

# **Energy Use and Biodiversity Loss**

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## Energy use and biodiversity loss

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#### **SUMMARY**

This paper evaluates the proposition that rates of population and species extinction can be assessed by using an indirect measure: total consumption of energy (industrial plus traditional) by man. This proposition rests on three assumptions. First, the rate of extinction is proportional to the rate of habitat destruction because most organisms are adapted to rather limited environments. Second, the rate of habitat destruction is correlated with the scale of human enterprise: the product of the number of people, average consumption, and the environmental damage done by the technologies used to supply each unit of consumption. Third, average energy can be used as a surrogate for the latter two factors, consumption × technology. Total energy use is therefore an indicator of trends in extinction rates, and thus could be used to estimate the rates themselves. I examine these premises and conclude that they are sufficiently well supported for biologists to use total energy consumption as an index of global extinction rates. That index, however, is not useful politically because the assumptions upon which it is based are not understood by decision makers and the general public.

#### 1. INTRODUCTION

Because every species and population can be assigned intrinsic (and perhaps practical) value, we should be concerned with both the number and rate of extinctions (Ehrlich & Ehrlich 1981, 1992). It seems reasonable also to place value on the proportion of a higher taxon that is disappearing: the annual loss of 1000 species from the class Aves would be considered as substantially more serious than the loss of 1000 species from the class Insecta, and the extinction of the only remaining coelocanth would be deemed a scien-

Here, however, I will limit my focus to population and species extinctions, and start with a plea to give adequate attention to the former (Ehrlich & Daily 1993). It is easy for the naive to imagine there is no species extinction crisis, and complex analyses are required to show that the situation could actually be extremely serious (see, for example, Smith et al. 1993b). However, little sophistication is required to see that populations are disappearing at a high rate, and that will have disastrous consequences (Ehrlich & Daily 1993), regardless of the fate of species. After all, if population extinctions reduced all remaining species to single minimum viable populations, no further species extinctions would have occurred. None the less, an extinction catastrophe would have taken place that might well, through interruption of ecosystem services (Holdren & Ehrlich 1974; Ehrlich & Ehrlich 1981), cause the demise of humanity as well.

Directly obtaining rates of loss of species and populations requires overcoming a daunting array of problems. First, no one is sure how much diversity

there is, however defined (see, for example, May 1988). At the species level, estimates range from 5 million to 30 million or even 100 million (see, for example, Wilson 1992), and there are probably billions of distinct populations (Ehrlich & Daily 1993; Daily & Ehrlich 1994). Needless to say, even knowing present absolute extinction rates would be of little use in obtaining proportional rates of extinction when there is roughly an order of magnitude of uncertainty on the size of the stock.

Biologists should initiate steps to narrow the uncertainties about the magnitude of biodiversity and compute present loss rates for a stratified sample of taxa. These tasks are so enormous, however, that it behoves us to examine indirect ways of determining the rate of decay of biodiversity. After all, it is not necessary to have counted, named and established measures of similarity among the grains of sand, pebbles, shells and rocks on a beach to determine for practical purposes how rapidly the beach is eroding.

Here the following propositions are evaluated to see whether an indirect index of the rate of biodiversity loss can serve in place of direct estimates that are not available now and are unlikely to be available in the critical decades ahead.

- 1. Rates of extinction of both populations and species are related to the rate of habitat loss.
- 2. The rate of habitat loss increases with the scale of the human enterprise.
- 3. Total energy use is a reasonable, if imperfect, surrogate for the scale of the human enterprise and its environmental impact. Thus, use is positively correlated with extinction rate, and a doubling of energy use leads to roughly a doubling of the rate. By

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applying data on increase in energy use to historical data on extinction rates, current rates can be estimated.

# 2. PROPOSITION 1: EXTINCTION TRACKS HABITAT LOSS

No organisms occur in all habitats, and most have quite narrow habitat requirements. Plants often require characteristic soils, régimes of temperature, humidity and light. In one sample of British plant species, about half were restricted to one or a few specialized habitats (Rabinowitz *et al.* 1986). Members of the most species-rich taxonomic group, phytophagous insects, each tend to feed on relatively few plants (see, for example, Futuyma 1991; Bernays & Graham 1988; Ehrlich & Murphy 1988).

