ECOSYSTEM EXPLOITATION, SUSTAINABILITY AND BIODIVERSITY:
ARE THEY COMPATIBLE?

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Introduction

The intention of this contribution is really three-fold. First, to offer some
tangible basis for describing sustainability, in relation to what are the
supposed threats to the preservation of global ecosystems and to the
survival of species. Second, it seeks to place these concepts on an
energetic basis by reference to recent advances in the understanding of
patterns and processes in (mainly pelagic) fresh waters. Third, by relating
these to terrestrial ecosystems, it is shown how their sustainability may
be attained through encouraging healthy fresh waters. In order to
increase the accessibility of the concepts, I also draw on familiar non-
aquatic examples where these assist the argument.
Exploitation

Our first task is to recognise the problems which are currently posed to the sustainability and viability of global ecosystems by human socio-economic development. Individuals of the species Homo sapiens are no different from those of any other species in having to exploit their environments, both for their resources and as a sink for wastes. It is recognised that many species provide the resources and, in some instances, dominate the environments of others (consider woodland herbs and animals). Indeed, natural communities function by serial exploitation, through food chains which themselves support microbial loops that recycle the resources for renewed exploitation. This complex processing is driven almost wholly by radiant solar energy. Our own species is not excluded from this scheme; however, the technologies which we have developed to support our agriculture, mining and extractive industries, industrial manufacturing, mechanised transport and urbanisation, are fuelled not on the current account of solar energy but by drawing on the deposit of the unoxidised organic products of past ecosystems. The same technology supports what many ecologists suspect is too great a human population. Paradoxically, it is the numbers which make the technology so threatening (Rattray Taylor 1970): the exploitation of the planet’s living resources verges upon over-exploitation. Thus, "Give us this day our daily bread" is a modest-enough exploitative exhortation. When we attach to the request a serving of meat and a beverage, to have it transported half way round the Earth, for it still to be fresh and unputrefied within a layer or more of polymerised hydrocarbon, and five billion other people may be doing the asking, the request begins to sound excessive.

Human overexploitation of the biosphere certainly threatens the well-being of its other inhabitants, through the disproportionate harvesting of common resources, destruction of their habitats and in damaging the gross biospheric functioning in which all species play a part. Thus, human overexploitation is ultimately self-destructive. The dilemma raises the question, "Do we know what the right balance of exploitation is and how might we recognise it, save with the pragmatism of failure?"

Sustainability

We are entitled to assume that the present capacity of the planet to support a range of well-developed self-sustaining ecosystems of forests, grasslands and oceans, if not changelessly then at least around a stable organisational norm, would have been recognisable thousands or millions of years previously. The structures of these ecosystems are
supposed to have withstood external change and internal fluctuations. The perception now is that overexploitation, pollution and environmental degradation may have impaired, perhaps irrevocably, their ability to go on sustaining their normal functioning against the additional exploitation imposed upon them. The distinction is relevant to attitudes: clearly, we have to have some means of judging what might or might not be sustainable. The political challenge to the signatories of the "Rio Declaration" of 1992 is how to so manage exploitation that it does not threaten the economic performances of nations and does not impact unacceptably on "the environment". Since the signatories still have not much idea on how to achieve this broad goal, the declaration is a commitment to the unknown (Younes 1995). One challenge to the ecologist is to determine the extent to which ecosystems can be managed or cropped safely, without prejudice to human living standards, and to set targets for their attainment. Another is to determine how important to ecosystem function is the number of participatory species and how many are functionally redundant anyway.

### Biodiversity

Biodiversity is another term assimilated into popular and political parlance without clear definition. The general understanding is that there is an enormous number of species of plants and animals out there and, a few black-listed species apart (we might cite rats, tsetse flies and Salmonella, just to convey the idea), we have a duty to perpetuate their stocks. Apart from the challenge to name and classify them, there needs to be a consensus on WHY there are so many species and HOW they came to be here at all, when most of our ecological theory (density interdependence, food-web regulation, competitive exclusion) should lead us to conclude that many of them should, by now, have become extinct anyway.

