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The Croonian Lecture, 1995: Natural Communities: Structure and Dynamics

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THE CROONIAN LECTURE, 1995

Natural communities: structure and dynamics

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CONTENTS

PAGE
1. Introduction 1113
2. Species richness 1114
3. Species diversity 1117
4. Functional and trophic groups 1118
   (*a*) Guild structure 1118
   (*b*) Niche structure 1120
5. Stability and change 1122
   (*a*) Constancy of structure 1122
   (*b*) Succession 1122
6. The bionomic profile of communities 1124
7. Conclusions 1125
References 1126

SUMMARY

A review is undertaken of various concepts in community ecology that relate to observed patterns in nature; these are species richness, diversity, guild structure, niche structure, constancy of structure, succession and the bionomic profile of communities. This understanding may allow us to better predict the effects of changes we are making in our environment.

1. INTRODUCTION

Knowledge of its environment is vital to any organism. Mankind's power to modify the environment is greater than that of any other organism. For mankind, therefore, especially as technological prowess increases, there is no limit to the information that may be of value. Every Fellow of the Royal Society is committed to the improvement of natural knowledge at the time of admission, but as such knowledge is 'improved', the search for its systematic organization (a feature of science as the dictionaries remind us) becomes pressing. A major organising principle, such as Mendeleev's periodic table, Einstein's mass–energy equation or Crick and Watson's double helix, provides a framework for a vast array of individual observations and a basis for prediction, which is vital as our ability to bring about environmental change accelerates.

As Peter Medawar pointed out, biology may be viewed on several scales of complexity: from the molecular, through the cellular and organismal, to the population and, eventually, the community. In recent Croonian lectures my colleagues R. M. May (1986*a*) and R. M. Anderson (1995) have illuminated the striking progress that has been made in developing a general understanding of the dynamics of populations. Here the position in the other component of ecology, that concerned with the greatest levels of complexity, natural communities, is reviewed. The living organisms that occur in an ecosystem constitute its natural community. To what extent can predictions be made about the various features of communities?

The features considered here are:
(i) the number of different types of organism (species richness);
(ii) the relative abundances of the species (diversity);
(iii) the division of the community into functional groups (guilds);
(iv) the composition of guilds themselves (a series of niches);
(v) how communities change (succession and stability);
(vi) whether habitats can be defined by certain features to indicate the suites of traits of the species in their community, i.e. by templet theory.

I will say at the outset that, although I consider that there are some useful emergent principles, one of the fascinating (and infuriating) aspects of this area of ecological work is the extent to which as layers of

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complexity are peeled away yet another pattern is revealed in which the organizing principles appear to be different.

Often a first and superficial impression of what appear to be communities in similar environments is of their differences. On the grasslands of Africa there are a variety of large grazing and browsing mammals: elephants, rhinoceros, zebras, giraffes, as well as many bovoids (antelopes and buffalo). However, on the prairies of North America the only large mammals are bovoids, the pronghorn antelope (*Antilocarpa*) and the American bison (*Bison*); before the arrival of the gun the latter was present in vast numbers. But before some other change this difference between the continents was much less, for in the middle Miocene there were eleven different species of equid and ruminant (bovoid) browsers living on the central plains – savannah habitats – of North America (Janis *et al.* 1994).

By contrast one may be struck by morphological parallels between the components of different communities. Bourlière (1973) pointed to five forms of rainforest animal in both Africa and South America; the representatives of each morphotype on the different continents were phylogenetically unrelated. However, a variety of forms may not imply phylogenetic diversity. In the classical case of Darwin's finches in the Galapagos a variety of morphotypes, resembling various families of birds elsewhere, have evolved from one ancestor (Grant 1986). A somewhat intermediate situation with regard to the extent of phylogenetic differences between analogous morphotypes is represented by the small desert rodents, which occur in two distinct forms, one that hops and the other that runs. These forms are represented by quite different genera in Eurasia and North America. Turning to invertebrates or to plants one could point to other striking examples of convergence. Does each form represent a complete and distinct role in the community? Can we predict from form to function?

If predictions are to be made then the search must be made for answers to a range of questions. Are there rules that govern the features in my initial list? Are there uniform mechanisms underlying apparently similar patterns? Are there rules we can discover to allow a forecast of the new community if we change the environment? This review seeks to explore the answers to these questions. The number of examples that can be utilized is limited; frankly my selection is strongly biased in that I tend to use work with which I have been associated.

2. SPECIES RICHNESS

In their seminal work on island biogeography, MacArthur & Wilson (1967) pointed out that there was a positive relation between the size of an island and the richness of its fauna: the species–area equation ($S = cA^z$). This pattern was first recognized in 1948 by Eugene Munroe for butterflies in the West Indies. There the many islands of greatly varying size, within a limited geographical range, could provide a large data set; a further detailed investigation of this relationship on 65 islands has been undertaken by Davis & Smith (1996). They found that, although there was a good fit to the equation ($r^2 = 0.72$), the slope was small ($z = 0.20$) and they concluded that this was due to high immigration rates.

The concept has been applied to ecological islands, such as trees, as well as to geographical ones (Janzen 1968; Opler 1974; Strong 1974; Southwood & Kennedy 1983). Several studies of the insect fauna of plants have shown that species richness is correlated with the abundance of the plant (see, for example, Southwood 1960*a*; Lawton & Schröder 1977; Kennedy & Southwood 1984). Over half the variation in the numbers of insect species associated with British trees can be accounted for by the tree's abundance as represented by distribution records. In all such studies care has to be taken to avoid sampling effects (Kuris *et al.* 1980). If limited taxa are considered, as by Claridge (1987), then evolutionary associations may dominate; thus such work is not a falsification of the species-area relation for faunas. There are also statistical reasons why small samples may not show the relation (Graffen in Kennedy & Southwood 1984).

Area, then, explains much of the variation between environmentally comparable 'islands', but the real level of species richness (i.e. c and z in the equation) is related to other factors. One set of these factors are those that determine the capacity of an area, the resources of its habitats. These may be categorized into those influencing productivity and those influencing structure. The third factor is the role of history.

Variation in productivity, that is in the amount of energy available from the photosynthetic capture of sunlight by the plants (the primary producers), does underlie the long-recognized latitudinal gradient in species richness (Stevens 1989). Some recent data on Canadian entomofauna (Danks 1993) illustrate this: the boreal and subarctic regions have a higher species richness than the most northerly, but comparably sized, region. Where the productivity varies naturally, independently of latitude, as in deserts, species richness has been shown to correlate with it (Brown & Davidson 1977). However, there is much evidence that when productivity is enhanced by enrichment with nutrients species richness falls and, because the commonest species become especially abundant, diversity falls even more. Examples of this can be observed in the vegetation of grasslands (the classic Park Grass experiment at Rothamsted (Tilman *et al.* 1994)), in the algae in freshwater lakes (Reynolds & Bellinger 1992) and in the benthic fauna of shallow seas (Gray 1979). The conclusion that we must draw is that the relation of productivity to community structure is expressed as increased biomass. It is not necessarily true that some or all of this additional biomass will represent new species. It seems that there is no simple universal rule relating species richness to this aspect of habitat capacity.

The second factor that influences habitat capacity is its structural complexity. This was originally demonstrated by Lawton & Schröder (1977) in relation to the number of insects associated with different types of plant. As Lawton succinctly expressed it, 'there are more ways of making a living on an oak tree than on a rush'. Species richness of macroinvertebrates on plants increases with increasing structural complexity, through the series: monocotyledons, annuals, perennial herbs, bushes or shrubs, trees. This is related both to the architectural complexity (the different types of plant structures) and to the spatial complexity (the distribution of plant structures in space). These studies were concerned with the insects associated with particular species of plant; the same association can be seen in communities of plants. During succession the structural complexity of the plant community increases. The number of species of Hemiptera and Coleoptera occurring through four stages in a secondary succession could be closely correlated ($R^2 = 0.86$) with measures of structural complexity of the plant community (Southwood *et al.* 1979). On a large scale, vegetational structure has been found to be an important determinant of bird species diversity (see, for example, James & Wamer 1982; Bersier & Meyer 1994). On the smallest of scales, fallen logs increase the structural complexity of the rain forest for rodents, providing 'an extension' of the environment for the ground-dwelling species of *Oryzomys* (Woodman *et al.*1995).