Thus, when habitats are destroyed, populations and, eventually, species inevitably become extinct. When the sand dune habitat of the butterfly Cercyonis sthenele sthenele was developed as San Francisco grew in the last century, that distinctive population (subspecies) disappeared. When the mature swamp forest habitats of southeastern U.S.A. were fragmented, the Ivory-billed woodpecker, which required large tracts of such habitat, lost population after population, and finally became extinct. In Australia, I was once told by a forester not to worry about the destruction of Queensland's tropical forests 'because they'll grow back'. That is a highly dubious proposition for the plants unless sources of propagules are preserved and appropriate microclimates for their germination and growth (often provided by the forests themselves) can be restored. But it is nonsense for organisms such as parrots and canopy butterflies, which cannot remain in orbit for the many decades needed to reestablish their habitat.

# 3. PROPOSITION 2: HABITAT LOSS INCREASES WITH THE HUMAN ENTERPRISE

#### (a) Habitat loss

Determining the overall rate of habitat loss with precision is very difficult for several reasons. First, comprehensive numbers on even total destruction of habitats, such as clearcutting of forests, ploughing of grasslands, and draining of swamps, are not available. Existing statistics are limited to some habitats in some nations, leaving little basis for making 'bottom up' global assessments (see, for example, World Resources Institute 1990, 1992).

The figures that are available do give a feel for how extensive such damage can be. Percentages of total forest area that has been lost are available for a sample of 40 African nations, and range from 30% in Zambia to 91% in the Gambia, with an average of 68%. Losses in 14 sampled Asian nations range from 34% to 96%, with an average of 69%. China, largely deforested, is not included; India has lost 78% of its forests. Unhappily, estimates are only available for four Western Hemisphere nations: U.S.A. 26%,

Argentina 50%, Guatemala 60%, and Mexico 66% (World Resources Institute 1990).

The extent of total habitat destruction varies among habitat types and regions. Nearly all the old-growth forests of the Pacific Northwest of U.S.A. are gone. Approximately half of all tropical moist forests have been cut since 1950. Other kinds of habitat have suffered similarly. In U.S.A., virtually 100% of natural grasslands have been lost since 1492. Both Germany and the contiguous 48 United States have lost half their wetlands. About three quarters of the coastal mangrove wetlands of India, Pakistan and Thailand are gone (World Resources Institute 1992; Brown et al. 1992).

Second, much habitat that is not destroyed is 'lost' to some organisms through various forms of habitat conversion short of outright destruction. For example, converting many old-growth pine forests in the southeastern United States to even-aged stands of pines made them uninhabitable by red-cockaded woodpeckers, but had less impact on various species of warblers.

Third, orbital or airborne sensors cannot provide comprehensive estimates of rates of habitat destruction. Remote sensing might seem an ideal solution to the precise measurement of those rates, and it can be useful in measuring deforestation, desertification and other dramatic forms of habitat destruction. However, remote sensors have a variety of limitations. One is that they often cannot make subtle but important discriminations. For instance, over forests they tend to measure surface (crown) characteristics, and thus they may not be able to detect major changes in forest biomass that do not disrupt the canopy significantly. Synthetic aperture radar is incapable of distinguishing different amounts of biomass above a level that excludes from analysis over half of the Earth's vegetated area, including all mature tropical moist forests (Imhoff 1993).

Remote sensing is now of little value in detecting critical alterations of freshwater habitats. One study of New Zealand stream habitats found the fish communities in most sites depauperate in both species diversity and abundance (Swales & West 1991), a condition not apparent to many indirect means of assessment. The habitat changes responsible were clearance of native forests, drainage of wetlands, and river channel works for hydropower, agricultural development and other uses. In theory, data acquired by remote sensing might, given the proper algorithms, eventually be used to determine extinction rates in lakes, rivers and streams caused by such changes, if the remote sensing could distinguish native from exotic forest (as streams in the latter had few fish species).