### Pelagic ecosystems

My own studies on the ecology of plankton have led me to two important deductions. One is that despite the microscopic size of the plants, the smallness of the herbivores and the conspicuousness of the carnivores, the basic relationships and processing of the components of pelagic ecosystems are entirely analogous to those of tangible terrestrial systems, even to their intimate involvement of microbial pathways. Also, the structural organisation of their communities invokes the analogous strategic organismic adaptations to invasiveness or acquisition or disturbance-tolerance (Grime 1979; Reynolds 1993). The second is that,
measured in terms of the generation times of the dominant plant species, the times required for species to colonise a new habitat, develop populations, establish communities and to competitively exclude all but the eventual dominant, are hierarchically shortened, so that the seasonal onset of spring blooms, summer and/or autumn maxima and the late autumn decline is comparable to the re-establishment, changes in main species and subsequent recession of forest associated with the great Pleistocene interglacial periods (Reynolds 1995). Because they operate on small spatial scales, it is relatively easy to study things like resource exploitation rates and overconsumption by herbivores or by their predators. Because they occupy absolutely short time-scales in human terms, it has proved practical to gauge the authenticity of some ecological theories and to experiment meaningfully with plankton successions, to disturb them and to study their reconstitution.

**Phytoplankton succession**

Through this work, it has been possible to follow planktonic successions from the first colonisers to competitively-excluded dominance and to verify many of the properties hypothesised by Margalef (e.g. 1968) and Odum (1969); for more details see the review by Reynolds (1995). These include the following suppositions: the successful species are initially invasive species, selected by virtue of their reproductive strategies and rapid growth rates, but they are replaced by dominant resource-conserving species with elaborate survival strategies; they transfer resources into biomass, to the capacity of the relatively least plentiful of them (see Fig. 1a); although progressively more biomass ($B$) is sustained and the primary production ($P$) per unit area increases through the succession (Fig. 1 b), because a progressively greater proportion of production is consumed in maintenance ($R$, Fig. 1c) the productivity, *sensu* net production per unit biomass ($\frac{P-R}{B}$), steadily declines (Fig. 1 d). At climax, the material cycling is closed, the primary products of the resource-limited capacity of the plants and their dependents being devoted entirely to their maintenance. The rate of change in the species make-up of the community is suppressed towards the point where the species that will eventually dominate accounts for over 50% of the supported producer biomass; as it excludes its competitors, the

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**FIG. 1.** *(On facing page 193)* (a) Accumulation of total biomass ($B$) in a generalised ecological succession involving three species: one colonist (1), one climactic (3) and one intermediate (2), to the limit of the carrying capacity of the system, (b) Representation of community production ($P$, in units of, for example, carbon fixed per unit area per unit time) and community maintenance and respiration ($R$, in similar units) through the succession, (c) shows the difference between them ($P-R$) and (d) the quotient ($P-R/B$).
LIMITING CAPACITY

BIOMASS = B

(a)

P

R

(b)

(P−R)

(c)

(P−R)/B

(d)

TIME

(c)
equitability of the community is reduced and, ultimately, the diversity is suppressed as the last of the other species is outcompeted (Fig. 2a, based on experimental field data). In the end, there should be only as many species left as there are simultaneously definable niches to support them (Tilman 1982). That natural, unperturbed successions should lead to a species-poor unproductive outcome is against popular intuition ("look at the biodiversity of rain forests") but it is exactly what is predicted by competition theory (Hardin 1960).

