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ECOSYSTEM ORGANIZATION: MUTUALISM AND CYBERNETICS OR PLAIN DARWINIAN STRUGGLE FOR EXISTENCE?

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For an evolutionary ecologist, nature is both the ecological theater where the evolutionary play is being performed and a direct product of this play. The struggle for existence is its sole organizing principle, and the physical environment is its only external constraint. Some systems ecologists of the Odum school do not seem to share this view of nature. According to Patten and Odum (1981), cybernetic organization is a necessary condition for the persistence of ecosystems. They stated clearly that regular Darwinian interactions are not a sufficient basis for understanding this supposedly cybernetic structure of ecosystems: "Either the ecosystem is orderly in the [cybernetic] way we described or its lack of chaos just happened to develop from unregulated Darwinian struggles between competing populations, all alone and uninfluenced, except by each other, on a neutral slate of life. The latter seems implausible for us." (1981, p. 891.)

Thus, Patten and Odum suggested that natural selection also operates between ecosystems with "survival of the cybernetic" as its fundamental principle. In the ecosystems that we observe, the boundary condition of proper cybernetic design is satisfied, and other kinds of ecosystems have been eliminated. Odum and Biever deviated still farther from standard evolutionary thinking by suggesting that "over evolutionary time, movement of energy from autotrophs to heterotrophs is donor-recipient controlled or mutualistic" (1984, p. 364). The only explanation provided by Odum and Biever for such supposedly widespread cooperation is a vague statement about the occurrence of positive-feedback loops between consumers and resources. The examples discussed in greater detail refer to tightly linked mutualistic associations between green plants and fungi. These cases can, however, be readily interpreted on a purely Darwinian basis as examples of mutual exploitation between organisms having shortages and surpluses of different commodities. The mutualism hypothesis of Odum and Biever (1984) thus needs to be specified before it can be assigned the status of a scientific proposition.

The Patten-Odum hypothesis of elimination of non-cybernetic ecosystems is better formulated, although it apparently refers to several attributes of ecosystems that would be better treated separately (Reiners 1986). Patten and Odum sug-

gested that a major shortcoming of standard evolutionary ecology is its failure to account for the existence of a ready environment where the interactions take place: "For us, we must also ask why the environment is always prepared and ready: why did it not become chaotic long ago, a disorganized heap of unprocessed and partially processed energy-matter residues from the evolutionary biology of past ages?" (1981, p. 894.) In a biogeochemical context, this question is easy to answer. In the current biosphere, where oxygen is present, organic wastes of animals and plants are the resources of many fungi and bacteria (Rich 1984). Mineralization takes place because these organisms gain from it as individuals. Under anoxic conditions, unprocessed and partially processed energy-matter residues (peat, mud) accumulate, and disorganized heaps of such residuals (fossil fuels) abound in many areas. Lovelock (1979) pointed out that in some geochemically important microbial processes, the immediate energy balance is negative. However, these reactions increase the individual fitness of their performers by yielding oxidants for microbes living in anaerobic conditions (Brock 1966; Schlegel 1969).

In the context of population dynamics, the point of Patten and Odum is not so trivial. Simple models with difference equations or differential equations easily generate extremely violent cycles or chaotic population dynamics (Gilpir 1975; May 1981). Although the view of essentially chaotic behavior in natural populations has its proponents (Ehrlich and Birch 1967), most ecologists seem to agree that the current diversity of life and the persistence of highly specialized organisms in many ecosystems cannot be reconciled with the idea that pure chaos or violent cycles are typical for most populations in most ecosystems. However, chaos and violent cycles arise most readily from oversimplified single-population and two-population models, whereas interactions between populations on three successive trophic levels are quite likely to result in a stable equilibrium, especially if interference competition is common in consumer populations (Rosenzweig 1973; Wollkind 1976). In fact, the central message of these models was already proposed a quarter of a century ago (in Hairston et al. 1960, conventionally referred to as HSS). The original HSS hypothesis has its problems, but these can be, and have been, solved. Moreover, the solution of these problems has greatly increased the predictive power of the HSS approach, as shown below.

