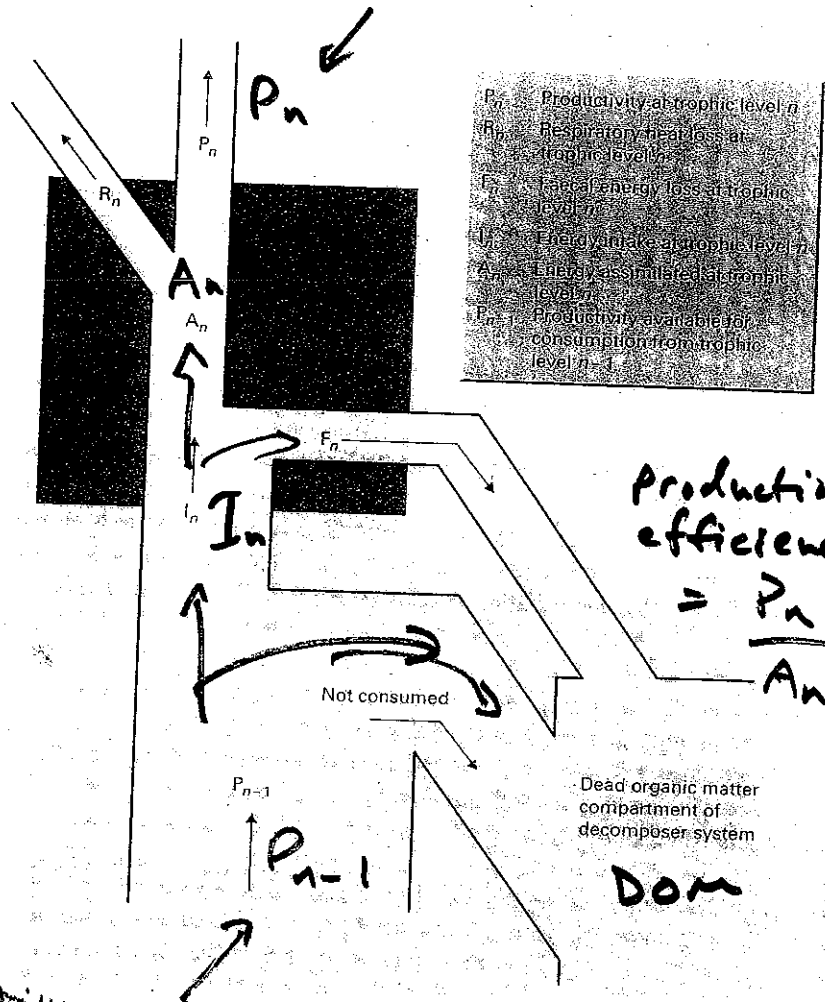


Assimilation
Efficiency
 $= A_n / I_n$

Trophic level
transfer efficiencies
 P_n / P_{n-1}

$\frac{I_n}{P_{n-1}}$ = consumption
efficiency



Production
efficiency
 $= \frac{P_n}{A_n}$

Dead organic matter
compartment of
decomposer system
DOM

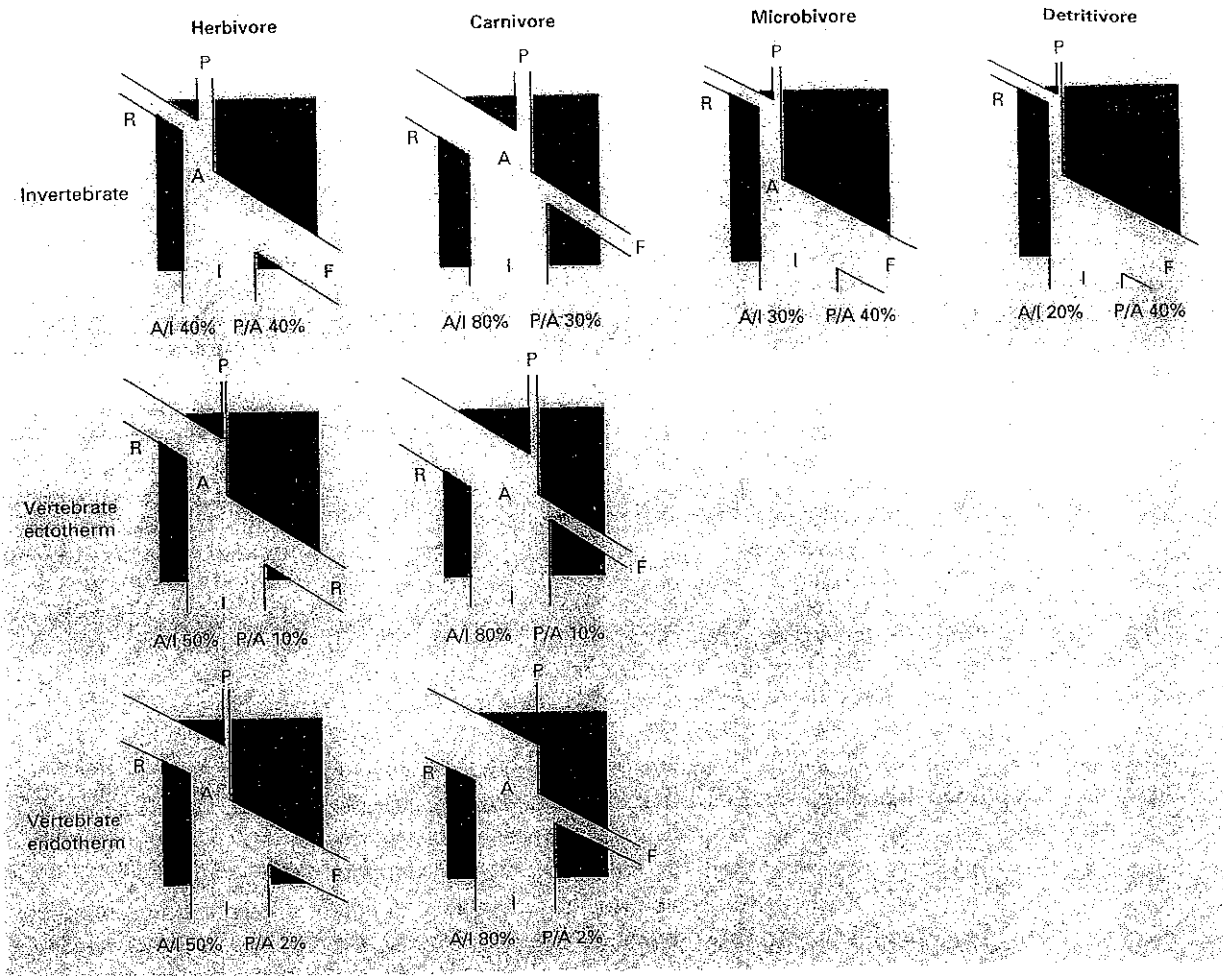


Figure 18.22 Pattern of energy flow through each trophic compartment (in Figure 18.19) and the values of assimilation and production efficiencies used in Heal and MacLean's (1975) grassland model.

proportion of NPP goes to the decomposer system, but, in addition, decomposers consume well in excess of 100 J for every 100 J of NPP! This comes about simply because energy that is consumed is not all assimilated on its first trip through the decomposer chain and so is available for consumption again. The decomposers are responsible for 84.8% of the consumption of matter. However, they carry out 90.8% of the assimilation (mainly because of the importance of microbial activity and their assumed 100% assimilation efficiency). Once again, the apparent discrepancy in total joules assimilated by the decomposers (157 J per 100 J of NPP) results from their ability to 'work over' organic matter on a number of occasions.