However, habitat changes caused by introductions of exotics may never be detectable remotely, and invasions account for 20–40% of known species extinctions (World Resources Institute 1989). Consider the dramatic modification of the Lake Victoria habitat that occurred with the introduction of Nile perch (*Lates niloticus*), which promptly devoured most of the endemic cichlid species (Lowe-McConnell 1987), or

Table 1. Decline of British butterfly populations as indicated by records from grid squares

		extinct by		
	total (all periods)	1940	1969	extant in 1970-1982
average number of squares occupied	807	68	107	632
average percent per species	100	23	17	60

the introduced brown snake that virtually wiped out the avifauna of Guam. Several individuals of the snake have now been found on the runways at Honolulu International Airport (apparently having dropped from aircraft wheel wells). They pose a severe threat to the remnants of the distinctive endemic avifauna of the Hawaiian Islands, but would not show up in satellite images. Indeed, invasions are one of the most insidious and potent forms of habitat conversion, and one of the most difficult to evaluate from afar (Drake et al. 1989).

Habitat can be 'lost' in other very subtle ways, difficult to detect even on-site. For instance, even minor incursions into forest that do not significantly change vegetative structure can be catastrophic for larger forms of wildlife. As Terborgh (1983) noted: 'a skilled hunter equipped with a standard one-shot 16 gauge shotgun can single-handedly eliminate large birds and mammals within a radius of several hours' walk from his dwelling.' Before he found the undisturbed Cocha Cashu in the Peruvian Amazon, he, like most of us, did not realize that a tropical forest could have abundant mammals (especially primates).

In Costa Rica, hunting pressure has removed agoutis (*Dasyprocta punctata*) and creasted guans (*Penelope purpurascens*) from many remnant forest patches. However, extinction patterns are often complex: in southern Costa Rica, despite heavy hunting pressure, guans persisted in a recently converted (18–30 years ago) agricultural landscape with small (*ca.* 3–30 ha) forests patches from which even many forest butterfly species had already been eliminated (Daily & Ehrlich 1994).

In addition to these difficulties, data acquisition and analysis on the important conditions and processes to which remote sensing is ideally suited (such as rates of change in land-use patterns) fall far behind need (see, for example, Myers 1989). Overall, it might actually be better to use changes in distribution of well-known organisms (such as butterflies) as indirect measures of habitat loss (see discussion in Ehrlich (1994)).

### (b) Population extinctions

Trying to determine rates of population extinctions is even more difficult than establishing rates of species extinctions. Populations are more difficult to define than species, and to my knowledge no systematic attempt is made anywhere to keep track of population extinctions in any major taxonomic group.

There is one data set that casts some light on the extinction of butterfly populations (and thus, perhaps, on the extinctions of herbivorous insects in general). The British butterfly distributions mapped by Heath *et al.* (1984) are based on records of presence or

absence in a National Grid consisting of 3600 10-km squares covering the entire British Isles. The maps show records of pre-1940 presence gathered from the literature (and showing, in combination with other records, the maximum historical extent of each species), records from 1940–1969 gathered from field notes and collections by early contributors in a comprehensive scheme to determine which grid squares had which species, and field records as they were received by those collaborating in the intensive survey between 1970 and 1982. Thanks to the enthusiasm of British lepidopterists, although the maps are admittedly incomplete, 98% of the grid squares had been surveyed to some extent.

By using these maps, the shrinkage in number of populations in 54 of the 62 British butterfly species can be estimated. I excluded three migratory species, two widespread agricultural pests, and three species that had contracted and then re-expanded their ranges to equal or greater area. The exclusions did not change the picture significantly, but did reduce the average maximum number of squares occupied from 927 to 807. The results are given in table 1.

One assumption made in table 1 is that all squares were occupied in previous periods: if there were butterflies in a square in 1978, butterflies were assumed to have been there in 1938. This is certainly not exactly true but, as the three species that were noted as expanding their ranges were excluded, it seems a reasonable assumption for the level of conclusions drawn here. A more interesting issue is how square occupancy corresponds to population number (Daily & Ehrlich 1994). Here it is simply assumed that if a species disappeared from 50% of the grid squares, it lost 50% of its populations. That is almost certainly a conservative assumption, as most British species have geographically restricted, closed populations. Consequently, some species are known to be still present in grid squares even though one or more populations have gone extinct in those squares. For example, five populations of Hesperia comma have disappeared from squares in Dorset which still contain extant colonies and thus remain 'occupied' on the grid square maps, and the same is true of virtually all other Dorset butterflies (Thomas & Webb 1984).