HSS: SUCCESSES AND PROBLEMS

In a short and somewhat provocative paper, Hairston et al. (1960) explained how order can arise from plain Darwinian struggles without ecosystem-level selection: carnivores severely exploit their resources and have guilds structured by competition. Regulated by predation, the resources (i.e., herbivores) are unable to have much impact on the vegetation. Consequently, plant communities are structured by competition.

The initial response of ecologists to the HSS hypothesis seems to have been cautious. In the mid-sixties, HSS became the storm's eye of an intense debate. According to Ehrlich and Birch (1967), HSS explained an order that does not exist. Thus, they seemed to argue for an essentially chaotic view of population

dynamics (see above). Murdoch's (1966) critique contained two qualitatively different parts. One of these, that the statements in HSS are untestable and thus not scientific, was rebutted by Slobodkin et al. (1967). Murdoch's other chief point was that HSS failed to consider the alternative hypothesis that consumers are regulated by the defensive mechanisms of their resources. This point was apparently in concert with the spirit of the time and emerged as the winner in the debate. For two decades, the prevailing hypotheses of plant-herbivore interactions (e.g., Haukioja and Hakala 1975; White 1978; Rhoades 1985) have been elaborations of Murdoch's defense hypothesis. The exploitation view of HSS has survived as an implicit basis of predation and competition models, but direct and positive references to HSS in influential papers have been rare.

The defense approach might have seemed plausible in the late sixties and early seventies. Current evidence suggests, however, that the enthusiasm for Murdoch's viewpoints might have been premature. The apparent defensive responses of plants are often too small to be significant for the dynamics of herbivorous populations, and some celebrated cases are based on dubious statistical procedures (Fowler and Lawton 1985). The results of consumer-removal experiments are even more damaging to the Murdoch-White approach. In these experiments, more than twofold increases in resource populations have been frequently observed (Sih et al. 1985); these observations are clearly inconsistent with Murdoch's and White's ideas of populations regulated by their resources, not by their consumers.

A good measure of how forgotten HSS had become is the way in which Sih and his coworkers related their results to HSS. Instead of stating that their report refutes Murdoch's critique of HSS, they placed emphasis on the fact that positive results were common in the herbivore-removal studies included in their review. This was interpreted as evidence against HSS. However, Hairston (pers. comm.) has pointed out that the positive responses were obtained mainly in studies focusing on granivores or on introduced herbivores and in studies performed in disturbed habitats. In all these cases, the strong impact of herbivores on the vegetation is compatible with HSS (see Slobodkin et al. 1967). The prevalence of such systems (and the virtual absence of studies performed in undisturbed mesic forests) is, in fact, a further piece of evidence for HSS. The prevailing attitude among plant ecologists is that herbivory is usually unimportant. Thus, an experimental demonstration of this trivial point would not look like a promising project.

As a test of HSS, the field experiments reviewed by Sih et al. (1985) had a clear shortcoming. They did not include a single case in which predators of herbivorous vertebrates had been controlled. Two such studies have been performed recently in Sweden, one on voles in an old-field area in Scania (Erlinge 1987), and another on gallinaceous birds of the Baltic islands (Marcström and Engren 1982). In both cases, the numerical responses of the prey would qualify as "large effects" in the terminology of Sih et al., and the impact on survival has been dramatic. Yet, the experimental designs were extremely conservative. The fence used by Erlinge allowed free movements of voles out of the relatively small enclosure (0.5 ha). Thus, predators in surrounding areas could influence population dynamics in the enclosure both by maintaining a dispersal-provoking density gradient and by

preying on the voles as they visited outside areas. Marcström's team, in turn, removed foxes and martens but not stoats or weasels, thus leaving a potential source of clutch predation unaffected.