the decomposer system is responsible for 98% of secondary productivity in this grassland community

The most significant result of this study is the overwhelming importance of the decomposer system. Even though the grazer system consumes 29% of NPP, it only accounts for 2% of secondary productivity. Of every 100 J of NPP, more than 55 J find their way into decomposer production per year but less than 1 J into grazer production. Overall, in this steady-state community, losses through animal respiration balance NPP so that standing crop biomass (not illustrated) stays the same.

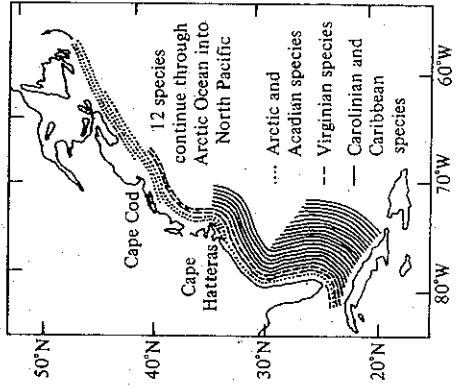


Fig. 8-9

Diversity gradient of gastropods along the eastern coast of the United States and Canada. Each line stands for ten species. (From Fischer, 1960, after Abbott.)

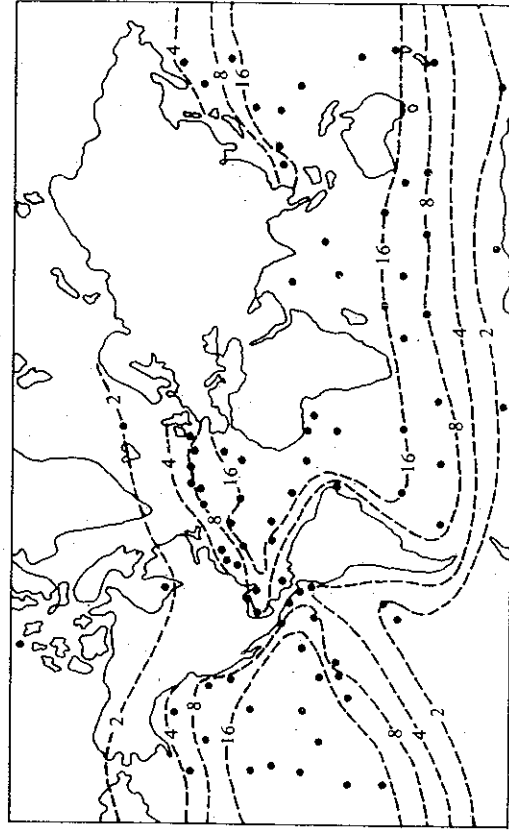


Fig. 8-10

Contoured raw diversity for recent species of planktonic Foraminifera. (From Stehli, 1968.)