This structural space provided by other organisms is often referred to as 'ecospace'. The increase in surface area is often quite dramatic: for example, an old beech tree occupying 6 m^2 of ground surface was found to have a surface area in summer of 11 000 m^2. The extent to which an animal (or epiphyte) can exploit this ecospace depends on size: there will be many more habitats (more strictly, trivial ranges) for small animals than for large ones (Southwood 1978*b*). The communities in apparently similar habitats in different parts of the ecospace may be quite distinctive: working in the coastal spruce forests of northwest Canada, Winchester (1996) found less than 20% similarity between the species composition of the oribatid mite community living in the moss mats high in the canopy and that of the forest floor.

There is a general similarity in the form of the relation between the frequency of availability of trivial ranges of various sizes as predicted from the structure of ecospace (Southwood 1978*b*; Morse *et al.* 1985) and that between the number of species and their size, demonstrated by May (1978, 1986*b*), which is $S \approx L^{-2}$. However, several studies have failed to demonstrate a consistent relation between size and abundance in natural communities (Blackburn *et al.* 1993; Stork & Blackburn 1993), but such a relation may have been obscured by the restriction of some of these studies to a particular taxon. Although there must be a measure of causality in these patterns, the exact relations and mechanisms remain a matter of conjecture (May 1986*b*).

Coral reefs and tropical rain forests are two of the most species-rich biotopes; their apparent stability and high productivity are traditionally cited as the factors responsible. They are, however, dominated by organisms that provide a great deal of ecospace. I suggest that this could be a major factor in their species richness.

As well as area and capacity, the history of a habitat will determine the species richness of its fauna and flora. The history will indicate the time that has been available for colonization. The time that a tree species has been present in Britain is the second most significant determinant of the species richness of its entomofauna (Kennedy & Southwood 1984) and the number of years an animal species has been domesticated is closely reflected in the number of diseases (parasitic organisms) shared with humans (Southwood 1987*a*). When a new habitat arises the physical conditions may initially be biologically harsh, as with a new volcanic islands (e.g. Krakatau (Thornton & New 1988)), or relatively benign, as with a landslide face or a small pool; in either case the species richness of the colonizing flora and fauna will rise, slowly in the former case, more rapidly in the latter, but eventually the rate at which new species are gained will fall and the community will have become diverse. This is neatly shown by a study the species of two families of water bug (Notonectidae and Corixidae) colonizing 13 subsidence pools in north England; the pools varied in age from 6 to 54 years. Many factors were tested for a correlation with species richness, but only pond age was significant (Williams 1993). The extent in time of the steadiness of a community's environment is clearly a major determinant of its species richness.

When the numbers of species in an area eventually cease to rise and any additions (immigrations) are being balanced by subtractions (extinctions), the changes constitute the turnover rate. This has been well demonstrated in several instances; not surprisingly, most of these have involved the vertebrate fauna of islands, where species richness is relatively small. For instance, detailed information on the breeding bird population on the Farne Islands, gathered over a period of 29 years, was analysed by Diamond & May (1977). Of the 16 species recorded, only four bred every year; the others became extinct and mostly recolonized, some several times. The probability of extinction was less in those species that bred in more than one successive year and that had larger populations. The high extinction rate can be related to the very small populations concerned: with one exception (the colonial-nesting house martin) all the species that became extinct never had more than three breeding pairs present on the islands in any year. Whether the habitat was unsuitable in the years when species were not present or whether the extinction was merely a reflection of demographic stochasticity (May 1971) cannot be determined. The key features of a community that demonstrates such a dynamic turnover are the small sizes of the species' populations and continuous exposure to the full species pool from which the flora or fauna are drawn.

If we turn to ecological 'islands' such as an isolated clump of trees or a small pond the species dynamics pattern is likely to show a high turnover rate and be analogous to that of the Farne Island birds. However, if larger areas and hence larger numbers are considered, as MacArthur and Wilson postulated, species turnover becomes a much less significant process in relation to the total number of species involved. The

Table 1. *The proportion of the total British fauna of certain taxa collected in individual gardens* (0.3 *ha or less*) *in England*

taxon	number of years collecting	number of species found	% British list	reference
Coleoptera	46	730	20	Allen 1951, 1964
Coleoptera	20	950	26	Welch 1994*a*
Syrphidae	22	92	38	Owen 1994
Ichneumonidae	1	355	17	Owen 1994
Aphidoidea	8	120	24	Martin 1994

species-pool exhaustion model is the more appropriate paradigm when considering the species-richness dynamics of the flora of a forest, the insect fauna of a woodland or of a species of introduced tree. Some species pools will be rich for biogeographical reasons: Churchfield & Sheftel (1995) describe a community of nine species of shrew (*Sorex* and *Neomys*) in the mid-taiga of central Siberia, the exceptional diversity arising from the presence of both eastern and western palaearctic faunas.

Species pools reflect the latitudinal and altitudinal gradients in species richness. The effective pool will be determined also by the vagility of the species, their active and passive movement and the prevailing wind or ocean currents. Thus there is the assumption that given enough time every organism that can be carried in air or water currents will turn up everywhere that those currents can take it. There are several accounts of avid entomologists finding a high proportion of the total national list of species of a particular group in a small area in which they have collected steadily over a number of years (table 1).

So in such communities the number of immigrant species at apparent equilibrium will not be the significant measure; the key variable is the number of new species that become established, producing a slow increase in species richness (increased packing of species). This occurs proportionally to time since the last disturbance, that is while the environment remains stable. The probability of establishment (successful colonization) will depend on the extent to which the new habitat meets the ecological requirements of the immigrants. I suggested (Southwood 1961) that this might be termed the species' predilection for the new habitat; individual immigrants with a high predilection are likely to become successful colonists, but the probability is that those with lower predilections will fail on numerous occasions, perhaps always. Thus species accumulation curves for the species richness of a flora or fauna will be of the form

$$S_t = S_\mathrm{p}(1-\mathrm{e}^{-\epsilon t})$$

where S_t is the total number of species at time t, S_p is the species pool and ϵ is a measure of the success rate of immigrants (Southwood & Kennedy 1983). Applying this to the fauna of a newly introduced species of plant or other novel habitat, the increase in species richness will depend on the level of predilection in the species pool and the frequency of exposure of a species (an evolutionary process somewhat analogous to the development of resistance to an insecticide). As Singer *et al.* (1993) have shown, this can be a rapid process when the plant composition of a habitat changes; their careful work strengthens comparable interpretations of earlier, more anecdotal, evidence (Southwood 1961). Thus species-accumulation curves for these large habitats flatten out (become asymptotic), not because a rising proportion of the species are becoming extinct, but mainly because the species pool of potential colonists becomes progressively exhausted. If the habitat itself changes the rate of extinction will be enhanced (Lawton & May 1995), but otherwise species richness will continue to rise, very slowly, as some of the species that arrive and 'challenge' the community succeed (figure 1). Changes in the British entomofauna this century, in which establishments exceed extinctions in most adequately known groups, provide data to support this interpretation of the mechanism (Southwood & Kennedy 1983), although the losses among the butterfly species are, exceptionally, high (Thomas & Morris 1995).