If the world is green because of predation, as proposed in HSS, then removal of predators should have profound cascading trophic impacts on the vegetation (Carpenter et al. 1985). No such impacts were reported in the two studies cited above, whose conservative designs made expectations of cascading effects unreasonable indeed. However, much more radical experiments, in which native grazers were protected against all predators, have been performed, some on a very large scale. Sometime during the Neolithic Stone Age, three ungulate species—the ancestors of the present cattle, sheep, and goats—started to enjoy protection by man against their predators. For these experiments, the evidence of cascading effects is plentiful; when the domestication process began, major changes in the vegetation of the Old World started to occur. The current heaths of western Europe, the low scrublands of the Mediterranean region, the “hedgehog” vegetation of the mountains in the Middle East, and the secondary grasslands that abound throughout the Old World are all products of this change and occur in areas formerly covered by forests (Walter 1968; Gimingham 1972).

The changes in the vegetation were accelerated by logging. However, according to the current wisdom of forestry, heavy logging alone is compatible with the persistence of forests. The semi-open wooded grazing lands around Scandinavian farms and chalets, in turn, suggest that forests can gradually disappear as a result of grazing and browsing alone: grazers (especially sheep and goats) prevent regeneration, and the established trees get old and gradually die off. In northern Europe, domesticated animals can be regarded as introduced aliens dependent on the provision of food and shelter. However, the changes in the vegetation have been especially pronounced in areas formerly inhabited by the wild ancestors of these animals and characterized by mild winters, allowing at least sheep and goats to graze outdoors throughout the year. For these areas, it is rather clear that the essential human impact was protection against predators, not the introduction of exotic species or the provision of supplemental food during the winter.

Corresponding large-scale experiments have also been performed by nature without human influence. During the Pleistocene, rising sea levels have periodically created medium-sized islands, large enough to harbor fair population sizes of herbivores but so small for carnivores that extinctions have been very likely. On these islands, body sizes of herbivores have converged toward a size of 10–20 kg (Kurtén 1972; see also Lomolino 1985). A plausible explanation for this, as suggested by Kurtén, is that the enormous diversity in size of continental herbivores is a consequence of predation (i.e., an herbivore that is outside the prey range of existing predators can always invade), whereas grazers of about the size of a sheep are best able to survive on severely depleted vegetation.

In a parallel case, herbivores (tortoises) invaded an island in the Indian Ocean, but predators failed to follow. On the eastern half of the island where drinking water is available, tortoise densities (mean body weight 24 kg) range from 20 to 60 individuals per hectare. Trees, established after the tortoise population had been depleted by humans, have died, and the woodlands have been replaced by pecu-

liar vegetation called tortoise turf: a dense mat of graminoids and herbs about 5 mm tall, with many endemic and genetically dwarfed species (Merton et al. 1976). Parallel changes have also occurred on the southern and eastern coasts (Hnatiuk et al. 1976), whereas woody vegetation continues to flourish in northern and western parts, where tortoises are rare or absent (Merton et al. 1976; Hnatiuk et al. 1976).

A further line of evidence is provided by the competition experiments reviewed by Schoener (1983). As predicted in HSS, removal of competitors has created clear and positive responses in most experiments with terrestrial plants and carnivores, whereas terrestrial herbivores have generally failed to respond to corresponding treatments. (Notice that the more ambiguous results in Connell 1983 can be attributed to a smaller data base and to the consequently prominent role played by a rather peculiar group of insects in the data; see Hairston 1985; Schoener 1985.) The pattern is probably meaningful, because the current controversy about the importance of interspecific competition has created a situation in which even experiments yielding negative results have, *a priori*, a relatively high likelihood of being performed and then published.

Schoener's (1983) review did, however, contain information that cannot be readily reconciled with the HSS hypothesis. Although many competition experiments with plants yielded unambiguously positive results, some did not. In part, the negative cases could be explained away as consequences of recent disturbance, but some experiments conducted in relatively mature vegetation nevertheless yielded ambiguous or negative results. When evaluating these results, it is useful to recollect the observation that HSS attempted to explain: the world is green. When the data are re-analyzed so that "truly green" habitats (forests and successional stages leading to forests, meadows and tallgrass prairies) are regarded as one category, "somewhat green" habitats (grasslands, heaths, arid scrublands) as another one, and "definitely not green" habitats (deserts) as a third category, an interesting pattern arises (table 1). The overwhelming majority of cases in which results were negative or ambiguous stems from somewhat-green habitats accessible to grazers.