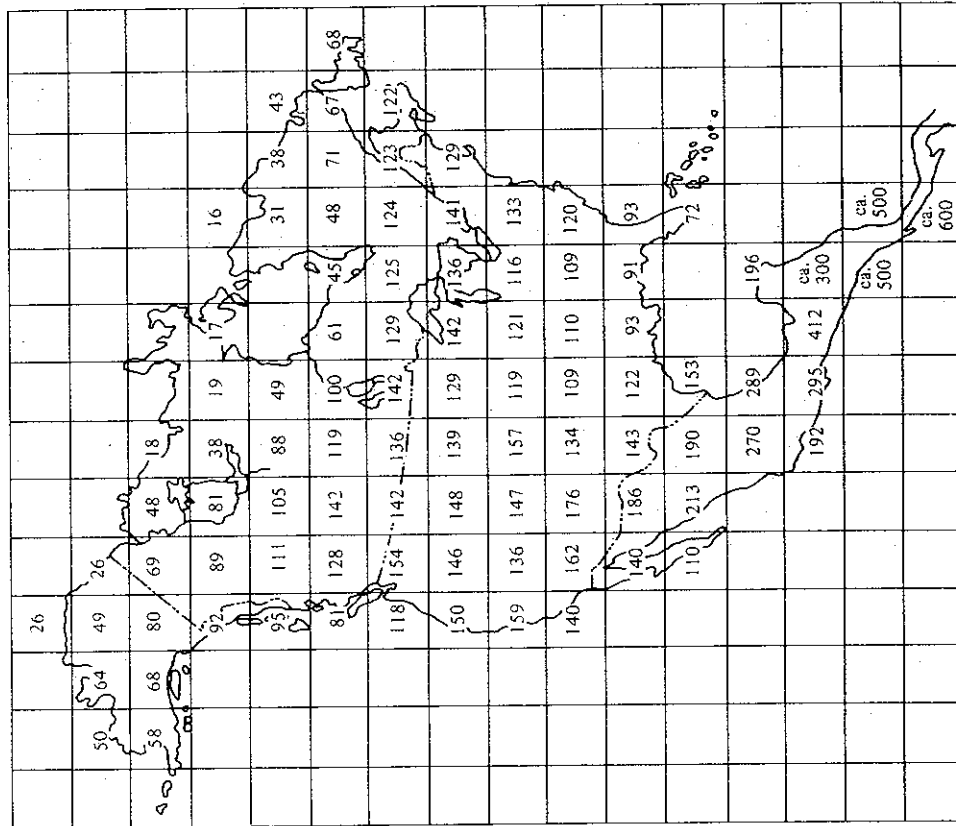


Fig. 8-8

Number of breeding land bird species in different parts of North America, from various sources. (From MacArthur, 1969, after MacArthur and Wilson.)

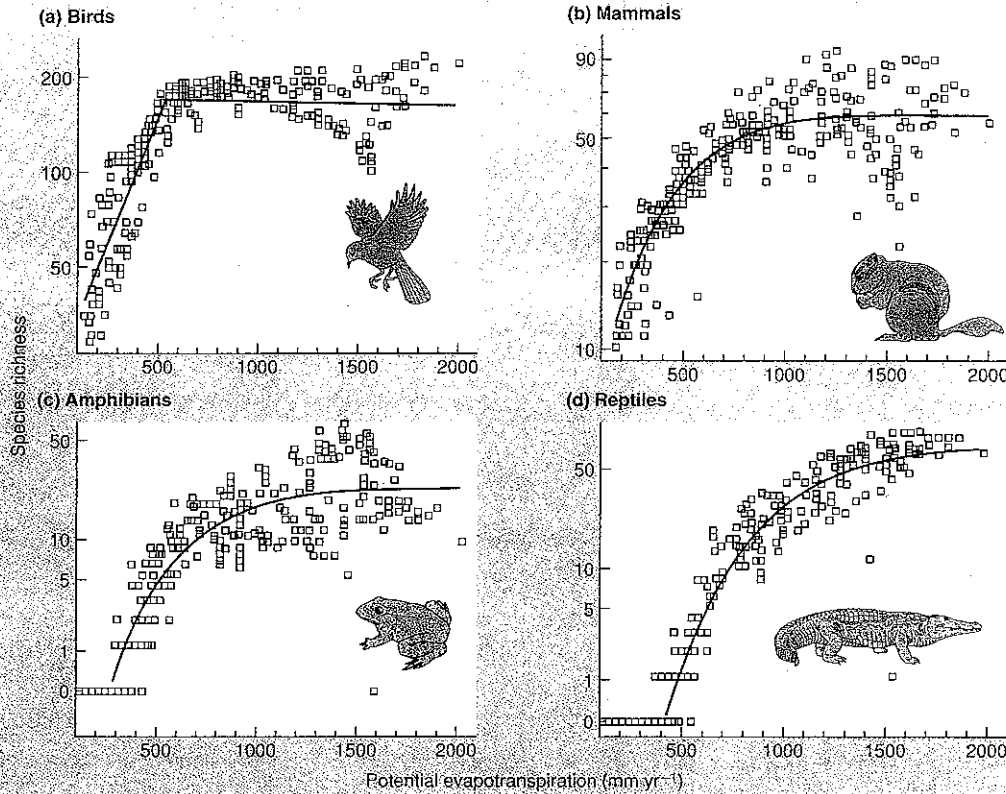


Figure 21.4 Species richness of (a) birds, (b) mammals, (c) amphibians, and (d) reptiles in North America in relation to potential evapotranspiration. (After Currie, 1991.)

available. It is particularly noteworthy that in species-rich sites, the communities contained more species of very large ants (which consume large seeds) and more species of very small ants (which take small seeds) (Davidson, 1977). It seems that either the range of sizes of seeds is greater in the more productive environments (see Figure 21.1a) or the abundance of seeds becomes sufficient to support extra consumer species with narrower niches (see Figure 21.1b).

On the other hand, an increase in diversity with productivity is by no means universal, as noted in the unique Parkgrass experiment which started in 1856 at Rothamstead in England (see Section 16.2.1). A 3.2 ha (8-acre) pasture was divided into 20 plots, two serving as controls and the others receiving a fertilizer treatment once a year. While the unfertilized areas remained essentially unchanged, the fertilized areas showed a progressive decline in species richness (and diversity).