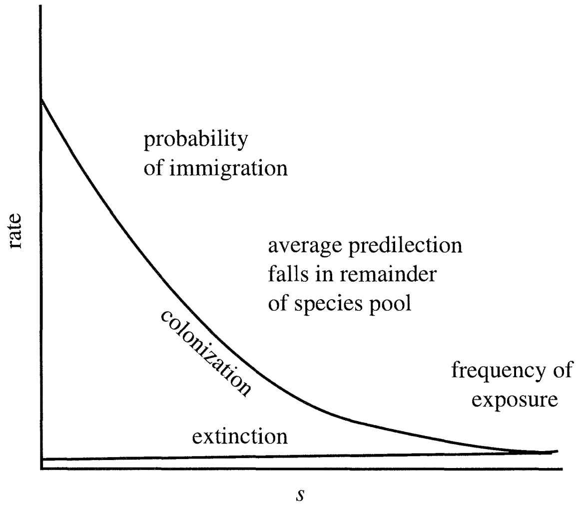

Figure 1. The rates of colonization (addition to species richness) and extinction against the species richness (s) in large islands, either geographical or ecological, with a large species pool; indicating the factors that successively dominate the determination of the rate.

When a community is being studied the inventory of species will at first build up quickly, but eventually it flattens out as even the rarest species are recorded: in this manner the inventory mimics the theoretical species-accumulation curve for the habitat. With certain caveats, incomplete curves may be used to estimate the species richness of a community (Soberón & Llorente 1993; Walther *et al.* 1995). An example of

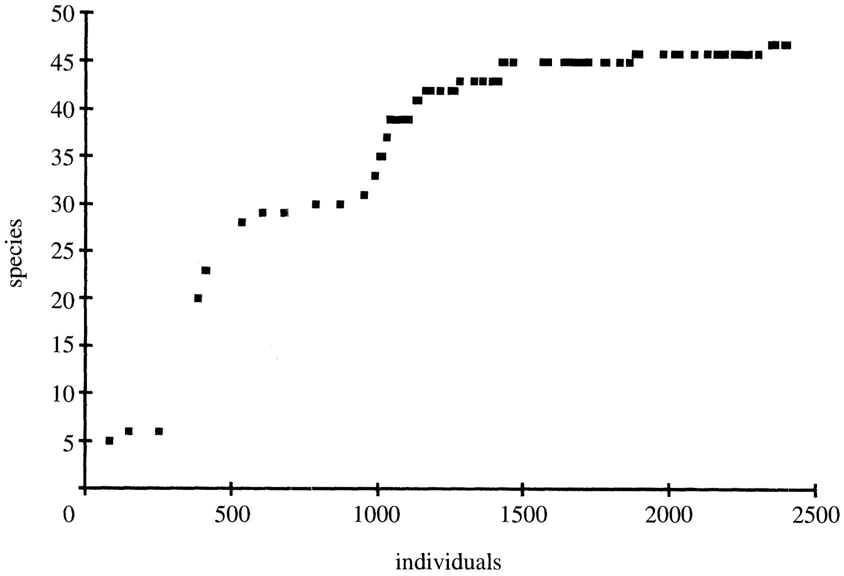

Figure 2. The species-accumulation curve for Heteroptera collected in knockdown sampling of oak trees (*Quercus robur*) in Wytham Wood (T. R. E. Southwood, G. R. W. Wint, C. E. J. Kennedy, J. Killick and S. Greenwood, unpublished).

such a species-accumulation curve is provided by the plot for Heteroptera (figure 2) on oak trees (*Quercus robur*) sampled by insecticide knockdown over five years (T. R. E. Southwood, G. R. W. Wint, C. E. J. Kennedy, J. Killick and S. Greenwood, unpublished). The point of inflection of the curve is around 35, close to the recorded number (38) of 'associated species' (Kennedy & Southwood 1984). The final total of 47 contains single examples of species that are in no normal sense part of the community on oak in central England, the most bizarre of which is *Piesma quadrata*, normally a saltmarsh dweller. The occurrence of such individuals underlines the point already made about the unbounded nature of the species pool that can challenge a community.

3. SPECIES DIVERSITY

Communities with the same species richness may differ in the number of individuals they contain (i.e. in their diversity) and in the manner in which the individuals are distributed between the species (equitability) (Southwood 1978*a*; Magurran 1988). Two distributions have been found to describe the diversity of communities: the log-series (Fisher *et al.* 1943) and the log-normal (Preston 1948). May (1975) showed on theoretical grounds that the log-series distribution would be expected to best describe unsaturated communities and the log-normal communities that were near their equilibrium composition. It is axiomatic in these models that samples from the same community will have the same index of diversity (Williams 1947). However, when samples of macroinvertebrates from oak, taken in the study referred to above, were successively summed it was found that the index of diversity continued to rise, achieving extremely high values of William's α. Dr S. Nee has determined that this rank-abundance curve is best described by a power-law or a log-normal distribution.

When some of the component sets of species-richness data are examined separately, the following results are obtained.

1. For all insects on *Quercus ilex* (6700 individuals, 435 species) (figure 3*a*) neither the log-normal nor the log-series distribution provides a good description of the abundance distribution. However, a power-law distribution (Kendall 1961) provides an excellent fit. There are numerous models, differing in their details, that can generate power-law distributions, but their generic feature in terms of this analysis is that the species abundances are determined independently of eachother. This accords with the supposition that the community developing on the introduced *Q. ilex* is a non-equilibrium one.
2. All phytophages on *Quercus robur* (7644 individuals, 266 species) (figure 3*b*) have a distribution that is best described by the log-normal, although it is not as good a fit as the next example.
3. The Heteroptera on *Q. robur* (2400 individuals, 47 species) (figure 3*c*) are well described by the log-normal distribution apart from the excess abundance of species represented by a single individual; the number of species in this class is inflated by the recording of vagrants, such as the saltmarsh species mentioned already. The fact that this distribution shows an inflection indicates that the sample is large enough relative to the community to have extended beyond the veil line (in comparison with the previous distribution). Such a good fit of the log-normal distribution can be interpreted as describing an equilibrium community in which the multidimensional niche space has been partitioned among the species.

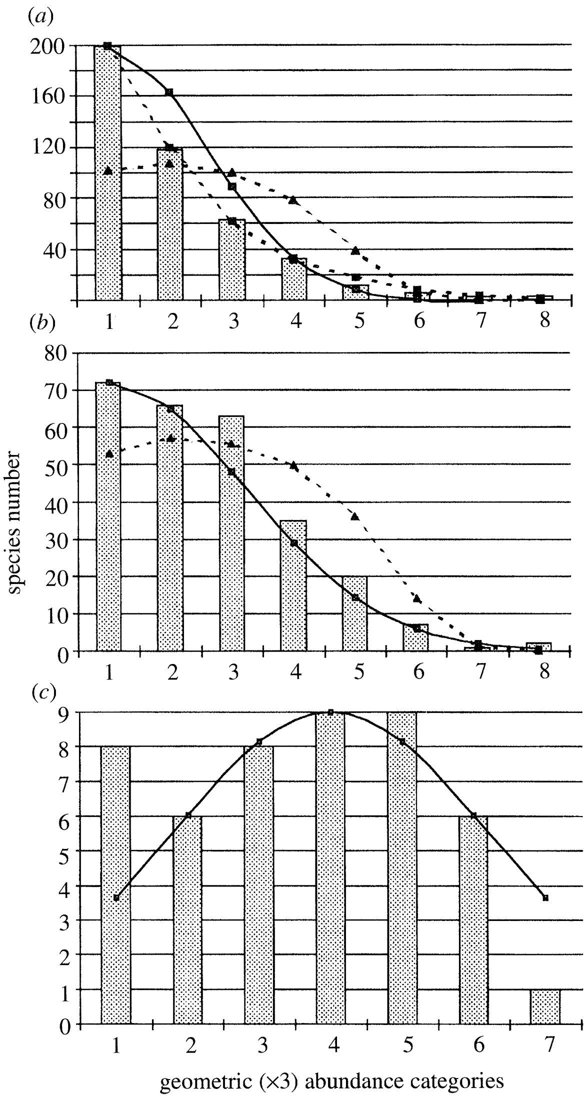

Figure 3. Species diversity profiles for different communities. (*a*, *b*) Rank (geometric categories) – log abundance curves; (*c*) frequency of geometric abundance classes. (*a*) All insects (excluding tourist guild) on *Quercus ilex*; (*b*) phytophages on *Q. robur*; (*c*) Heteroptera on *Q. robur*. Data from Southwood *et al.* (unpublished, as figure 2).