The apparent weakness of competition between plants in relatively stressful habitats might appear to be evidence for Grime's (1979) hypothesis that stress prevents competition from becoming an important ecological factor for plants. However, such an interpretation is clearly untenable. In the most stressful habitats (deserts), field experiments on competition between plants yielded positive results (table 1). The same was true even for somewhat-green habitats if the access of grazers to the study plots was restricted. Moreover, Parker's (1984) grasshopper-exclusion experiment, conducted in an arid grassland area, represents a case in which Hairston (pers. comm.) could not fault the interpretation of Sih et al. (1985) and tacitly accepted the possibility that HSS might not be valid for this particular system. There is also good evidence that herbivores are limited by resources in relatively barren regions (Batzli et al. 1980; Thomas and Edmonds 1983). Instead of looking at direct impacts of stress on plants, it might be useful to study how stress constrains trophic interactions and influences plants via its impact on trophic dynamics.

TABLE 1

A REANALYSIS OF SCHOENER'S (1983) REVIEW OF COMPETITION EXPERIMENTS WITH PLANTS

HABITAT	FREE ACCESS TO GRAZERS ^a		RESTRICTED ACCESS TO GRAZERS ^b	
	COMPETITION		COMPETITION	
	Clearly Demonstrated	Unclear or Apparently Absent	Clearly Demonstrated	Unclear or Apparently Absent
Green worlds (forest, meadow, tallgrass prairie, seral scrubland)	31	6	15	1
Habitats with scanty vegetation (grassland, mesquite or sagebrush, heath)	4	25	3	1
Extremely stressful habitats (desert)	4	0	4	1

NOTE.—Studies performed in clearly disturbed habitats (field, old field, pasture) have been removed, and the remaining studies have been grouped in three classes on the basis of the "greenness" of the habitat. Each class has been further subdivided on the basis of free or restricted access by grazers (including the domesticated ones, which are the only larger ones left in many temperate areas). The numbers in the cells refer to the number of species for which competition was or was not unambiguously demonstrated.

^a For a test of between-habitat differences, $\chi^2 = 45.36$, $P < 0.001$.

^b Enclosure, partial enclosure, or livestock excluded. For a test of between-habitat differences, $\chi^2 = 1.44$, NS.

THE PRODUCTIVITY CONNECTION

The HSS hypothesis was derived from two specific assumptions beyond the authors' basic Darwinian view of nature: (1) trophic interactions are exploitative, and (2) order emerges out of these interactions in a basically uniform way all over the world. Although empirical support is available for the first assumption, the second assumption is empirically implausible (see above) and leads to logical problems. It makes no sense to ask why the world is green while standing in the middle of the Atacama Desert or on the northern shores of Greenland. These extreme cases are linked to the green worlds of HSS by continuous gradients. The realism of the HSS approach could thus probably be increased by studying how trophic dynamics interact with the physical factors ultimately responsible for these gradients. Such a biogeographical modification of HSS was outlined by Fretwell (1977) and formally presented later (Oksanen et al. 1981, hereafter referred to as OFAN). The logic of these propositions can be illustrated by considering the dynamics of two man-managed ungulate populations in Fennoscandia.