Based on those assumptions, the loss of population diversity of British butterflies is clearly much more extensive than that of species diversity, as table 1 shows.

# 4. PROPOSITION 3: TOTAL ENERGY USE IS CORRELATED WITH EXTINCTIONS

One can view the impact (I) of humanity on Earth's life-support systems as the product of three factors: the size of the human population (P), average affluence

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(A) (as measured by average consumption), and an index of the environmental damage of the technologies (T) used to supply each unit of consumption (Ehrlich & Holdren 1971; Holdren & Ehrlich 1974; Ehrlich et al. 1977; Ehrlich & Ehrlich 1990). The  $I = P \times A \times T$  identity is important as a heuristic device but, because only P is reported in national statistics, the identity's usefulness in analysis depends upon estimating A and T. That problem can be largely solved by substituting average energy use (for which numbers are generally available) for  $A \times T$  (Ehrlich & Ehrlich 1991; Ehrlich 1993).

Even where habitat loss can be quantified, determining its relation to energy use can be very difficult. Several studies suggest that local or regional population growth is not a major trigger of rapid tropical deforestation (see, for example, Kummer 1991). However, external factors, such as demand for timber and beef in rich nations and the industrialization of agriculture (often to grow produce for sale to the wealthy), leading to the invasion of tropical forests by displaced farm labourers, clearly are related to the global scale of energy use.

One can hope, then, that changes in global energy consumption might average over the manifold regional differences and provide a satisfactory general index of extinction rates. To test this idea, consider the increase of extinction rates over background levels that would be predicted from the expansion of the human enterprise as measured by energy consumption. An estimate of the average species 'life span' of higher vertebrates is 200 000 years to 2 million years (Ehrlich *et al.* 1977), giving a background extinction rate of species between 0.2 and 2 species per million species per year. This estimate incorporates that of Raup (1988) and Wilson (1992) of 1 species per million species per year, which will be used here as the best available.

I assume that the impact of the human enterprise did not begin to move the extinction rate out of the background range before the agricultural revolution roughly 10 000 years ago. An exception to this might be found among the large mammals, because of the widespread extinctions of the Pleistocene megafauna in which *Homo sapiens* is almost certainly implicated. Megavertebrates, however, are a tiny portion of biodiversity, and the invention of agriculture was clearly the step that put our species on the road to being a global force.

Just before the revolution, there were perhaps 5–10 million people (Biraben 1979). A conservatively high guess of their average energy consumption would be about 0.2 kW, consisting mostly of wood burning. The total impact of humanity then was, therefore, on the order of 0.001–0.002 TW (1 TW =  $10^{12}$  W). Under those assumptions, human impact had multiplied roughly 7000- to 13 000-fold by 1990, when total energy consumption reached about 13 TW. Wilson's (1992) rather conservative appraisal based on island biogeographic theory is that human activity has increased the species extinction rate in rainforests (by reduction in area) between 1000- and 10 000-fold. So those estimates overlap, and a reasonable (but not

conservative) impact-based evaluation would be the loss today of about 10 000 species per million species per year.

Since 1600, a very conservative estimate of the number of bird and mammal species that have gone extinct is 175 (Smith et al. 1993a). That is an annual rate of roughly 30 species per million species in those taxa. From 1986 to 1990, 15 bird and mammal species disappeared, a rate of over 250 per million species per year. That rate is about an order of magnitude lower than Wilson's (1992) conservative appraisal that rainforest species (of all groups) are disappearing at a yearly rate of 2700 per million species per year, and is even further below the 10 000 per million species (1%) per year implied by the above calculation on human impact. So, from the viewpoint of species extinction, the increased scale of the human enterprise suggests rather higher overall rates than the admittedly conservative estimates based on known vertebrate extinction rates. The correlation of species extinction with that scale would be stronger if insect species were currently suffering a relatively high rate of extinction. That would be occurring if, in the extremely rich, poorly known, and unmonitored fauna of tropical moist forests, many insect species had relatively restricted distributions.

