on Earth are declining at a rate unprecedented since the late Cretaceous, it is difficult to underestimate the need to understand the ecological processes behind species richness.

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