4. FUNCTIONAL AND TROPHIC GROUPS

(*a*) *Guild structure*

Some of the most basic concepts of ecology, the pyramid of numbers, the food chain and the food web (Elton 1927), concern the division of communities into major trophic groups. At the other end of the scale Root (1967) reintroduced the concept of the guild to define a group of species that exploit the same class of environmental resources in a similar way. It was originally used by Schimper (1903) to describe major functional groups of plants (climbers, epiphytes, etc.), but as Jaksic (1981) and Simberloff & Dayan (1991) have pointed out the interpretation of this useful term has been very varied. I will use it in a broad sense, as did Schimper (1903) and Root (1973), to divide the community into the major functional components for which the term 'major guilds' has been used (Moran & Southwood 1982). Intuitively one might suppose that in terms of biomass, if not of individuals, there would be some fairly constant relation between the predator guild and those that constitute its prey (making allowance for metabolic rate, i.e. whether warm-blooded or not); indeed, this has been observed by several workers (Arnold 1972; Cohen 1972; Cole 1980; Jeffries & Lawton 1985). Measured in terms of individuals, the phytophagous and predatory arthropods were found by Hendrix *et al.* (1988) to be a relatively constant proportion of the total arthropods in the first two years of secondary successions in both Britain and Iowa, but the proportions were different in the two continents. Data obtained on the macro-invertebrates on oak (Southwood *et al.*, unpublished) throughout the year allow the comparison of the ratio of phytophages to predators by using the three different measures of guilds' size: biomass fluctuates most and species number the least (figure 4). It should of course be noted that when, in the late spring, there is that particularly high ratio of prey biomass to predator biomass, vertebrate predators, namely birds, are actively foraging on the trees, taking large numbers of caterpillars and undoubtedly some the invertebrate predators too.

Thus for the description of composition, species number seems the more constant measure and this has been used in many studies. In an analysis of the trophic structure of the terrestrial fauna of mangrove islands Heatwole and Levins (1972) maintained that there was a proportional uniformity in the numbers of species within guilds before and after recolonisation. Simberloff (1976, 1978), who had undertaken the original work, challenged their conclusions on conceptual and statistical grounds. A comparison of the proportions of the major guilds (in terms of species) in late summer samples of macroinvertebrate faunas from ten broadleaved deciduous trees (differing either in species or in location: South Africa or Britain) also showed evidence of some constancy in pattern (Moran & Southwood 1982). It is now possible to include this data with a variety of subsequent studies, also based on field data from samples of real communities. All these studies contain data from samples taken over some months (Stork 1987; West 1986), or over several seasons and several years (Southwood *et al.*, unpublished) (over 55000 individual insects were collected on nearly 200 sampling occasions). This further information (figure 5) supports the preliminary conclusion that there is indeed some constancy in proportionality, more especially in relation to the phytophage guild. What is perhaps more interesting is the suggestion that tree type (broadleaved, evergreen, etc.) and biogeographical region (wet tropics, dry tropics, temperate), but not exact geography, act as major modifiers of guild proportionality. Variations in the other guilds need to related to this picture; the lack of data make that more problematic, although I suspect that it is the variations in these that largely drive the above patterns.

An alternative to using field samples is to consider the recorded fauna of a geographical region. The analysis of the factors influencing the species richness of the phytophagous arthropod fauna of British trees

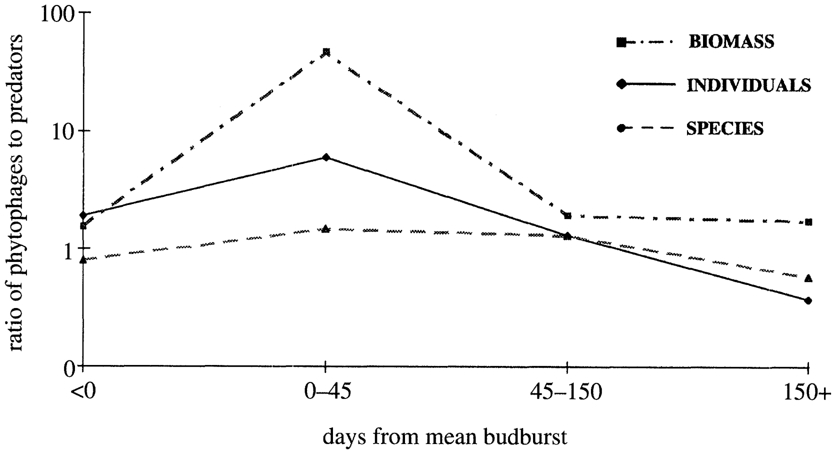

Figure 4. Comparison of changes in the relative sizes of predator and phytophage guilds with season, using three different measures of size (numbers of individuals, numbers of species and biomass). Data from knockdown survey of *Q. robur* entomofauna (Southwood *et al.* (unpublished, as figure 2)).

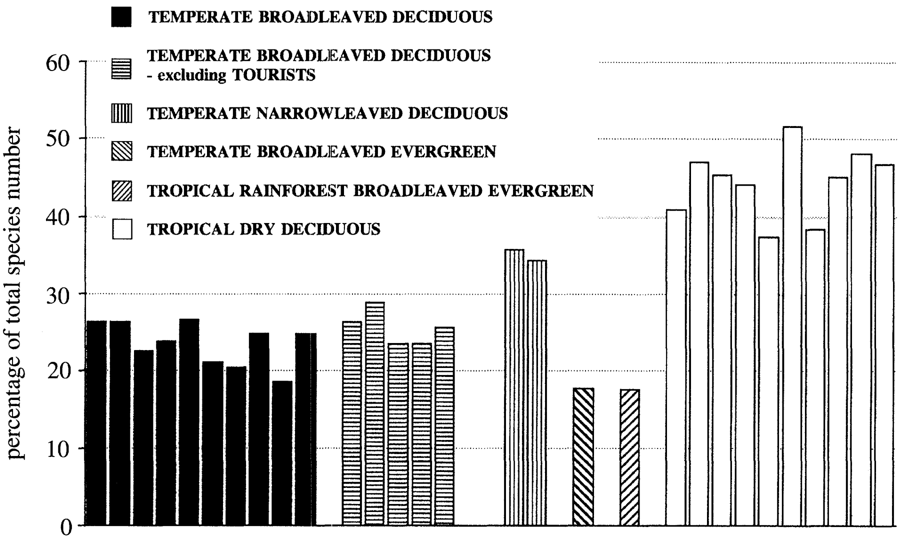

Figure 5. Species in the phytophage guild as a proportion of the total entomofauna found in different surveys. Temperate data from Moran & Southwood (1982) and Southwood *et al.* (unpublished, as figure 2); rainforest data from Stork (1987) and dry tropical data from West (1986).

discussed above (Kennedy & Southwood 1984) was based on faunal lists. This data has been further analysed by Cornell & Kahn (1989), who divided the arthropod species recorded for each genus or species of tree into chewers, leaf-miners, gall-formers and sap-suckers* and within these guilds into fifteen arthropod taxonomic categories. They found a great deal of unexplained variation; more particularly, the proportional contribution of different taxa to the guilds varied enormously. For example, Symphyta make a large contribution to the chewer guild of *Salix*, but are very poorly represented on *Fagus*, although the chewer guilds of both trees constitute very similar proportions of the overall phytophage guild on both. Cornell & Kahn conclude that there is a strong historical component contributing to the functional structure of this fauna. This is undoubtedly true in relation to both coevolution and colonization. Incidentally, their analysis highlights the importance in community studies of avoiding 'taxonomic myopia' (Southwood 1987*b*); a guild should be studied in its entirety independent of taxonomic divisions. But in spite of Cornell & Kahn's general conclusion concerning variation there are certain patterns. Averaged across all trees, chewers make up 61.6% of the phytophage guild. There are 16 native deciduous tree taxa in Britain; for only two (*Salix* and *Betula*) is the proportion of chewers significantly oversized. It is noteworthy that the proportional sizes of the guilds associated with introduced trees are generally widely different from the average values and taxonomic representation is limited. Perhaps there are some 'rules' for major guilds that are fully 'obeyed' only when a fauna has reached the asymptotic region of the species-accumulation curve.