Such declines have long been recognized. Rosenzweig (1971) referred to them as illustrating the 'paradox of enrichment'. One possible resolution of the paradox is that high productivity leads

to high rates of population growth, bringing about the extinction of some of the species present because of a speedy conclusion to any potential competitive exclusion. At lower productivity, the environment is more likely to have changed before competitive exclusion is achieved. An association between high productivity and low species richness has been found in several other studies of plant communities (reviewed by Cornwell & Grubb, 2003).

It is perhaps not surprising, then, that several studies have demonstrated both an increase and a decrease in richness with increasing productivity – that is, that species richness may be highest at intermediate levels of productivity.

Species richness is low at the lowest productivities because of a shortage of resources, but also declines at the highest productivities where competitive exclusions speed rapidly to their conclusion. For instance, there are humped curves when the species richness of desert rodents is plotted against precipitation (and thus productivity) along a gradient in Israel (Abramsky & Rosenzweig, 1983), when the species richness of central European plants is plotted against soil nutrient supply (Cornwell & Grubb,

... or decreased richness ...

... or an increase then a decrease (hump-shaped relationships)

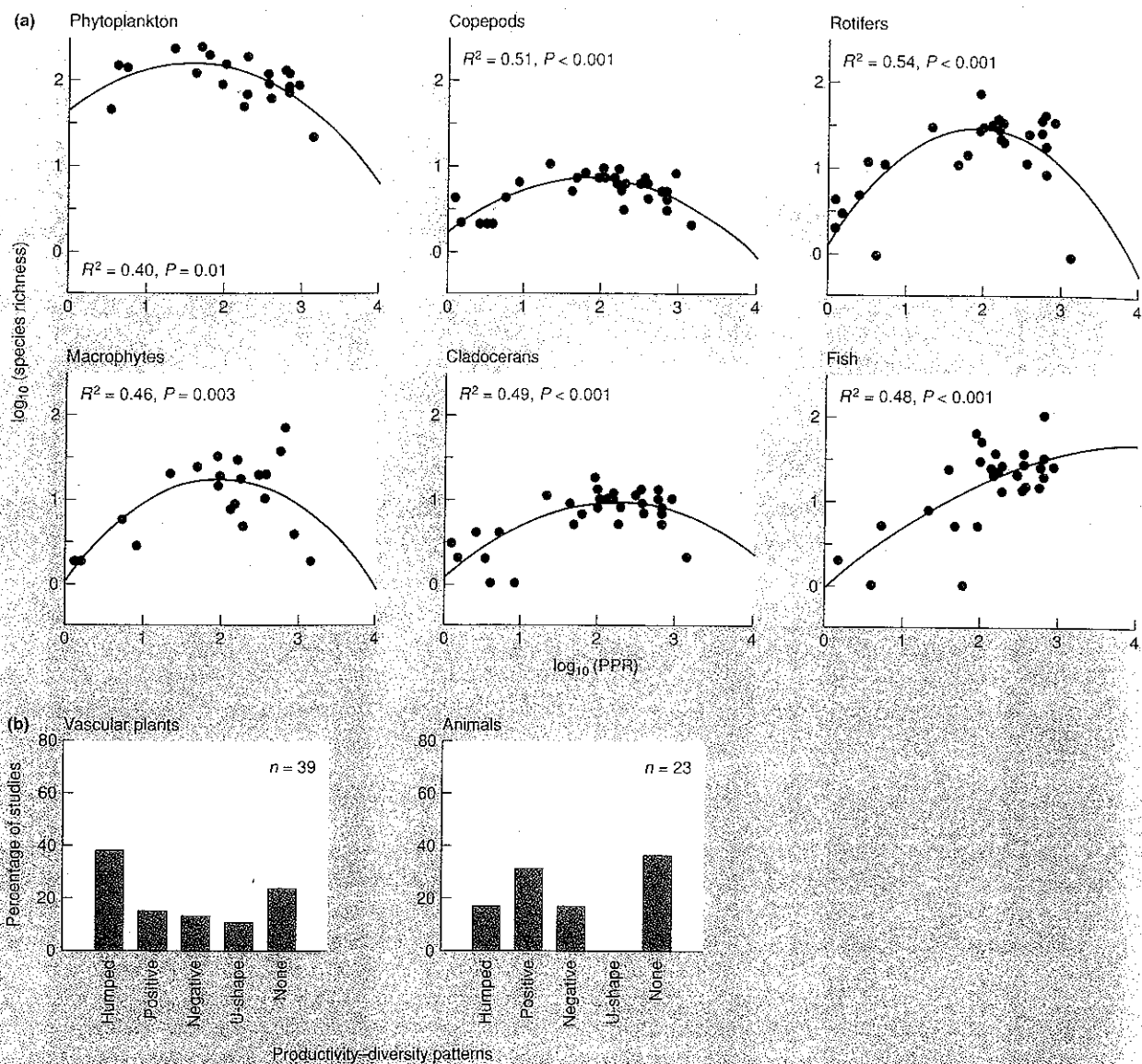


Figure 21.5 (a) Species richness of various taxonomic groups in lakes in North America plotted against gross primary productivity (PPR), with fitted quadratic regression lines (all significant at $P < 0.01$). (After Dodson *et al.*, 2000.) (b) Percentage of published studies on plants and animals showing various patterns of relationship between species richness and productivity. (After Mittelbach *et al.*, 2001.)