If we use the rate of increase of total energy use from 1970 to 1990 (2.3% annually (Holdren 1991)) as an index to future rates of extinction (2.3% of species or populations annually), then the time to extinction of half of all species or populations is about 30 years. This figure, which is based on a constant exponential decay of diversity, seems quite high for species compared with other evaluations, but it could be low for populations.

Is there a relation between species and population extinction in the British Isles and energy consumption in the U.K.? Between 1925 and 1955, commercial energy consumption increased by roughly 40%, but between 1955 and 1975 it went up only about another 5%. Over the entire 1925–1982 period, it climbed about 50% (Darmstadter 1971; United Nations 1988). If population extinction rates were proportional to regional energy use, a loss of about 33% of populations would be expected in the 1925–1982 period.

Assuming these U.K. energy numbers are adequate surrogates for the scale of the human enterprise in the British Isles, since 1955 the rate of butterfly population extinctions in Britain has been faster than that of the increase in human activities, but that of species extinctions has lagged (as only one species, 2% of the fauna, has disappeared in the last 40 years). The observation that extinction rates for populations are much higher than species extinction rates (as one would assume on general principles) certainly conforms with massive anecdotal data from continental Europe (see, for example, Kudrna 1986) and other parts of the temperate zones. Extinctions of butterfly populations in North America north of Mexico have also been observed on numerous occasions. Most populations recorded by early collectors in the Los Angeles Basin are long gone, and my research group

has observed the extinction of several populations of the Bay checkerspot butterfly, Euphydryas editha bayensis, over the roughly three decades that we studied it (Ehrlich et al. 1980). In contrast, no butterfly species has gone extinct in North America in historic times, although two distinctive subspecies in the San Francisco area were extirpated by urban expansion, one around 1880 and the other in the early 1940s (Scott 1986).

Similarly, many butterflies are declining in Japan, and population extinctions are common, but none of the 238 resident butterfly species has yet wholly disappeared from the Japanese islands (Sibitani 1989). In fact, to my knowledge, there has been no well-documented extinction of a continental butterfly species anywhere in the world. The complete disappearance of the Italian endemic *Polyommatus exuberans* would be an example if it actually was a distinct species (Kudrna 1986). It is likely that some species have disappeared unheralded in tropical areas (such as the unique *Styx infernalis* of the Chanchamayo Valley in the Peruvian Andes).

#### 5. INTERPRETATION

Obviously, attempting to compare rates of extinction with rates of habitat destruction involves dealing with incomplete information and pyramiding assumptions. Data on species extinctions in even the most thoroughly monitored groups are at best incomplete (see, for example, Diamond 1987), and pathetically little information of any sort exists on population extinctions. However, overall evaluations of habitat destruction involve extrapolation from data on energy use as a surrogate for the scale of the human enterprise, then assume that scale to be well correlated with the loss of habitat, and finally assume that loss of habitat is closely related to rates of extinction. With the exception of the relation between habitat loss and population extinction, all these assumptions are quite oversimplified.

None the less, estimates based on them seem to fall between those generated by other methods for species and population extinctions. The power function relation between habitat destruction and species extinction, and the cascading effects of disrupting metapopulations, could explain this. We know on both theoretical and observational grounds that reducing a habitat area by half does not lead to the extinction of half the species in it. We also know that the loss of key habitat patches in a metapopulation system can cause the disappearance of all component populations.

### 6. CONCLUSION

If the human enterprise expands to anything roughly like the scale envisioned by the Brundtland report (World Commission on Environment and Development 1987), it will increase at least tenfold, until the world uses 130 TW, before growth stops. As a thought experiment, a 130 TW world today could imply, based on numbers in Smith et al. (1993a) for the actual

current 13 TW world, only about 30 years to the extinction of half of all species of birds and mammals, and about 7 years for half of all species of palms. However, if the world were instantaneously transformed into the 30 TW world of the optimistic Holdren scenario (Holdren 1991), then those times to 50% extinction would be extended to about 130 years and 30 years, respectively. Compare these with the global estimate of 30 years to 50% extinction based on current growth rates of energy consumption.