Guilds may also be considered on a finer scale: for phytophagous insects a matrix can be constructed for the feeding site and the feeding mode. The phytophagous insect fauna of bracken (*Pteridium aquilinum*)

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* Moran & Southwood (1982) 'lumped' the first three categories together as defoliators/chewers.

in two locations, in Britain and in Mexico, showed marked differences in their guild structure, but the number of species in the two communities was very different (Lawton 1982). However, comparisons between red oak and aspens in Britain and Canada shows some striking similarities (Ashbourne & Putman 1987).

In summary, then, the proportional size of various guilds may be expressed in terms of individuals, biomass or species, the latter based on field sampling or faunistic lists. Naturally these different measures reveal different patterns, but restricting any conclusions to insects on plants, where much work is current, there is some evidence of constancy in proportionality, particularly in terms of the species richness of phytophages. There are indications that these patterns are different on particular types of plant, e.g. trees of the dry tropics with finely divided leaves compared with deciduous broadleaved trees of temperate regions. A similar pattern is emerging from studies of guild structure in bird communities. A recent example is the work of MacNally (1994) on the species richness of ten guilds of forest birds in Victoria, Australia. He found that there was consistency in foraging guild proportions within each of the five different types of forest. Taken more broadly, the overall guild patterns in terms of all three measures will contribute to the size-dependent features that have recently been detected in food webs (Martinez 1994).

At an even finer level, individual species may be considered. In the introduction reference was made to the apparent convergence in morphotypes in the mammalian faunas of similar habitats in different parts of the world. With seed-feeding desert rodents it is easy to postulate that there are two morphologies that reflect different niches in deserts, and that the functioning of the communities converge in parallel with the morphologies. However, recent comparative studies in the North American desert (Brown 1989) and the Negev desert (Brown *et al.* 1994) have shown, *inter alia*, that there may not be a shared convergence. The kangaroo rats (*Dipodomys*) of the former coexist with pocket mice (*Perognathus*) through seasonal variations in foraging efficiencies, but in the Negev it appears to be differences in diet that separate the niches of the jerboa (*Jaculus jaculus*) from the gerbils (*Gebillus*). Comparing the more abundant phytophagous insects found on birch (*Betula*) in South Africa, where it was introduced, with its fauna in Britain, Southwood & Kennedy (1983) were able on the basis of taxonomy and morphology to list possible analogues: whether this apparent morphotypic convergence mirrors a measure of ecological convergence is of course uncertain.

There is one particular guild that must be considered separately: the tourist guild, defined as non-predatory species that have no intimate or lasting association with the plant (primary producer), but which may be present in the habitat by chance or for shelter, for temporary sustenance (for example, for substances such as honey-dew) or for a site for sunbathing or sexual display (Moran & Southwood 1982). Tourists make up a small proportion of the biomass of most invertebrate communities studied. However they may be of particular significance in that they are not part of the main trophic system or any feedback loop on the community, but may fall prey to local predators and so modify trophic patterns and stability.

(*b*) ***Niche structure***

Within an existing community and within its guild each species will occupy a niche. A distinction is made between the fundamental niche (the organism's tolerance limits for resources and physical conditions) and the realized niche (that actually occupied). The realized niche is generally smaller than the fundamental niche. Species will differ in the size (in multidimensional space) of their fundamental niches: polyphagous species will have broader fundamental niches in the resource dimension than those with specialized feeding habits. If two species overlap in all their niche dimensions then they must compete in the area of overlap; in theory one species could exclude another. A number of theoretical studies (MacArthur & Levins 1967; May & MacArthur 1972; May 1975) have indicated a limit to niche overlap on any one resource dimension (one standard deviation between the midpoints of the two resource curves). I want to consider two aspects: first, the extent that species in communities do appear to be 'spaced' out, and secondly the extent to which field data suggest that communities are not 'fully saturated', that if another species arrives it could squeeze in, either into vacant niche space or by restricting the realized niche space of existing species.

In 1959 G. E. Hutchinson pointed out, on the basis of a range of examples, that coexisting members of a taxon differed in size by a constant ratio: 1.3. Much earlier Dyar (1890) had pointed out that an insect's successive instars have that ratio: Dyar's rule. Since then many other examples have been described (Diamond 1975; Horn & May 1977; Uetz 1977; May & Seger 1986; Schoener 1984, 1986), although others have questioned whether the size distribution is different from the one that would arise from random assemblage (Simberloff & Boecklen 1981). I will not rehearse these arguments (that has been done on many occasions); rather, I wish to revisit certain patterns and consider biological evidence as to whether when there is major overlap on one niche dimension there is particular separation on another. If so, does this suggest a way of analysis?

The studies I want to review have been made on two groups of insects that are part predatory and part herbivorous. Therefore the relations between them may be those of predator and prey, rather than interspecific competition for resources. Predator–prey relations are often governed by size: late-instar mosquito (*Culiseata*) larvae may prey on small toad (*Bufo*) tadpoles (Blaustein & Margalit 1994) and large belostomatid bugs may kill newly hatched crocodiles. These are dramatic reversals of the general relations between vertebrate predators and insects, but such reversals of competitive interactions – in the widest sense – are often a feature of community dynamics

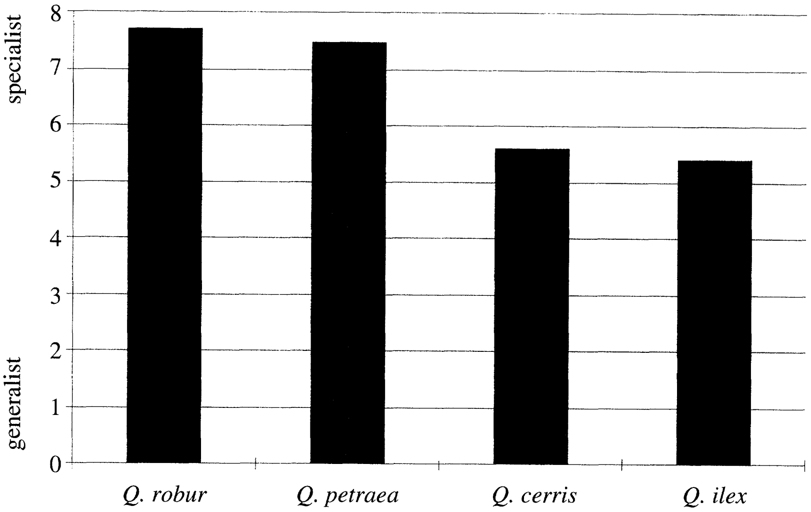

Figure 6. The degree of specificity to oak (*Quercus*) of the phytophages on the different oak species (native and non-native) in Wytham Wood. (Data for knockdown survey from Southwood *et al.* (unpublished, as figure 2).)

(Buss & Jackson 1979; Tanner *et al.* 1994). The 28 species of ground beetle (Carabidae) found in a study at Silwood Park (in southern England) (Greenslade 1961, 1963) range in length from 3 mm to 25 mm. Taking the Hutchinsonian ratio, this range should permit merely nine species. However, if they are arranged by season and by their diurnal cycle, one may see that where they are closest in size they are spaced out in time, seasonal or daily (Southwood 1978*b*). Where species packing seems particularly tight on all these resource dimensions, one species, *Harpalus rufipies*, is partly phytophagous.

The second study was also made at Silwood Park and involved five species of mirid bug living on broom (*Sarothamnus*) (Waloff & Southwood 1960). They are all very similar in size, and four in superficial appearance; their niches are, however, largely separated by time (Southwood 1978*b*). Where occurrence is almost concurrent the species have very distinct feeding habits (Dempster 1964).