2003) and when the species richness of various taxonomic groups is plotted against gross primary productivity in the open water zones of lakes in North America (Figure 21.5a). An analysis of a wide range of such studies found that when communities of the same general type (e.g. tallgrass prairie) but differing in productivity were compared (Figure 21.5b), a positive relationship was the most common finding in animal studies (with fair numbers of humped and negative relationships), whereas with plants, humped relationships were the most common, with smaller numbers of

positives and negatives (and even some unexplained U-shaped curves). When Venterink *et al.* (2003) assessed the relationship between plant species richness and plant productivity in 150 European wetland sites that differed in the nutrient that was limiting productivity (nitrogen, phosphorus or potassium), they found humped patterns for nitrogen- and phosphorus-limited sites but species richness declined monotonically with productivity in potassium-limited sites. Clearly, increased productivity can and does lead to increased or decreased species richness – or both.

DISTURBANCE: IDH

Figure 21.10 Diagrammatic representation of the time course of species richness in three gaps, and in the community as a whole, at three frequencies of disturbance. The disturbance is unphased. Dashed lines indicate the phase of competitive exclusion as the climax is approached.

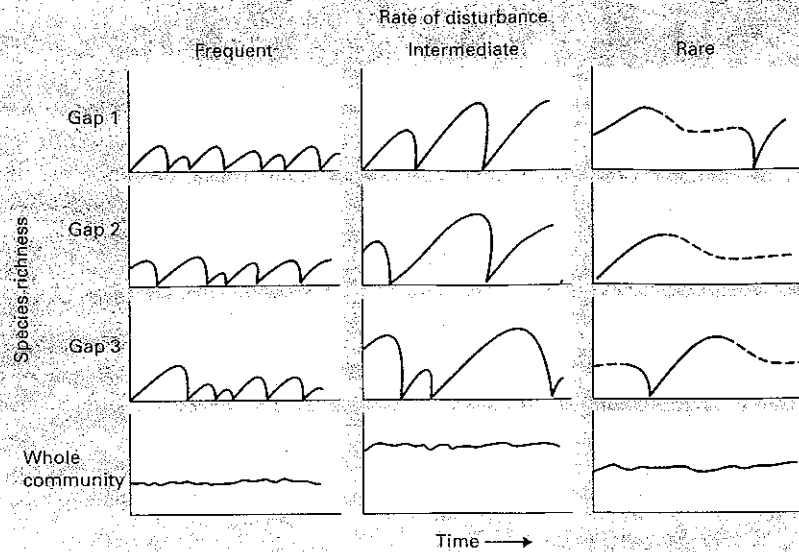


Table 21.2 Seasonal patterns in bare space and species richness on boulders in each of three classes, categorized according to the force (in newtons) required to move them. (After Sousa, 1979b.)

Census date	Boulder class (N)	Percentage bare space	Species richness		
			Mean	Standard error	Range
November 1975	< 49	78.0	1.7	0.18	1-4
	50-294	26.5	3.7	0.28	2-7
	> 294	11.4	2.5	0.25	1-6
May 1976	< 49	66.5	1.9	0.19	1-5
	50-294	35.9	4.3	0.34	2-6
	> 294	4.7	3.5	0.26	1-6
October 1976	< 49	67.7	1.9	0.14	1-4
	50-294	32.2	3.4	0.40	2-7
	> 294	14.5	2.3	0.18	1-6
May 1977	< 49	49.9	1.4	0.16	1-4
	50-294	34.2	3.6	0.20	2-5
	> 294	6.1	3.2	0.21	1-5

MecArthur (1955)

↑ Div → Stability

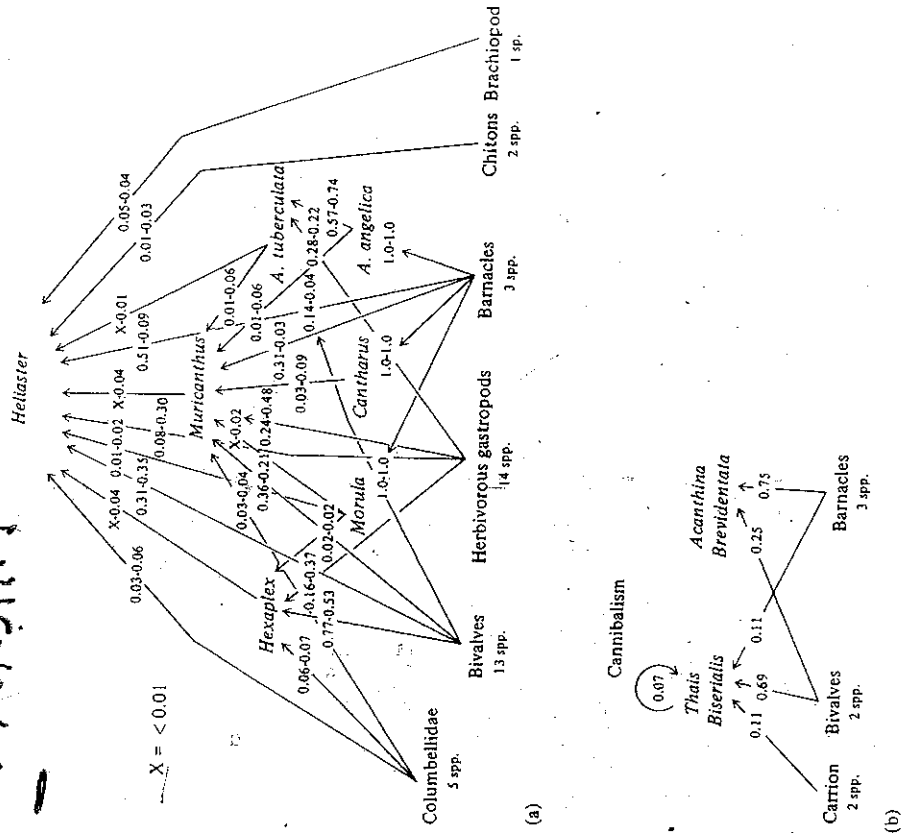


Fig. 7-9

(a) The complicated food web of a predator-rich community in the Gulf of California (genus *A* is *Acanthina*). Numbers on the left are fractions of numbers of food items in the predator's diet; numbers on the right are fractions of calories in the predator's diet.
 (b) A simpler food web in Costa Rica without a secondary carnivore. Numbers are fractions of numbers in the predator's diet. (From Paine, 1966.)

