

### 3.3 Density, Diversity and a General Model of Ecosystem Evolution

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The late Professor D. Ager has argued that the Panda, a WWF heraldic species, is not worth protecting, for, being a slow reproducing, slow moving and dietarily fastidious animal, it is doomed by evolution itself (Ager 1991). Conservationists feel differently, however, although they seem lacking any scientific arguments for caring for the Panda. The situation resembles the evolutionist versus humanitarian controversies of the 1870s–1880s when Tolstoy (also Turgenev, Flaubert, Daudet, Dostoevsky, Meredith, Bourget, etc.) tried, on sentimental grounds alone, to protect people from selectionism. They have failed and the political ‘solutions’ of the controversy have been left to the Nazi and Marxian rulers.

Evidently, our notions of what adaptation is and how it is achieved lay at the core of the problem. In essence, the Darwinian model of adaptation held that a population (P) starting at a particular variation (V<sub>1</sub>) and fitness (F<sub>1</sub>) arrives, through selection of the constituent gene frequencies, at a different variation (V<sub>2</sub>) resulting in a superior fitness (F<sub>2</sub>) manifested through the population growth (dP):

$$P(V_2, F_2) - (\text{selection}) = P + dP(V_2, F_2)$$

If  $dP > 0$  then

$$F_2 > F_1$$

To this R. Fisher has added an assumption that the larger the V the faster the increase in F (Edwards 1995).

This model does not explain a progression from the lower forms of life to the higher, nor the origin of species nor, for that matter, any other natural phenomena of general interest. Rather, it succeeded in separating natural science from natural human interests. But this is a side issue at the moment, for we are interested primarily in population growth as a measure of fitness. In the Darwinian model any trait actually or potentially enhancing population growth is considered as increasing fitness, thereby an evolutionary achievement. Incidentally, since plant communities produce more seeds under heavy grazing or browsing, the plant fitness must be increased by herbivory (McNaughton 1986; Belsky 1986). How good to be eaten! Despite the constantly repeated claims to the contrary, the logic of the Darwinian model is falsifiable and even readily so. As is discussed later in this paper, a positive dP disrupts density ratios of a balanced ecosystem and is eventually deleterious for the growing population itself — a fitness loss rather than a gain. In the alternative model population growth is interpreted as an evolutionary failure for only the maladapted organisms rely on sheer numbers for their survival.

In organisms of high reproductive potential population growth is typically regulated by a negative environmental feedback inflicting the high amplitude density fluctuations (e.g. in drosophilid flies, tundra rodents, etc.). Such organisms tend to surpass their sustainable density (D<sub>s</sub>) by a certain number of individuals constituting a redundant density component (D<sub>r</sub>), which then is sacrificed to environmental hazards serving as a buffer from complete extinction. The necessity to produce D<sub>r</sub> render these populations over-consumptive and destructive to their environments, thereby an adaptation failure. On the other hand, organisms arriving at a sustainable density typically obtain an innate control of their reproductive potentials (e.g. hatch size regulation negatively correlated with life expectancies in birds or even in wasps (Mangel & Clark 1988), or estrus periodicity regulation in mammals, notably in the Panda), thus minimising the redundant component of their populations. Consequently, D<sub>r</sub> can serve as a negative measure of fitness.

The ‘psychology’ under the Darwinian model above seems to have been inherited from those pioneer herdsmen who pleaded in their prayers for their progeny being multiplied as sand in the desert. Recently social priorities have shifted from growth to sustainability. ;

Similar shifts regularly occur in biotic communities in the course of their succession, or sere, from pioneer stages to climax (this does not imply that all communities inevitably arrive at their potential climax and is fairly compatible with the modern view of community systems as fluctuating mosaics of various successional stages (Hendry & McGlade 1995). For not only Abraham’s tribe, but any pioneer population tends to produce larger D<sub>r</sub>. As a consequence, their dead mass (M) accumulation is large relative to their comparatively small standing biomass (B). The B/M ratio typically increases through seral stages, and this process is accompanied by a rise of taxonomic diversity. The later appearing species are, as a rule, more effective in their use of trophic resources (Bridham, Pastor, McClaughert & Richardson 1995), which makes them less destructive than their preceding seral species and even allows them to confer a stabilising influence on their habitats.