These patterns, and many others (see, for example, Uetz 1977), show co-occurring species spacing themselves out in a variety of niche dimensions; where they overlap closely in time and size, another dimension, in these instances unusual feeding habits, can be identified. As I have already indicated, the construction of null models to test whether these patterns differ significantly from a random assemblage poses many problems (see, for example, Hastings 1987). Another approach might be to analyse the patterns sequentially; the probability of the separation in niche dimension y being distributed inversely in relation to the niche spacing in dimension x, taken with a similar probability calculation for niche dimension z in relation to dimension y. Dr S. Nee is currently undertaking, with me, such an analysis of the above data.

We can also investigate niche dimension by following the sequence of changes during the development of a community. A most interesting example of this is the study of the bird community on the Hawaiian islands during the past 150 years (Moulton & Pimm 1983, 1986). During this period many species have been introduced and the island habitat has undergone extensive changes. Moulton & Pimm found that the chances of a species becoming extinct was closely correlated with the extent of the closeness in size between it and related species. During the process of succession, which I will discuss shortly, the number of animal species increases and their size and other morphological features become more diverse. The structural diversity of the vegetation also increases, but the extent to which morphological diversity increases in groups as diverse as the Heteroptera (Brown 1982) and birds (Southwood *et al.* 1986*b*) is striking.

We can perhaps visualize the resource base of a habitat as rather like a peg-board, with irregularly distributed irregular holes (niches); with the passing of time, since the establishment of the habitat, more and more of the holes are occupied by a unique peg (species) that exactly fits the hole. Put more precisely, this is an aspect of May's (1986*a*) prediction that connectance will fall as species number rises.

Applied to the fauna of a plant introduced to a new region, this model predicts that the initial fauna would contain a relatively large proportion of phytophagous species with wide host ranges. There is an indication of this in the entomofauna of *Buddleia* in Britain, where the genus was unrepresented until about 100 years ago (Southwood & Kennedy 1983; Keenlyside 1989). More quantitative data conforming to the prediction come from the current study of oak entomofauna undertaken at Oxford. Each of the nearly 300 species of phytophage was coded to indicate the degree of its association with oak (*Quercus* spp.) as recorded in the literature. Those species with a monophagous association with oaks were coded 12; progressively lower codes (to 1) were allocated to species that either were more polyphagous or whose normal (recorded) associations were with plants at an increasing phylogenetic distance from oaks. The code of each species was weighted by the number of individuals of that species found, to give an average 'oakcode'. As may be seen from figure 6, the two native species of *Quercus* have higher values, that is their phytophage fauna is more closely associated with oaks, than the community on the introduced species. In this connection it is interesting to note Welch's (1994*b*) record of a leaf-mining weevil normally confined to beech (*Fagus*) living on a non-native oak (*Q. rubra*).

5. STABILITY AND CHANGE

(*a*) *Constancy of structure*

Early ecological observations suggested that certain habitats, such as woodlands, were stable; it was believed that this was a causal reflection of their complexity (Elton 1958; Hutchinson 1959). However, there were particular data sets that led to a questioning of the simplicity of this relation (Watt 1964; Southwood & Way 1970) and in 1973 May explored and illuminated the whole area in his benchmark book *Stability and complexity in model ecosystems*. He showed on theoretical grounds that, far from increasing stability, an increase in links in a randomly assembled web would decrease it. May recognized that in the 'real world' many complex ecosystems are stable and, emphasizing that there could be no paradox, proposed two explanations: firstly, that it is the stability of the habitat that permits stability; and secondly, that in nature the parameters governing the connectance are not, as in the model, a random set, but a selected one. Much further work has confirmed May's conclusions. Most recently Tilman & Downing (1994) have reported results from a study of grassland communities showing the association of diversity and stability in the extent of change in the community in response to drought (see also Givnish (1994) and Tilman *et al.* (1994)).

Another general rule of community ecology has been that food chains from the primary producer to the top predator are limited to a maximum of five links (Cohen *et al.* 1990). This observation holds, but doubt has been cast on the traditional explanation, which was that the energy losses at each trophic transfer are such that another level of predator cannot be sustained; for example, it would not be possible for a 'superbear' to maintain a positive energy balance by hunting polar bears. Pimm & Lawton (1977) questioned this reasoning, pointing out that if this explanation was correct those communities where primary production per area was greatest should have food chains that were longer than where production is low. An experiment using small water containers (artificial tree-holes) in which the initial energy level could be manipulated falsified the energy-attenuation hypothesis (Pimm & Kitching 1987). In what is essentially an extension of May's (1973) conclusions about stability, Pimm & Lawton (1977) proposed that the limit on length was imposed by the inherent instability of a food chain of more than five links. Stochastic population fluctuations at lower levels become amplified through the chain so that a stable population cannot be maintained at a higher level.

How constant are the populations of individual species? If organisms are considered on a wide geographical scale, there is a predictable constancy about their relative abundance. For well over a hundred years guides to flora and fauna have given descriptions such as 'common' or 'rare' for plants and animals. The great majority of these descriptions hold today, although there are some notable exceptions. A flora published in 1801 recorded the eight sites in England from which the rosebay willowherb (*Chamaenerion angustifolium*) had been recorded (Withering 1801) and as recently as 1940 the collared dove (*Streptopelia decaocto*) was unrecorded from Britain; now both are widespread and common.

In general, this predictability also holds to a remarkable extent on a smaller scale. I have already drawn attention to the stability in the relative abundance of the most numerous Heteroptera caught in a light trap at Rothamsted Experimental Station over nine sampling years in the period from 1933 to 1956: three species out of 95 were always among the six most abundant (Southwood 1960*b*, 1987*b*). It is noteworthy that this work was done in an agricultural environment and the host plants of these species are weeds: in other words, not a particularly stable system. Lawton & Gaston (1989) recorded the abundance of phytophagous insects on two patches of bracken over seven and fifteen years and found that relative abundance changed hardly at all.

(*b*) *Succession*

In both the studies just referred to, a natural process of community change, succession, had effectively been absent for the timescales considered. On Rothamsted Farm, agricultural practice eliminated it; and bracken is a long-lasting community. However, in all natural communities change occurs over time and there are abrupt perturbations: lightning fires, floods, landslides, hurricanes and other natural phenomena as well as the changes brought about by human activities. Long-term observations show that many of the apparently stable and complex ecosystems are in fact unstable when viewed over centuries. Extensive studies of the tropical rainforests of New Guinea led Johns (1986; R. J. Johns, personal communication) to conclude that there were few, if any, areas that had not had a major perturbation within the past 100 or so years. Likewise in Europe many areas of apparently well-established forest show evidence of change (Schütt & Cowling 1985; Schlaepfer 1993). Such evidence tends to support May's theoretical conclusions, that these complex habitats are indeed fragile and their apparent stability depends on the stability of all the factors that contribute to their physical environment. Perhaps we should note that the oldest organisms in the world, bristlecone pines (*Pinus aristata*), live in apparently relatively simple ecosystems.

Secondary succession, the changes that follow from a perturbation of a habitat, is a more widespread phenomenon than primary succession, the development of a community in new, previously unvegetated sites (Miles 1987). What are the rules that underlie secondary succession? A number of models have been put forward for the mechanisms determining the space-holding organisms (e.g. plants, corals) in a succession (Connell & Slatyer 1977; Lawton 1987), as follows.

1. *Facilitation*: the organisms of a successional stage need the changes that are brought about by organisms present in earlier stages. An interesting entomological example is provided by Cappuccino & Martin (1994).
2. *Tolerance*: species that come later tolerate the presence of those that come earlier, eventually outcompeting and replacing them.
3. *Random colonization*: the survival of those species that by chance arrive first.
4. *Inhibition*: those that arrive first hold the site until they die, an extension of 3 (above).