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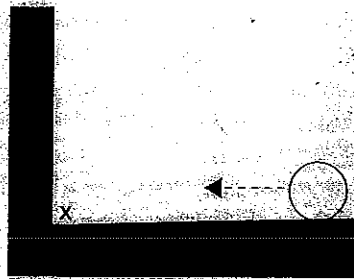
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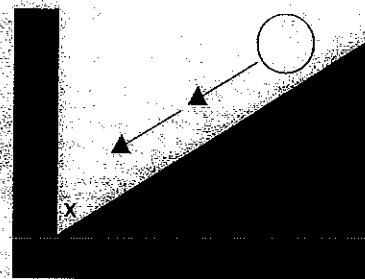
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Low resilience



High resilience



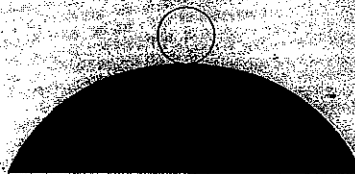
Low resistance



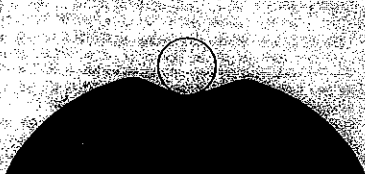
High resistance



Low local stability
Low global stability



High local stability
Low global stability



Low local stability
High global stability

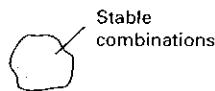


High local stability
High global stability



Environmental parameter 1

Dynamically fragile

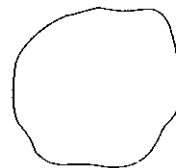


Stable combinations

Environmental parameter 2

Environmental parameter 1

Dynamically robust



Environmental parameter 2

Figure 22.5 Various aspects of stability, used in this chapter to describe communities, illustrated here in a figurative way. In the resilience diagrams, X marks the spot from which the community has been displaced.

of interaction or some combination of all of these things. Elton (1958), amongst others, brought together a variety of empirical and theoretical observations in support of the view that more complex communities are more stable (Table 22.1). Nowadays though, the points Elton made can be seen as either untrue or else liable to some other plausible interpretation. (Indeed, Elton himself pointed out that more extensive analysis was necessary.) At about the same time, MacArthur (1955) proposed another argument in favour of the conventional wisdom. He suggested that the more possible pathways there were by which energy passed through a community, the less likely it was that the densities of constituent species would change in response to an abnormally raised or lowered density of one of those species. In other words, the greater the complexity (more pathways), the greater is the stability (less numerical change) in the face of a perturbation. However, the conventional wisdom has by no means always received support from more recent work, and has been undermined particularly by the analysis of mathematical models.

Table 22.1 Summary of Elton's arguments (1958) in support of the 'conventional wisdom' prior to 1970 that complexity begets stability in communities. Each observation is consistent with the complexity/stability hypothesis. However, each can be explained in terms of reasonable alternative hypotheses or questioned because of lack of a control.

Statement	Assessment
1 Mathematical models of interactions between two or a few species are inherently unstable	No longer held to be true after recent development of two-species models (see Chapter 10). In any case, there was no evidence at the time that multispecies models would be any more stable (none had been developed)
2 Simple laboratory communities of two or a few species are difficult to maintain without extinctions	True, but no evidence that multispecies laboratory communities would be more stable. The probable reason that laboratory cultures are difficult to set up and maintain is because it is virtually impossible to reproduce the natural environmental conditions
3 Islands, which usually possess few species, are more vulnerable to invading species than are species-rich continents	There have also been well-documented and remarkable examples of introduced species assuming pest proportions on continents (see Chapter 17). Nevertheless, statement 3 may be true. However, vulnerability to invasion has only a tenuous link with more conventional definitions of stability and resilience
4 Crop monocultures are peculiarly vulnerable to invasions and destruction by pests	Differences between natural and agricultural communities could derive from the long periods of coevolution to which natural associations may have been subject (Maynard Smith, 1974). Note also that arable crops are typically early successional species, naturally subject to rapid change. Natural monocultures such as salt-marsh and bracken seem to be stable (May, 1972)
5 Species-rich tropical communities are not noted for insect outbreaks when compared to their temperate and boreal counterparts	Such a pattern, if real, could be due to the destabilizing effects of climatic fluctuations in temperate and boreal communities (Maynard Smith, 1974). Wolda (1978) has produced evidence suggesting that insect abundances fluctuate just as markedly in the tropics