These projections are not reassuring. Furthermore, ecological (including climatic) systems often display nonlinearities, long time lags, and threshold effects that could make such projections conservative. For example, many tropical pastures contain isolated rainforest trees that were left standing to shade cattle and now are utilized by forest birds. They have limited lifespans and are not being replaced as they die. When they go, they may trigger a surge in population (and perhaps species) extinctions. Moreover, neither species nor population extinctions occur independently (see, for example, Paine 1966; Daily et al. 1993). Consequently, extinction cascades may become commonplace in the next century.

Furthermore, Homo sapiens now threatens to alter the climate dramatically and already uses, co-opts or destroys roughly 40% of terrestrial net primary productivity, the food supply of virtually all animals and most microorganisms that live on land (Vitousek et al. 1986). Finally, there is no guarantee that technological changes (as have already occurred in forest harvesting techniques) will not accelerate the expansion of the human enterprise and accelerate the exponential rate of diversity decay. In light of such considerations, it seems only sensible to conclude that projections based on past and current rates of anthropogenic extinction could easily be low. In my view, there is ample justification for society to pay substantial premiums to insure against the loss of a large fraction of biodiversity.

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### REFERENCES

Bernays, E. & Graham, M. 1988 On the evolution of host specificity in phytophagous arthropods. *Ecology* **69**, 886–892.

Biraben, J.-N. 1979 Essai sur l'évolution du nombre des hommes. *Population* 34, 13-25.

Daily, G. & Ehrlich, P. 1994 Preservation of biodiversity in small rainforest patches: a rapid evaluation using butterfly trapping, with an application. *Biodiv. Cons.* (Submitted.)

Daily, G., Ehrlich, P. & Haddad, N. 1993 Double keystone bird in a keystone species complex. Proc. natn. Acad. Sci. U.S.A. 90, 592-594.

Darmstadter, J. 1968 Energy in the world economy. Baltimore: Johns Hopkins.

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- Diamond, J. 1987 Extant unless proven extinct? Or extinct unless proven extant? *Conserv. Biol.* 1, 77–79.
- Diamond, J. 1991 The rise and fall of the third chimpanzee. London: Radius.
- Drake, J., Mooney, H., di Castri, et al. 1989 Biological invasions. Chichester: Wiley.
- Ehrlich, P.R. 1964 Some axioms of taxonomy. Syst. Zool. 13, 109–123.
- Ehrlich, P.R. 1984 The structure and dynamics of butterfly populations. In *The biology of butterflies* (ed. R. I. Vane-Wright and P. R. Ackery), pp. 25–40. London: Academic Press.
- Ehrlich, P.R. 1994 The scale of the human enterprise and biodiversity loss (In the press.)
- Ehrlich, P.R. & Daily, G.C. 1993 Population extinction and saving biodiversity. *Ambio* 22 (2-3), 64-68.
- Ehrlich, P.R. & Ehrlich, A.H. 1981 Extinction. New York: Random House.
- Ehrlich, P.R. & Ehrlich, A.H. 1990 The population explosion. New York: Simon and Schuster.
- Ehrlich, P.R. & Ehrlich, A.H. 1991 Healing the planet. New York: Addison-Wesley.
- Ehrlich, P.R. & Murphy, D.D. 1988 Plant chemistry and host range in insect herbivores. *Ecology* **69**, 908–909.
- Ehrlich, P.R., Ehrlich, A.H. & Holdren, J.P. 1977 Ecoscience: population, resources, environment. San Francisco: W. H. Freeman.
- Ehrlich, P.R., Murphy, D.D., Singer, M.C., Sherwood, C.B., White, R.R. & Brown, I.L. 1980 Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia (Berl.)* 46, 101–105.
- Ehrlich, P.R. & Holdren, J.P. 1971 Impact of population growth. *Science*, Wash. 171, 1212-1217.
- Futuyma, D.J. 1991 Evolution of host specificity in herbivorous insects: genetic, ecological, and phylogenetic aspects. In *Plant-animal interactions: evolutionary ecology in tropical and temperate regions* (ed. P. W. Price, T. M. Lewinsohn, G. W. Fernandes & W. W. Benson), pp. 431–454. New York: Wiley.
- Heath, J., Pollard, E. & Thomas, J. 1984 Atlas of butterflies in Britain and Ireland. New York: Viking.
- Holdren, J.P. 1991 Population and the energy problem. *Popul. Env.* 12, 231–255.
- Holdren, J.P. & Ehrlich, P.R. 1974 Human population and the global environment. *Am. Scient.* **62**, 282–292.
- Imhoff, M.L. 1993 The dependence of synthetic aperture radar backscatter on forest structure and biomass: potential application for global carbon models. Unpublished Ph.D. thesis, Stanford University.
- Kudrna, O. 1986 Aspects of the conservation of butterflies in Europe. Butterflies of Europe, vol. 8 (ed. O. Kudrna). Weisbaden: Aula-Verlag.
- Kummer, D.M. 1991 Deforestation in the postwar Philippines. University of Chicago Press.
- Lipscomb, C.G. & Jackson, R.A. 1964 Some considerations