**Disturbance and diversity**

Counter-intuition will also point to the vastness of species numbers existing before the major impact of man. The planktonic flora is also extensive: I estimate that there are upwards of 8,000 species in lakes, rivers and seas. Hutchinson (1961) found this array to be particularly paradoxical. The only way that this scale of diversity can have evolved and still be selected is if competitive exclusion has never occurred, at least, not everywhere at once, or if some other forcing mechanism routinely intervenes to prevent it from doing so. Certainly, the instances of very advanced ecological successions with competitively-excluded outcomes are rare. It has been shown by observation, analysis and experiment that the major force for change in planktonic communities is brought about by external agencies, such as seasonal variations in radiation income and day-to-day fluctuations in weather - wind, rain and sunshine, especially (Reynolds 1988). The effects of water-column stability, mixing and exposure to light on phytoplankton dynamics are profound. The changes can select among species of algae, just as storms or tree-fellers or farmers can influence the vegetation of a piece of land. Most of all, their effect is not merely to prevent the rightward progression through Fig. 2a but actually to make sharp leftward jumps. Moreover, the frequency of such incursions will determine how advanced a stage can be in the succession at the particular time when it is observed. However, at a frequency approaching that of generation times, individuals have to be physiologically tolerant of the extremes to which they are exposed: indeed, high frequency disturbance becomes a non-disturbed constant to the adapted species and is often a more powerful selective agent than the chemical composition of the water. Sommer's (1993) comparison of two chemically-similar nearby lakes of different size showed that susceptibility to wind action was decisive in driving the community composition and the rate of its change. Temporal changes in the species composition of phytoplankton thus provide excellent case studies for the demonstration of Connell's (1978) hypothesis of intermediate disturbance; at the appropriate frequency (2-4 generations, some 5-15
FIG. 2. (a) Features of succession deduced from observations on phytoplankton by Reynolds (1988), all of which decline as succession enters its climactic condition: the rate at which the species-specific share of the biomass alters, the index of species diversity and the equitability, or how the total biomass is distributed among the species present; (b) represents the difference between the potential entropy of the abiotic system and the effect of the ecosystem's acquisition of structure taking it away from entropic equilibrium, i.e., its exergy or negative entropy. Fragments of this sequence are represented in (c) and (d), subject to exploitative biomass removal (cropping) wherein the crop yield (Y) either (c) is within or (d) exceeds the current exergy of the system.
days), diversity of plankton is kept high. For most of the time, the algae have more trouble in coping with environmental variability than in competing with each other (see Padisak et al. 1993 for further examples). When we compare the representations in Fig. 1, it is apparent that the maximum diversity is coincidental with high net production (P - R).

The thermodynamics of disturbance

If delaying ecosystem progress is good for diversity, it is also good for species productivity. If disturbance is always disruptive, what can we infer is its impact upon sustainability? To do this, we need to elect some common (thermodynamic) units of measurement. As an example, we may appreciate that the mass of wheat harvested from a field, or fish trawled from an area of sea, or timber felled from a forest, can be expressed by the energy content, or what we once called its calorific value, per unit area (Joules per square metre). Quantitatively, this yield (Y) will be a small fraction of the energy consumed in its production (P + R) and a still smaller proportion of the aggregate flux of solar energy (f, in J m\(^{-2}\) day\(^{-1}\)) which was received by that area of the earth's surface during its production. Let us for a moment assume that the solar energy is constant at its daily maximum at the latitude 52°N (about 26.7 MJ m\(^{-2}\) day\(^{-1}\)). Much of this is consumed by reflection, by evaporation of water and long-wave radiation of heat. High quality radiative fluxes are dissipated, as irreversible heat losses, according to the second law of thermodynamics. The proportion which may be siphoned off into biological production depends on the proportion of the photosynthetically-active radiation (ca. 47%, or 12.6 MJ m\(^{-2}\) day\(^{-1}\)) and the ability of the biological system to conserve the high-energy carbon bonds of its photosynthates for internal consumption. I have calculated (Reynolds 1995) that the maximum sustainable active biomass of planktonic algae at the above energy flux, under which the visible wavelengths are reduced to zero, is 10.5 moles of cell carbon per square metre. Terrestrial plants can do better than this because they have opportunities to store photosynthate, accumulated over many days or years of photosynthesis, or to build inactive mechanical tissue (wood). In fact, observed standing-crop maxima of phytoplankton in lakes in Britain amount to 1.0-1.5 grams of chlorophyll per square metre, equivalent to 4-5 moles of carbon per square metre.

We must now assume that respiration in these self-shaded, climactic populations, together with the yield to other trophic levels (R + Y), balances the photosynthetically-available radiative flux of 12.6 MJ m\(^{-2}\) day\(^{-1}\). This, of course, is distinguishable from the heat shed by the same area of surface completely lacking any living organisms, and differs only in that it has been
processed biologically. Thus, the biological succession has re-routed the energy exchanges of the abiotic equilibrium into sustaining an elaborate biotic structure. Again, in thermodynamic terms, the entropy (S) of the abiotic system has been reduced by a quantity, being that required to sustain the assembly of the community (P) and which is expressible in the same units of areal energy-flux. Following the ideas of Jorgensen (1982) and his co-workers (Mejer & Jørgensen 1979; Nielsen 1992), we may now take the view that the energetic role of the ecosystem is to maintain itself as far as possible from the thermodynamic equilibrium. Then the "distance" from equilibrium is measured by the difference between the entropy due to maintenance of the biological system (R) and the total entropy of the system (S); Jørgensen calls this negative entropy the "exergy" of the system, which is represented graphically in Fig. 2b. It is quantitatively small at first but grows with total biomass B until the maximum value of [P - R] is attained.