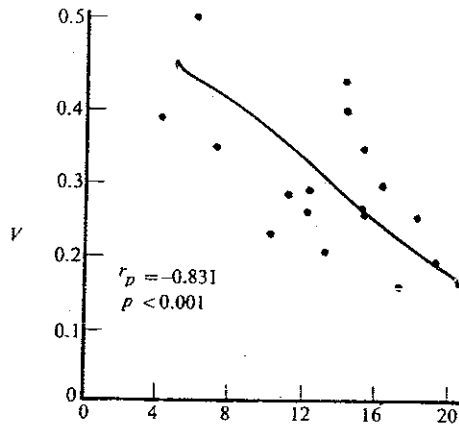
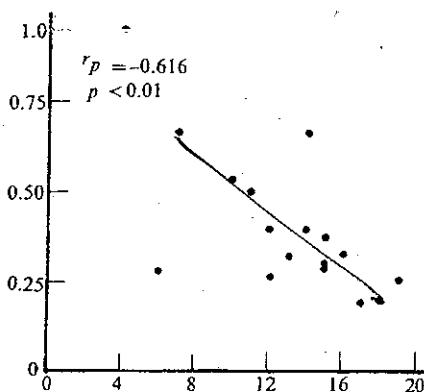


Fig. 1 relationship between average interaction strength among species and number of species in African grassland samples. r_p is the partial correlation coefficient with sample size held constant.

organisation may affect relationships between community diversity and stability. First, species-poor communities are likely to be characterised by strong interactions among the species while species interacting with many others are likely to do so weakly¹⁷. Thus, diffuse competition¹⁸, becomes more important as species diversity increases. Second, it suggests that communities are organised as blocks of species which interact among themselves but interact little with species in other blocks. May¹ remarked that such an organisation might reduce the destabilising effect of greater system complexity. I suggest that such interacting blocks of species represent guilds¹⁹ of species segregating along similar resources, and that they are only weakly connected with other guilds segregating along other gradients. Guild size may be estimated from sc . I found this product remarkably uniform for the 17 grasslands sampled: $sc = 4.7 \pm 0.7$ (0.95 interval) species per guild. For the Serengeti grassland, then, a guild may consist of remarkably uniform blocks of four to five species. Speculation about the environmental gradients organising such guilds in plant communities seems injudicious at this time. Numerous alternatives are possible.

The ratio, $i/(sc)^{-1/2}$, may be used as an instability index; if it is greater than 1, the system has a zero probability of being stable; if it is less than 1, it will be stable. Since both interaction strength and connectance declined with species richness, and $sc = \text{constant}$ in these samples, it is obvious that the ratio also must decrease. There was a significant negative correlation

Fig. 2 Relationship between connectance and number of species in African grassland samples.



between the index and s ($r_p = -0.594$ for $P < 0.02$ with $df = 14$). Mean value of the ratio was 0.65 ± 0.12 (0.95 interval). Only one stand, with a ratio of 1.39, fell above the critical limit of 1. In general, these grasslands would be expected to return to their equilibrium relative abundance relations if perturbed. They are stable by May's criterion¹.

Fragmentary evidence is available indicating that relative abundance relations are more stable, with environmental changes, as $i/(sc)^{-1/2}$ decreases. I reexamined in 1975 a series of four exclosures built in the early 1960s²⁰, evaluating the stability of relative abundances by the coefficient of similarity²¹ between protected and unprotected vegetation. The closer the similarity was to 1, the less species composition had changed subsequent to protection from grazing. As the ratio of interaction strength to the richness-connectance function increased in the unprotected vegetation, the less similar were species abundance relations in protected and unprotected vegetation (Table 1). Sample size is so small that statistical comparison seems inadvisable, but these data suggest a greater tendency for vegetation with weak interactions and low connectance to maintain species abundance relations when the environment changes.

In conclusion, I believe May's arguments do not contradict the traditional ecological hypothesis that ecosystem stability increases with ecosystem diversity. Rather, these arguments provide considerable fresh insight into the organisational constraints within ecosystems that may contribute to an association between diversity and stability. The occurrence of species as guilds with a relatively low number of participants, which interact weakly if at all with other guilds, may be an important component of ecosystem organisation. This is a consequence of

Table 1 Similarity of species relative abundance relations in unprotected grasslands and areas protected from grazing for over 10 yr and the instability index for unprotected areas

Similarity (C)	Instability ($i/(sc)^{-1/2}$)
0.022	0.571
0.365	0.537
0.419	0.433
0.539	0.348

a decline in connectance as diversity increases. If connectance were constant, the number of species per guild would be a linear function of the total number of species with slope = connectance. Even among those species which interact, the average strength of interaction may decline as diversity increases. Thus, more diverse ecosystems may be more stable than less diverse systems because (1) connectance declines as diversity increases, (2) species are therefore organised as relatively small guilds, and (3) interaction strength among species declines as diversity increases.