Remarkably, the historical process of biological evolution seems to follow the same path. The early Proterozoic microbial mats have produced enormous dead mass of coaly shales (shungites) and banded iron ores constituting about 20% of the total sedimentary rock of that age (Chang, Stolz & Kirschvink 1989; James 1983). Their descendant late Proterozoic mat communities, though much more diverse (Hofmann 1976), have left a relatively small amount of organic deposits. On land, the middle Devonian coal measures have been formed by

monodominant communities of primitive algae-like vascular plants (Krassilov 1981). The arboreal tropical vegetation of the Carboniferous Period was coal-producing, while the extant tropical rain forests produce very little dead mass in comparison with their immensely large biomass.

Direct quantitative comparisons of the Carboniferous and extant vegetation in terms of biomass and productivity are hardly feasible, but some inferences can be made from the arboreal species ratios (about 50% in the former versus 70% in the latter) and the tree size (up to 40 m versus 60 m respectively). The Carboniferous plant assemblages from a single locality typically accumulating plant debris from about 1 ha of a tree stand (Krassilov 1975) are oligodominant with no more than 10 arboreal species each, while the extant rain forest stands of comparable size are mostly polydominant (occasionally monodominant in more stressful environments) (Hart, Hart & Murphy 1989) containing about 40–100 arboreal species (Wilson 1988).

These distinctions are due to the later appearing groups of organisms, such as angiosperms, being superior to their predecessors in the ability to stabilise their physical environments (e.g. soil conditions in hardwood forests in comparison with conifer forests; in particular, the tropical rain forest soils, though nutrient-poor, have fairly stable nitrogen and phosphorus concentrations) (Lewis 1986) as well as in creating more potential ecological niches for their coevolving organisms (e.g. herbivores and pollinators). In effect, evolutionary appearances of new dominant groups raise biological diversity to a higher level (in the same way the highly creative human individuals provide new social niches for other, perhaps less creative, individuals around).

Ecological succession of biotic communities thus conforms to the general trends of their historical evolution — a succession of climaxes, or clisere (Krassilov 1975), in much the same way as, according to the 'biogenetic rule', ontogenesis is a brief reiteration of phylogenesis. While the biogenetic rule relates morphological evolution to individual development, the 'ecocenogenetic rule' of the clisere — sere parallelism bridges the gap between the evolutionary and ecological time-scales thereby allowing reciprocal inferences.

The ontogenetic — phylogenetic and cenogenetic — ecogenetic parallelisms are hardly accidental. They appear to be due to directional processes sustained by telic systems, such as genome, population, ecosystem, etc., striving at definable goals, such as viable organism, continuous reproduction, effective living matter — non-living matter turnover, etc.

Insofar as the ecosystem is a living biomass producing machine (see Galley 1993 for alternative definitions) the B/M ratio is a major criterion of its effectiveness. In the progressively evolving ecosystem, B, the positive result

of its activity, would increase with structural complexity (of the canopy levels, synusia, consortial assemblages, etc.), while M, the negative result, would decrease with building up tropical pyramids. As is evident from the foregoing discussion, this is what actually happens in the course of the large time scale biosphere evolution. Both processes would create potential ecological niches as a prepattern of taxonomic diversity.

There is no *a priori* reason why the entire ecological space might not be occupied by a single generalist species (which is what the human species is striving at at the moment). However, since tolerance depends on trophic conditions (Odum 1971), it would inevitably decrease with exhaustion of trophic resources impelling this species to abandon marginal environments (as humans have to abandon costly space projects), thus leaving space for other species. Each species entry opens potential niches at the higher and lower trophic levels, thus promoting more species entries. Such positive feedback enhancing would provide for exponential rise of biological diversity. Actually the species introduction curves could be exponential in their proximal segments alone showing gradual saturation at the widely discrepant levels (May 1978), which seem to be controlled primarily by residual niche overlap and sustainable population densities:

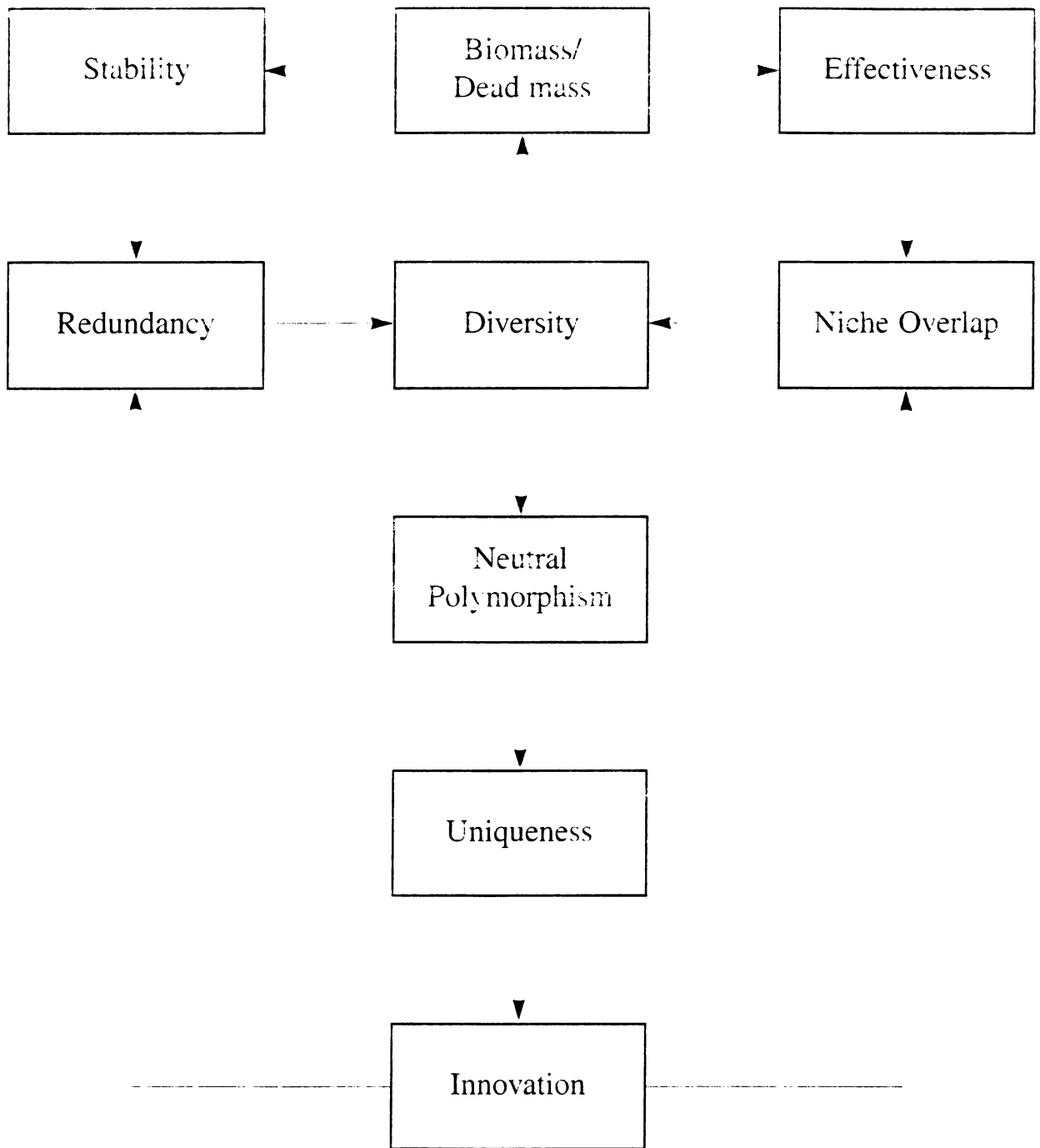
$$S_f \sim TR/NOM + D_{sm}$$

where  $S_f$  is a finite diversity of species, TR, the available trophic resources, NOM, the average niche overlap and  $D_{sm}$ , the average sustainable density.

Inasmuch as ecosystem evolutionary goals (above) impel a rise of  $S_f$ , there should be a reduction of NOM,  $D_{sm}$ , or both. Consequently, the constituent populations evolve towards a coarse-grained ecological strategy (Levins 1968) and minimal redundancy. Since the density fluctuations, the negative environmental feedback and the dead mass production relative to standing biomass tend to decrease in the process, we can identify this process as adaptation.