In terms of phytoplankton successions, I have argued that external disruptive forcing exerts a measurable energy cost (D) which should be cumulated with R against the exergy (Reynolds 1995). Quite simply, if [R + D] is less than P, the system continues to function and build towards its ecological climax. If [R + D] is greater than P, the existing structure becomes unsustainable, structural organisation and biomass are lost and regrouped around a "more minimal" (Pickett et al. 1989) level of organisation, or more primitive successional stage, pending its re-advance towards the climactic target. It has to be pointed out that when the very real, day-to-day differences in the radiant energy input, due to differences in atmospheric conditions (cloud, depth of wind mixing) are taken into account, differences in E, rather than D directly, provide the disruption against which a positive P must be sustained (Reynolds 1995).

The thermodynamics of exploitation

The argument may now be developed that human exploitation of the production, in the sense of removing some or all of the biomass, B, as a crop (VO, say, represents a form of imposed disturbance. The extent to which this kind of disturbance is energetically sustainable may be judged by substituting Y for D in our disturbance criteria: i.e. is [R + Y] less than P (Fig. 2c), and thus sustainable, or is [R + Y] greater than P (Fig. 2d), in which case the ecosystem is greatly altered? To illustrate the argument, we may compare the clear felling of a forest with the light grazing of cattle in a parkland with developing scrub. The forest will have been returned to a very open, primitive habitat indeed but has the opportunity to begin a new succession with new pioneers and achieve a new development of diversity. The parkland might continue a slow progress
to forest (not much good for raising cattle) but not if the cattle-grazing increases in the meantime. In the resource-limited plankton of an oligotrophic lake, the progress of the algal succession may be similarly delayed by copepod-grazing but the situation is opposite in a nutrient-rich lake where filter-feeding Cladocera flourish on the production of invasive algae and may advance the dominance of larger (and so unavailable), late successional species. It is also difficult to contrive a level of zooplankton-grazing in eutrophic lakes that maintains the phytoplankton at a consistent level and with a consistent species composition, in a way which apparently simulates the maintenance of agricultural pasture by herbivores; I use the word "apparently" because by "cropping" the herbivores, the grazing rate can be kept close to the growth rate of the grass. This can be achieved in biomanipulated ponds by ensuring that the planktonic herbivores are also maintained in some quasi-steady state (Reynolds 1991).

In either case, the scale of cropping (Y) is kept in approximate proportion to production (P) minus the biological expenditure on maintenance, so that \(R + Y\) approximately equals P. It may be noted that this condition meets the criteria of the climactic steady state. Indeed, just as high frequency disturbance selects for species which can tolerate the forcing, through their own physiological or morphological adaptations, and which perceive them as an environmental constant, so we find that the exploitation holds the succession in an incomplete state, called a plagioclimax. It should be remembered that the productivity \((P - R)/B\) is higher here than in more advanced successional stages but, because both P and B are absolutely larger in more advanced successional stages, then so may be the sustainable level of Y that may be cropped; perhaps we need to rediscover how to sustain our exploitative tendencies on more advanced ecosystems.

The sustainability of exploited ecosystems

We may deduce that it is thermodynamically quite sustainable to crop productive ecosystems when \(V\) is much less than \(P - R\). Moreover, if the cropping is more intensive in one period, successional theory should allow it to redevelop to a comparable condition. Thus it begins to seem that it is perfectly all right to exploit and otherwise regulate natural ecosystems in order to keep them rejuvenated and productive, and collectively - at least - to afford to them the best prospect of maintaining a wide diversity of species. Paradoxically, this does not sound like the correct deduction to make, yet it actually explains the enormous diversity of habitats and species supported by the Earth, hitherto and through many centuries of human settlement and agriculture. In fact, two further deductions need to be made. The first is the obvious one; a burgeoning
human population is imposing more cropping and more plagioclimaxes on arguably more marginal ecosystems, so the collective provision of habitat suitable for the totality of species is increasingly biased towards the primitive successional stages. There is thus an obvious priority to protect habitat types, although to do so presents politically, socially and economically difficult problems for developing and developed countries alike. Yet the question has ultimately to be faced; the exploitable ecosystems and the yields they can sustain are finite and are not limitlessly croppable. The second deduction is a little more subtle but is increasingly recognised; as the fragments of successional more advanced ecosystems become smaller and still more isolated from each other, it becomes more difficult for them to interact and supply inocula to each other, with a probability that diversity will shrink even in protected ecosystems. It is not enough to seek a diversity of habitats; they have to be effectively contiguous if the collective diversity of species is to be protected. For aquatic organisms dependent upon individual water-bodies, which by definition are relatively transient and are often physically isolated from each other though, evidently, contiguous in terms of the transportability of their cosmopolitan biota, the diversity of habitats needs to be continuous in the long term (Reynolds 1991).