- on some present day conditions as they affect the continued existence of certain butterflies. *Entomologist's Rec. J. Var.* **76**, 63–68.
- Lowe-McConnell, R.H. 1987 Ecological studies in tropical fish communities. Cambridge University Press.
- Martin, P.S. & Wright, H.E. (ed.) 1967 Pleistocene extinctions. New Haven: Yale University Press.
- May, R.M. 1988 How many species are there on Earth? Science, Wash. 241, 1441–1449.
- Myers, N. 1989 Deforestation rates in tropical forests and their climatic implications. London: Friends of the Earth.
- Paine, R. 1966 Food web complexity and species diversity. *Am. Nat.* **100**, 65–75.
- Rabinowitz, D., Cairns, S. & Dillon, T. 1986 Seven forms of rarity and their frequency in the flora of the British Isles. In *Conservation biology* (ed. M. E. Soulé), pp. 182–204. Sunderland, Massachusetts: Sinauer Associates.
- Raup, D.M. 1988 Diversity crises in the geological past. In *Biodiversity* (ed. E. O. Wilson), pp. 51–57. Washington: National Academy Press.
- Scott, J.A. 1986 The butterflies of North America. Stanford University Press.
- Sibitani, A. 1989 Decline and conservation of butterflies in Japan. In *Decline and conservation of butterflies in Japan. I* (ed. E. Hama, M. Ishii & A. Sibitani), pp. 16–22. Osaka: Lepidopterological Society of Japan.
- Simon, J. & Wildavsky, A. 1993 Facts, not species, are periled. *New York Times*, May 13.
- Smith, F., May, R., Pellew, R., Johnson, T. & Walter, K. 1993a Estimating extinction rates. *Nature*, *Lond.* 364, 494–496.
- Smith, F., May, R., Pellew, R., Johnson, T. & Walter, K. 1993b How much do we know about the current extinction rate? *Trends Ecol. Evol.* **8**, 375–378.
- Swales, S. & West, D.W. 1991 Distribution, abundance and conservation status of native fish in some Waikato streams in the North Island of New Zealand. *Jl R. Soc. N.Z.* 21, 281–296.
- Thomas, J. & Webb, N. 1984 Butterflies of Dorset. Dorchester: Dorset Natural History & Archeological Society.
- United Nations 1988 Statistic yearbook. New York: United Nations.
- Vitousek, P., Ehrlich, P., Ehrlich, A. & Matson, P. 1986 Human appropriation of the products of photosynthesis. *BioScience* 36, 368–373.
- Wilson, E.O. 1992 The diversity of life. Cambridge, Massachusetts: Harvard University Press.
- World Commission on Environment and Development 1987 Our common future. New York: Oxford University Press.
- World Resources Institute 1989 World resources 1989–90.New York: Oxford University Press.
- World Resources Institute 1990 World resources 1990–91.New York: Oxford University Press.
- World Resources Institute 1992 World resources 1992–93. New York: Oxford University Press.