With NOM reduced, there would be less competition, while species entries would be due primarily to evolutionary innovations, allowing the occupation of a new niche — rather than competitive superiority. Similarly, some people assess themselves as successful competitors within the existing social structure, others as innovators in the intellectual or economic spheres creating new social niches, thereby reducing the number of redundant people. It is due to creative, rather than competitive, species and people that progress occurs in both biological and social systems.

Population redundancy in turn depends on environmental constancy: the more stable environments, the less a need in the  $D_r$  buffering and *vice versa* (thus Romans had encouraged the prolific reproduction of redundant



**Figure 1** Suggested relationships between vital parameters in the course of ecosystem evolution (explanation in the text)

citizens called proletarians and all the later appearing militant states followed their example). The diversity — redundancy — environmental stability circuit provides a long-sought explanation of the positive correlation between stability and diversity (fig. 1). A destabilising factor would impel an increase of Dr, consequently decreasing of Sf and B. Ecosystem evolution, thus, can be reversed, which actually happens under geological, climatic or human impacts. If plants increase their seed production after being eaten (see above), this does not mean that herbivory benefits them (see Liebold 1989 on the effect of predation on productivity). They, rather, have to buffer their population from total destruction by a Dr, which actually decreases their fitness. Similarly, a Dr

increase in pests is a typical reaction to pesticide impact, which is devastating not only because of its direct effect on the pest populations but also due to the indirect destructive impact of Dr. In much the same way organic pollutants instigate a redundant productivity in aquatic organisms followed by a fall of diversity in hypertrophic reservoirs (Rapport, Regier & Hutchinson 1985). In both agriculture and conservation it seems impractical to simultaneously increase productivity and diversity if these parameters are negatively correlated.

The geological record of ecosystem evolution is punctuated by the falls of diversity, which are known as mass extinctions and are correlated with major tectonic,

eustatic and climatic events (Newell 1963; Erwin 1990; Retallack 1995; Stanley & Yang 1994; Wethey 1985). Mass extinctions are especially prominent in the dominant plant and animal groups of their time. Since these groups are widespread and, by inference, tolerant to a broad range of environmental conditions, their extinction could hardly have been caused by a direct action of cooling, drought or other environmental hazards. Rather they might be endangered just by their dominant status, i.e., by being confined to the later seral stages.

In heavily impacted environments, when disturbances occur at shorter intervals than is needed to restore the climax (Tanner & Hughes 1994), ecological successions never succeed to their potential later stages, thus cutting off their climax dominants. For example, at the Cretaceous-Tertiary boundary marked by a global regression, increased volcanism and cooling, the hitherto prevailing *Sequoia* and *Parataxodium* redwoods became extinct or semi-extinct, while their understory or gap-filling broad-leaved *Corylites*, *Tiliaephyllum*, *Ushia*, etc., formed the progenitorial Arcto-Tertiary forests (Krassilov 1994).

Typically the diversity response to environmental impacts can be divided into three stages. At the first stage, *Sf* would increase due to the rise of indigenous as well as invading pioneer species (this is why 'intermediate disturbance' appears beneficial for biological diversity) (Huston 1994). In the second stage, a tail of the climax rare species would be shed. Finally a truncation of ecological successions (particularly, under destruction or fragmentation of habitats) (Tilman, May, Lehman & Nowak 1994), would result in decline and fall of the climax dominants. The surviving pioneer and early successional species would practice a high redundancy strategy stimulating high reproductive rates, in turn impelling acceleration, abbreviation and/or condensation of individual development (of which a precocious sexuality is a familiar example, the evolutionary importance of which is evident in various groups of both vertebrates and invertebrates (Bemis, 1984; McNamara 1983)) or overlap of developmental stages. Major evolutionary novelties (e.g. new plant organs formed by fusion of separate ancestral organs) (Krassilov 1991) allegedly derive from such heterochronous developments (Gould 1977; Patel 1994; Muller & Wagner 1991).