A study of stages of secondary succession from bare soil, formerly an arable field, to woodland was made at Silwood Park some years ago; this was a directional succession, for a series of species were characteristic of the habitat at different ages (i.e. time since ploughing). A earlier, now classic, study was made in the U.S.A. by Bazzaz (1975) but was restricted to plants. At Silwood only one herbaceous species occurred throughout the sixty-year span covered: the grass *Holcus lanatus*. Certain trees were also found throughout, initially as very small seedlings. Information was obtained on the seed bank in the soil, and on the seedlings germinating in the field and their survival (Southwood *et al.* 1988). It was found that in the first year 27 % of the seed bank germinated in the spring and that these seedlings had a better than 50 % chance of survival to flowering. The much larger number of seedlings that grew in the autumn, many no doubt from the seeds of plants established that year, had a much lower survival rate. As individual seedlings could be observed, it was possible to identify mortality due to crowding (competition from the already established plants), herbivores, pathogens and the physical stresses of the winter period. Whereas over 6000 seedlings germinated per square metre in the first year, in an old-field site (7 years after being bare ground), the rate was only one per metre. The relatively small number of seedlings that could be observed on the old-field site all failed to survive a year, although they might remain alive, but hardly growing, for several months. The limited amount of free space restricted the extent of germination. Mortality was due to being quickly overshadowed by the existing vegetation and attacks by generalist herbivores, molluscs and probably small rodents. The tussocky vegetation of an old field provides shelter for these herbivores; in so much as they kill tree seedlings that would, if they flourished, eventually outcompete the existing vegetation, the association of tussock vegetation and herbivores may in fact be mutualistic. Some tree seedlings germinated in the very first year; those that reached a height of about 100 mm during that year survived for at least five years and are likely eventually to dominate the whole site.

In this succession there was no evidence of facilitation: the tree species, the final dominants, did not depend on changes brought about by the vegetation of the early years. Indeed, in the old-field stage (7+ years) there was definite evidence of inhibition of further succession: the existing tussocky vegetation shaded any seedlings and sheltered herbivores, small rodents and molluscs. The first colonists were largely a reflection of the seed bank. They, and especially the occasional tree seedling, conformed to the random-colonization model. The sequential change in floral composition, with species initially absent becoming dominant (Southwood *et al.* 1979) and showing a succession of growth forms (Brown & Southwood 1987) obeyed the tolerance rule. Thus three of these models apply, albeit with differing emphasis at different stages.

Coral reefs, species-rich tropical and subtropical ecosystems in which animals provide the ecospace, have provided many insights in community ecology. Contrary to superficial impressions, they are not stable systems. They are frequently affected by catastrophes such as hurricanes, cyclones, very low tides, earthquakes and their sequelae, or dramatic changes in the numbers of certain echinoderms; more recently there have been human disturbances leading to increases in nutrients and sediments (Hughes *et al.* 1987; Hughes 1989, 1994). The changes in species composition and abundance after such major disturbance can be described by transition matrices, which give the probability of one species being replaced by another after a certain interval of time (Tanner *et al.* 1994). In studies made in the Great Barrier Reef these authors found that transitions occurred to and from almost every species: there was no species that was universally dominant. Tanner *et al.* attribute this species richness to the length of time necessary for a species with a marginal overall competitive advantage to achieve dominance and the shortness of the time interval between disturbances. The pattern of replacement could be described as a first-order Markovian process. Horn (1975) was the first to demonstrate how well this process describes succession by using it to model the dynamics of tree-species succession in temperate forests. The applicability of the Markovian model to coral reefs and forest trees indicates that the transitions, from one species to the next, are dependent on the current situation and not on previous history. These studies on very different communities allow us to draw a number of common conclusions.

1. At the level of a unit space there is no continuous sequence of species: almost any species may replace any other. For example, in the Silwood study a grass could replace a tree seedling. Both inhibition and tolerance may occur in the same community; in a Markovian description they would be expressed by low or high transition coefficients, respectively.
2. The probabilities for these replacements are a reflection of the species and the habitat. For example, on the coral reef the probability of staghorn *Acropora* replacing tabular *Acropora* on the exposed crest is merely 5/1000, but in the exposed pools over the same interval of time it is 42/1000.
3. Succession may be viewed as a cycle of probabilities of replacement; given sufficient time the process, with constant probabilities, will result in a common endpoint, the climax, whatever the particular starting mix of species. The apparent stability of this stage is dependent on longevity and resistance to invasion, but there is, of course, always some change: for example, when the forest giant falls, the Markovian chain goes on and on.

4. Transition to the climax will be more rapid if all species can colonize free space (bare ground with sunlight in terrestrial plant communities), i.e. situations where the facilitation model does not apply. The extent to which space is available and the rate at which it is colonized, rapidly in the new field at Silwood, slowly in the coral reef, will be further variables determining the speed of the cycle.

5. Many natural communities suffer natural or human disturbances that disrupt the cycle before the climax has been reached. These disturbances create free space, the colonization of which may fit the random model.

6. Diversity is highest at intermediate stages (e.g. the second and third years of the arable to woodland succession followed at Silwood) and thus, as shown originally by Horn (1975), at intermediate levels of disturbance (Connell 1978; May 1994*b*). This has important practical implications for the maintenance of biodiversity, but it must be noted that the diversity of organisms other than the primary space-holders (plants, corals, etc.) depends on the structural diversity of the ecospace the space-holders provide.

6. THE BIONOMIC PROFILE OF COMMUNITIES

Organisms differ markedly in various biological attributes, their bionomics or species traits: their size, the length of their life cycle, the number of offspring each parent produces and the resources allocated to each, their investment in defence mechanisms, etc. Several studies have shown that in different communities certain suites of characters seem to go together and that these may be related to certain features of the habitat in which the communities occur (Grime 1977; Southwood 1977). The habitat may be viewed as the templet on which evolution forges characteristic life-history strategies, giving the community a particular bionomic profile. I have reviewed the development of these ideas elsewhere (Southwood 1988). Basically, there are two extreme sets of suites, which have been identified by many biologists, perhaps the first of whom was MacLeod (1894) (see Hermy & Stieperaere 1985). Their major features are:

(i) high reproductive rate, low input of resources per offspring but overall high allocation of resources to reproduction, high mobility, either passive (e.g. wind-borne seed) or active, low allocation of resources to defence, small size, short-lived (all characters relative to other species in the same taxon);

(ii) low reproductive rate, high input of resources per offspring, higher allocation of resources to survival than to reproduction, large size, long-lived.

Notwithstanding certain arguments about the precise meanings of the terms (Boyce 1984), it is, I believe, convenient to call the former *r*-selected and the latter *K*-selected species, a dichotomy pointed up by MacArthur & Wilson (1967). The major resource shortage operating in the habitat where *r*-selection occurs is time, thereby giving a premium to early colonization. These habitats will be those that change rapidly; they have a high frequency of disturbance (by natural events, people or other organisms). In the other habitats there is an absolute or relative shortage of other resources. These habitats may have a high level of productivity or a low one, having harsh climatic conditions. Under harsh conditions *A*-selection (adversity selection) occurs. These concepts are conveniently expressed by a quadrangular diagram (figure 7): there are not many communities that occur in adverse environments with a high frequency of disturbance, and hence Grime (1977, 1979) presented his formulation of the concept in a triangular form, but there is no essential difference between the models (Southwood 1988).

There have been studies on a wide variety of communities and organisms that have recognized the two fundamental axes in relation to species traits as disturbance and productivity, which normally marches with physical adversity. Clearly a habitat in which secondary succession is occurring is moving along the disturbance axis; it moves as the time since the last major perturbation lengthens.Therefore the predictions of the templet model can be tested by assessing the species traits exhibited in successive communities. Several studies have been made on plant populations (see, for example, Werner & Platt 1976; Grime 1979; Mortimer 1987) and on animals (Hendrix *et al.* 1988).