The biodiversity of isolated ecosystems

A third deduction needs to be made in respect of the observation that intensively exploited systems often do not maintain the diversity of early successional species that is suggested in Fig. 2a. It is well known that the managed pasture does not have the diversity of herbs of an ancient meadow. Proximal reasons have already been suggested, lack of nearby pools of species being one; moreover, the intensively-managed unit may represent a still more primitively successional stage at which the species have simply not arrived. It is not obvious, however, that the former is thermodynamically less sustainable than the latter. Does biodiversity matter to sustainability or must there be a large number of rare, functionally redundant species which, like the majority of phytoplankton species (Padisak 1992), are carried forward, if at all, as a sort of ecosystem "memory"? I am not sure whether we have more than an emotional answer to this question, though I suspect that species diversity is good for ecosystem health in ensuring alternative paths for the transfer of biologically-fixed energy to the higher trophic levels. More than functional fulfilment is needed to guarantee the health of the ecosystem. Once again, we can find an appropriate aquatic model in the ecosystem structure of small ponds. Many of these are known to recycle their nutrients efficiently and so are very responsive to eutrophication, and they can support intensive primary production. Many are also subject to
management as commercial or recreational fishponds. Exploitable fish biomass is sustained through primary production and its herbivorous and/or bacterivorous microconsumers in the zooplankton. Yet the fact that such ponds can remain in evidently quite different steady states is the subject of ongoing ecological study and debate (Scheffer et al. 1993). On the one hand, the fish may so dominate the system that the open water is depleted of zooplankton while the phytoplankton tends to be abundant and is comprised of only one or two main (invasive) species. This situation is unsustainable (the fish are in poor condition or do not grow well, unless they are benthic feeders). The alternative may be a primary-producer level dominated by submerged macrophytes, which supply organic detritus to a host of associated invertebrates as well as providing a physical refuge for zooplankton from predation. As a consequence, the water is clearer, the pond is more interesting and the variety and quality of the fish may be generally enhanced.

Look after water quality - the rest will look after itself

In recent years, freshwater ecologists have made great strides in understanding the structure, function and vulnerabilities of the aquatic ecosystems of lakes, ponds and rivers. They have grappled with the dynamics of species of plankton, nekton and benthos, involving a range of phylogenetic groups. Considerable progress has also been made in the fields of management and conservation of aquatic communities (summarised in Reynolds 1991) which should be of greater interest than perhaps it is to terrestrial ecologists. One common feature of the fresh waters that have been studied is their inseparability from their hydrological catchments, whether these are forested, agricultural, urbanised or industrialised. Much of the character and quality of these waters is therefore determined by the quantities and qualities of water received. How much they alter through exploitation of the land and through careless attitudes to deliberate waste disposal, or in accepting the inadequacies of its treatment, is the subject of penetrative and sometimes quite sophisticated mathematical models. Even the extent to which they can be altered back to an erstwhile better condition, or improved to bring about a new one of improved quality and greater biological and recreational interest, is within the realm of the limno-therapist. In many instances, the solution involves a change in the terrestrial processing of the water, before it becomes part of the aquatic ecosystem. In thus attempting to maintain and improve the quality of water, the diversity of its habitats and the sustainability of its biodiversity, it is inevitable that the exploitation of the land surface should be accorded greater care, in the end, to secure better terrestrial management practices.
These objectives are embraced in the recent moves adopted towards the management of water quality through an ecosystem approach and towards securing water-quality improvements by developing strategies of management for entire catchments. Against an ethos for defending water quality, significant improvements in the standards of land management can now be followed. With new attitudes towards the sustainability of the environmental systems, of which our own species is a part, perhaps their management will drive us towards a better strategy of self-management and persuade us that the proper approaches need not destroy the Earth's major resources in the process.

References