Since in the pioneer stage of ecological expansion a gene pool enrichment by hybridisation or non-sexual transduction of genetic material is potentially advantageous, there is no incentive for genetic insulation. There might be a tendency for species fusion by reciprocal genetic introgression. Species tend to be highly polymorphic and adaptively fine-grained. Contrary to the assumptions based on the fundamental theorem of natural selection (Edwards 1995), such species usually show the lowest, rather than the highest, evolutionary rates. Subsequently, while adopting a coarse-grained

strategy, they split into narrower species which are better protected from alien genetic material. A super species configuration of closely related but reproductively isolated species might arise from such speciation cycles (Krassilov 1989).

Concomitant with a switch to coarse-grained environmental strategy, a part of adaptive polymorphisms might turn non-adaptive by the narrowing of ecological niches and the loss of function. Actually, in the narrowly adapted stenobionts genetic variation appears selectively neutral at most of the polymorphic loci (Schopf & Gooch 1972). This may be accompanied by a loss of phenotypic plasticity, which correlates with moderately stressed and fluctuating environments (Kirzhner, Karol & Ronin 1995; Parsons 1991; Scheiner & Goodnight 1984; West-Eberhard 1989). Neutral polymorphism is potentially useful in acquiring new functions, e.g. marking off rare genotypes in the density-dependant mate choice. Human personality is based primarily on neutral variation of physiological and intellectual characters.

## Conclusion

In conclusion, an evolutionary model has been developed in this paper in which the ecosystem is defined as a living entity from non-living sources, the effectiveness of which can be assessed by living biomass to dead mass ratio. In the progressive evolution of an ecosystem as well as in its brief recapitulation by ecological succession, this ratio is increased (the genetic and intellectual immortality arise as a by-product) due to and concomitant with advancing structural complexity. To comply with this process, the newly added species have to be innovative — capable of opening new ecological niches — rather than competitive — capable of excluding other species. Ecosystem evolution thus promotes progressive organismic (morphological, physiological, intellectual, etc.) development. As a positive feedback, innovative species entries facilitate more species entries, thus making the increase of diversity self-sustainable. The level at which this process is slowed down depends on adaptedness — the sustainable use of environmental resources with minimal overlap of the other species' ecological niches, hence non-competitive coexistence — and a related parameter of fitness — an ability to maintain population at a low redundancy level. The latter depends on ecosystem stability buffering a sustainable density from environmental hazards.

Diversity is thus linked to stability through redundancy, a key parameter, the increase of which would reverse the ecosystem and, consequentially, organismic evolution inducing a truncation of seral and trophic chains, the corresponding decrease of biological diversity, primarily at the expense of top species, as well as developmental acceleration. Such turning points are amply documented in the fossil record and are invariably correlated with global environmental changes.

Human evolution complies to this model. Present day humans are inheritors of the early humans pioneer strategy of ecological expansion, unrestrained population growth, devastating use of trophic resources and the concomitant tense intraspecies competition. Incessant hostilities have encouraged proletarian demographic strategy. Even great empires might fall because of the ever-increasing masses of redundant people. There are, however, multiple signs of a turning point toward sustainability as a conscious goal of development including family planning, the conservationist and the animal rights movements — an incipient non-speciestic biospheric ethics. The individual priorities are gradually shifting from competitiveness to innovation. Technological developments have rendered adaptive variation, e.g. in the running speed or even in the memory capacities, non-adaptive.

The anti-Darwinian trend from useful to useless is manifested in both the biological and cultural evolution. The present day human individual variation is, for the most part, neutral (a comparison of prehistoric Venuses with modern beauties would readily show that our aesthetic ideals are shifting from the functional to the functionally neutral, and this process is faithfully reflected by the art evolution) and, with progress, more of it will turn from bearing on competitive interaction to facilitating noncompetitive coexistence of diverse individuals defining their unique sociocultural niches.