In the study I made with several colleagues at Silwood Park, to which I have already referred several times, we simultaneously assessed the species traits in plants and animals so that it constitutes, I think, the most comprehensive account of the changing pattern in succession (Brown & Southwood 1987). With plants we found that leaf-life expectancy increases through succession, as does damage, although palatability falls (Southwood *et al.* 1986*a*). The proportion of biomass allocated to reproduction falls through succession, whereas average germinule size (though very variable) increases and pollination modes change (Southwood *et al.* 1988). In the animals, the overriding pattern is for increased species diversity and variation in size associated with increased structural complexity in the vegetation (Southwood *et al.* 1979; Brown 1982; Southwood *et al.* 1986*b*); in certain groups of insects where these features were investigated in detail generation time lengthened and niche breadth narrowed with successional age. These general patterns conform to the predictions of the templet models, although there were often specific exceptions. In calculating the average characteristics for different stages we considered the average for the collection of species present and the average weighted according to the frequency of each species: the latter gave more consistent results.

A major test of the applicability of templet theory has been made on the data gathered in an extensive study of the Upper Rhône River (Statzner *et al.* 1994). The axes chosen by Townsend & Hildrew (1994) for this test were temporal and spatial heterogeneity. The former was based on the frequency and magnitude of excursions in environmental variables from some long-term average, which they considered would be related to the frequency of disturbance. Spatial heterogeneity

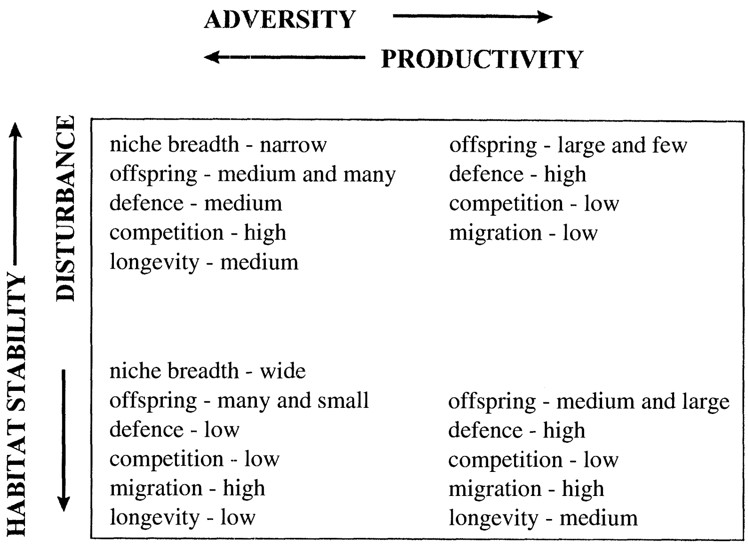

Figure 7. A habitat templet, indicating the features of the habitat (productivity, disturbance) that correlate with the bionomic profile of the community: some community and species attributes that contribute to the profile shown in the four corners of the templet. (Offspring characteristics: size and number.)

was assessed in physicochemical terms and is a reflection of patch size; it is not strictly equivalent to favourableness or its converse, adversity (or stress), used in most other models. Townsend & Hildrew predicted that such spatial heterogeneity would provide refugia that would ameliorate the effects of temporal change. The predictions were carefully tested against information, of varying levels of completeness, on 548 different taxa. They concluded, contrary to the view of Stearns (1992), that habitats and species traits can be matched. However, there was no overall confirmation of the precise predictions of Townsend & Hildrew's templet, for as Stearns (1992) and others have emphasized there are always individual species that have addressed the evolutionary challenge with unexpected trade-offs (Resh *et al.* 1994). Many examples of other generally more taxonomically limited studies from terrestrial and aquatic habitats are given in Southwood (1988).

Steneck & Dethier (1994) have shown how essentially the same concepts can be applied to marine algal communities from different seas. They point out that there is, in addition to the ruderal strategy, a disturbance-tolerant strategy, when the seaweeds have a structure that makes them resistant to damage when disturbed by, for example, boulders rolling. Seaweeds having ruderal and disturbance-tolerant strategies may coexist in the same habitat Indeed Resh *et al.* (1994) also point out that sometimes there may be alternative strategies (suites of species traits) for the same habitat. Emphasizing the significance of adversity selection, Greenslade (1972) originally described it as 'beyond K'. Perhaps the disturbance-tolerant strategy should be viewed as 'beyond r', which invites the construction of a three-dimensional model. But rather than embarking on further geometric diversification, I would prefer to endorse the conclusion of Hay (1994) commenting on Steneck and Dethier's paper and conclude that the two key variables for determining community structure are productivity and disturbance and these provide a basis for predicting how natural communities will respond to human-induced changes in the environment.

7. CONCLUSIONS

Various principles are emerging that indicate the patterns in the various levels of complexity in natural communities and which may allow us to predict the effects of changes we are making in our environments. These may be summarized as follows.

1. Taken across a broad taxonomic range, species richness is related to area and to capacity: the available resources. Capacity is dependent on productivity and structure. Increased productivity, itself dependent on metabolic resources, will be expressed as increased biomass, which may or may not be partitioned between more species. Increased structural (spatial and architectural) diversity increases species richness. This structure, may be physicochemical or be provided by other organisms (e.g. trees, corals); the latter can be termed ecospace.

2. Species richness is also dependent on the size and nature of the species pool from which immigration and establishment has taken place, and on the history of exposure to this pool. For establishment depends on the extent to which the organism is adapted to the habitat (widely defined), its predilection; the chance of selection of the more adapted forms will depend on the frequency of exposure.

3. The dynamics of the species richness of a community is described by MacArthur and Wilson's island biogeography theory, which postulates an equilibrium with a turnover rate, the balance between immigration and extinction. As MacArthur and Wilson recognized, the turnover rate will be particularly significant (i.e. involve a reasonable fraction of the species) in communities with species populations of tens or hundreds, such as vertebrates on offshore islands. But with large floras or faunas, such as the entomofauna of a forest or of a large island such as

Britain, species turnover rate is proportionally insignificant, and unless there are major changes in the habitat, the totality of the process is more realistically encapsulated by the species-pool exhaustion model. This model includes the effects of the predilections of immigrant species and of the frequency of their exposure to new habitats and constitutes an extension of zoogeography theory.

4. If a community is sampled thoroughly and over a period of time new species will continue to be recorded; most of these immigrants will fail to become established, but they provide the 'feed' for new evolutionary relationships dependent in part on the frequency of exposure.

5. Although biodiversity, in the form of rank-abundance curves, is generally well described by logarithmic distributions from which indications may be drawn as to whether the community is at equilibrium or not, data from a study of oak-tree fauna suggest that large samples taken over a period of time are better described by a power law. This may be because unsuccessful immigrants are recorded as well as the members of the community.

6. Evidence is presented that when the macro-invertebrates on various trees are separated into major guilds there is some consistency in the proportion that belong to the phytophage guild. This is modified by tree type and biogeographical type, but not by exact geographical location. It seems likely that these modifications are a reflection on the influence of these factors on the other guilds; for example, there is a small epiphyte-dwelling guild in dry regions so phytophages make up a greater proportion of the total.

7. Niche separation in co-occurring species needs to be considered in several dimensions and the extent that this departs from randomness analysed sequentially.

8. Studies of communities during secondary succession show the range of structural diversity of birds and insects increasing with successional age.

9. In studies on the entomofauna of oaks (*Quercus* spp.) it has been found that less specialized species (generalists) form a higher proportion of the community on non-native (introduced) trees.

10. Work on succession, in animal and plant communities, suggests the following conclusions.

(i) At the level of a unit space there is no continuous sequence of species.

(ii) The probabilities for these replacements are a reflection of the species and the habitat.

(iii) Succession may be viewed as a cycle of probabilities of replacement.

(iv) Transition to the climax will be more rapid if all species can colonize free space.

(v) Many natural communities suffer natural or human disturbances that disrupt the cycle before the climax has been reached.

(vi) Diversity is highest at intermediate stages.

11. The various models for succession (i.e. facilitation, tolerance, random colonization and inhibition) may all be observed in the sequence in one locality.

12. A wide range of studies, now including seaweeds, have shown that the habitat acts as a templet for the suites of bionomic characters evolved and exhibited in animal and plant communities. The habitat's templet can be described on two key axes: disturbance frequency (the converse of habitat stability) and productivity (the converse of adversity).

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