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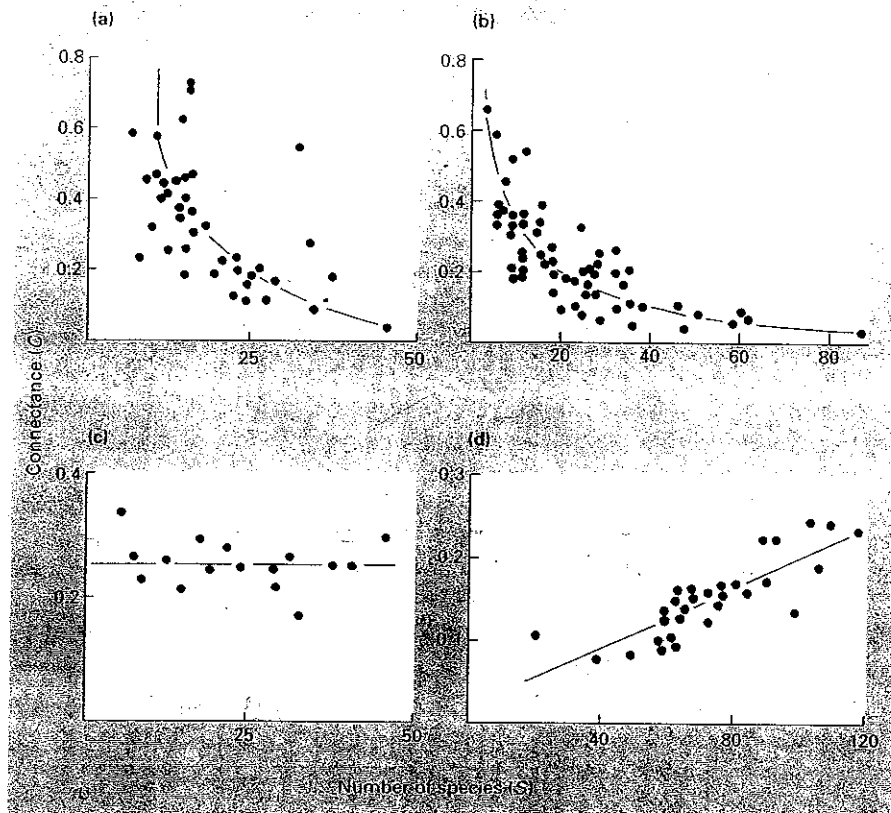


Figure 22.8 The relationships between connectance (C) and species richness (S). (a) For a compilation from the literature of 40 food webs from terrestrial, freshwater and marine environments. (After Briand, 1983.) (b) For a compilation of 95 insect-dominated webs from various habitats. (After Schoenly *et al.*, 1991.) (c) For seasonal versions of a food web for a large pond in northern England, varying in species richness from 12 to 32. (After Warren, 1989.) (d) For food webs from swamps and streams in Costa Rica and Venezuela. (After Winemiller, 1990.) (After Hall & Raffaelli, 1993.)

and another that is *more* stable

the importance of trophic level

perceived stability is apparently constant

stable in community composition) in the face of a severe summer drought in Yellowstone National Park (Figure 22.9). Enhanced stability may have resulted from the greater heterogeneity in soil conditions in the diverse communities. Once again, these 'experimental' studies provide conflicting results in relation to the predicted complexity/stability relationship.

The idea that the effect of complexity on stability depends on which trophic level is perturbed, gains some support from a study of simple, laboratory protozoan communities set up by Hairston *et al.* (1968). The first trophic level comprised one, two or three species of bacterium. These were consumed by one, two or three *Paramecium* spp. The percentage of cultures showing no extinctions of *Paramecium* spp. increased with diversity of bacteria. However, the extinction of the rarest *Paramecium* spp. was most likely when three species of *Paramecium* were cultured together as opposed to only two.

Finally, there have been a number of studies directed at the question of whether the level of 'perceived stability' (i.e. observed fluctuations in abundance) is roughly

Table 22.2 The influence of (a) nutrient addition on species richness, equitability ($H / \ln S$) and diversity (Shannon's index, H) in two fields, and (b) grazing by African buffalo on species diversity in two areas of vegetation. (After McNaughton, 1977.)

	Control plots	Experimental plots	Statistical significance
(a) Nutrient addition			
Species richness per 0.5 m ² plot			
Species-poor plot	20.8	22.5	n.s.
Species-rich plot	31.0	30.8	n.s.
Equitability			
Species-poor plot	0.660	0.615	n.s.
Species-rich plot	0.793	0.740	$P < 0.05$
Diversity			
Species-poor plot	2.001	1.915	n.s.
Species-rich plot	2.722	2.532	$P < 0.05$
(b) Grazing			
Species diversity			
Species-poor plot	1.069	1.357	n.s.
Species-rich plot	1.783	1.302	$P < 0.005$

n.s., not significant.

the same in all communities, or whether there are any noticeable trends. For instance, Wolda (1978) drew together an extensive array of data on annual fluctuations in the abundance of tropical, temperate and sub-Arctic insect populations. The old conventional wisdom assumed that the more diverse insect communities of the tropics were more stable (i.e. fluctuated less) than their depauperate temperate and sub-Arctic counterparts. However, Wolda concluded that, on

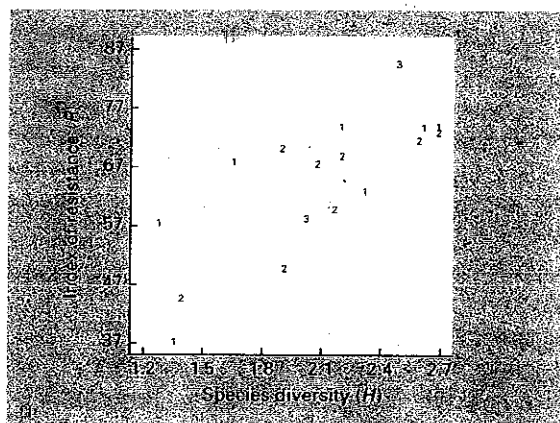


Figure 22.9 Relationship between resistance in grassland community composition and species diversity (Shannon's index, H) for a number of grassland areas in Yellowstone National Park, USA. The resistance measure (R) is designed to be inversely related to the cumulative differences in species abundances at sites between 1988 (a year of severe drought) and 1989 (a year of normal rainfall). Thus, a high value for R indicates that relative abundances changed little in the face of the drought, whilst a low value means they changed considerably. (After Frank & McNaughton, 1991.)