## References

- Ager, D. 1991, *New Scientist*, 128, pp. 56–57.
- Beisky, A. J. 1986, *Am. Nat.*, 127, pp. 870–892.
- Bemis, W. W. 1984, *Paleobiology*, 10, pp. 293–307.
- Bridham, S. D., Paster, J., McClougherty, C. A. & Richardson, C. J. 1995, *Am. Nat.*, 145, pp. 1–21.
- Chang, S. B. R., Stolz, J. F. & Kirschvink, J. L. 1989, *Precambrian Res.*, 43, pp. 305–317.
- Edwards, A. W. F. 1995, *Biol. Rev.*, 69, pp. 443–474.
- Erwin, D. H. 1990, *Ann. Rev. Ecol. Syst.*, 21, pp. 69–91.
- Galley, F. B. 1993, *A History of the Ecosystem Concept in Ecology*, Yale University Press.
- Gould, S. J. 1977, *Ontogeny and Phylogeny*, Harvard University Press, Cambridge, Mass.
- Hart, T. B., Hart, J. A. & Murphy, P. G. 1989, *Am. Nat.*, 133, pp. 623–633.
- Hendry, R. J. & McGlade, J. M. 1995, *Proc. R. Soc. Lond. B*, 259, pp. 253–259.
- Hofmann, H. J. 1976, *J. Paleont.*, 50, pp. 1040–1073.
- Huston, M. A. 1994, *Biological Diversity. The Coexistence of Species on Changing Landscapes*, Cambridge University Press, Cambridge, U.K.
- James, H. L. 1983, *Iron Formation: Fact and Problem*, Elsevier.
- Kirzhner, V. M., Karol, A. B. & Ronin, Y. T. 1995, *J. evol. Biol.*, 8, pp. 93–120.
- Krassilov, V. A. 1981, *Lethaia*, 14, pp. 235–250.
- Krassilov, V. A. 1975, *Paleoecology of Terrestrial Plants*, Wiley.
- Krassilov, V. A. 1994, in *Cenozoic Plants and Climates of the Arctic*, eds M. C. Boulter & H. C. Fisher, Springer, pp. 115–125.
- Krassilov, V. A. 1991, *Trends Ecol. Evol.*, 6, pp. 215–220.
- Krassilov, V. A. 1989, *Evol. Theory*, 9, pp. 37–44.
- Levins, R. 1968, *Evolution in Changing Environments: some theoretical explorations*, Princeton University Press, Princeton.
- Lewis, W. M. 1986, *Ecology*, 67, pp. 1275–1282.
- Liebold, M. A. 1989, *Am. Nat.*, 134, pp. 922–949.
- McNamara, K. J. 1983, *J. Paleont.*, 57, pp. 461–473.
- McNaughton, S. J. 1986, *Am. Nat.*, 128, pp. 765–770.
- Mangel, M. & Clark, C. V. 1988, *Dynamic Modelling in Behavioural Biology*, Princeton University Press, Princeton.
- May, R. M. 1978, *Scient. Am.*, 239, pp. 160–175.
- Muller, G. B. & Wagner, G. P. 1991, *Ann. Rev. Ecol. Syst.*, 22, pp. 229–256.
- Newell, N. D. 1963, *Scient. Am.*, 208, pp. 76–92.
- Odum, E. P. 1971, *Fundamentals of Ecology*, Saunders, Philadelphia.
- Parsons, P. A. 1991, *Ann. Rev. Ecol. Syst.*, 22, pp. 1–18.
- Patel, N. H. 1994, *Science*, 266, pp. 581–590.
- Kapport, D. J., Regier, H. A. & Hutchinson, T. C. 1985, *Am. Nat.*, 125, pp. 617–640.
- Retallack, G. J. 1995, *Science*, 267, pp. 77–80.
- Stanley, S. M. & Yang, X. 1994, *Science*, 266, pp. 1340–1344.
- Scheiner, S. M. & Goodnight, C. J. 1984, *Evolution*, 38, pp. 845–855.
- Schopf, T. J. & Gooch, J. L. 1972, *J. Geol.*, 80, pp. 481–483.
- Tanner, J. E. & Hughes, T. P. 1994, *Ecology*, 75, pp. 2204–2219.
- Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994, *Nature*, 371, pp. 65–66.
- West-Eberhard, M. J. 1989, *Ann. Rev. Ecol. Syst.*, 20, pp. 249–278.
- Wetney, D. S. 1985, *Ecology*, 66, pp. 445–456.
- Wilson, E. O. 1988, in *Biodiversity*, ed. E. O. Wilson, Nat. Acad. Press, pp. 5–18.

# Evolution of the Biosphere

edited by  
Alexei Yu Rozanov, Patricia Vickers-Rich  
and Chris Tassell

Records of the  
Queen Victoria Museum  
and Art Gallery  
Launceston  
No. 104

1997