The reindeer densities of northernmost Lapland (Finnmarken, Norway, and the tundra districts of Finland) range from 1 to 4 overwintering animals per square kilometer (Skjenneberg and Slagsvold 1968; Kurkela 1978; A. Riekkinen, pers.

comm.). The winter moose densities in southern and central Finland and Sweden are of the order of 0.5–2 animals per square kilometer (Nygren 1984; Cederlund 1988). Corrected for the more than fourfold size difference between moose and reindeer, these figures imply that the boreal parts of Fennoscandia have generally higher ungulate biomasses than the tundra and brushwood areas of Lapland. There is no doubt about the reason for the low reindeer densities in the far north: the ranges do not support higher numbers. Mass starvation occurs periodically, and the depleted lichen cover of the heaths in northern Lapland (Kalliola 1939; Hämet-Ahti 1963; Helle and Aspi 1983) differs strikingly from the thick and continuous lichen carpets characteristic of corresponding habitats in the reindeer-free mountains of southern Scandinavia (DuRietz 1925; Nordhagen 1943; Dahl 1956). The moose populations of boreal forest areas are, in turn, regulated by hunting. Except for pine heaths on especially barren soils, the impact of moose on the vegetation is moderate or slight (K. Danell, P. Niemelä, and K. Vuorisalo, MS), and moose densities of about 5 per square kilometer have been maintained in an enclosure in central Sweden since 1982 without the provision of supplemental food (Bergström 1987).

If game preserves were established both in northernmost Lapland and in central Fennoscandia, with both the ungulates and their predators being allowed to live without human interference, HSS would predict that predators start to regulate both moose and reindeer populations, keeping their impact on the vegetation at a modest level. For the moose, this view is plausible. The current moose densities are higher than those observed in a game preserve in southern Quebec, where a strong case for predator limitation can be made (Mesier and Crête 1984, 1985). In the case of the reindeer in northern Lapland, however, Caughley's (1976) idea of the primary importance of ungulate-plant interactions seems much more plausible than the HSS hypothesis. Even the impact of barren-ground caribou on the lichen tundra vegetation in central Canada is strong enough to keep the lichen cover more comparable to the conditions in Lapland than to those of the reindeer-free mountains in southern Scandinavia, in spite of relatively intense hunting and the presence of natural predators (Kelsall 1968). Moreover, the copious carpets of *Cladonia stellaris* (the competitively superior lichen species) on mountains of southern Scandinavia have turned out to be extremely sensitive to grazing and trampling and have become strongly decimated in many areas because of the current expansion of remnant reindeer populations (Höglund and Eriksson 1973; Gaare and Skogland 1975). The ultimate cause seems to be the low productivity of the lichen tundra vegetation. The vegetation can thus be under severe grazing pressure even when the reindeer (caribou) density is so low that predators cannot depress it any further.

The arguments in OFAN are no more complicated than those of the examples discussed above. Predators cannot possibly do more than set a ceiling for grazer densities. The height of this ceiling is determined by the food requirements of predator species (or such social units of predators) that are sufficiently efficient pursuers to subdue healthy prey. If the vegetation is so unproductive that a grazer density lower than this ceiling level is enough to create a serious shortage of forage, predators could not possibly control grazers within a large area of this

unproductive habitat. (Smaller patches could be affected by predators subsisting on prey populations supported by more-productive habitats; T. Oksanen, MS.) Consequently, the dynamically interesting part of the grazing chain in unproductive areas must be expected to consist of only two links. If the exploitation view in HSS is applied to these systems, the grazer community should be structured by competition, whereas the vegetation should be regulated by grazing.

When this approach is also extended to even less productive ecosystems, the positive results of competition experiments performed with desert plants become understandable. Assume that the hypothetical game preserve in northern Lapland contains one of the vast highland areas of the region, where non-glaciated land can be characterized as a "sea of boulders," with the "vegetation" consisting mainly of some isolated patches of glacial buttercups in the few sites where some soil is available. One cannot expect that the establishment of the preserve would affect the reindeer population of such an area because there is no reindeer population to be affected. On the stony fields, the forage basis simply does not allow the grazers to persist. Consequently, plants are largely left alone and, strange as it might seem, competition between plants should be relatively intense. In every environment, there is some maximum amount of phytomass that can exist; when this level is reached, neither an individual nor a species can expand without reducing the abundance of others. Competition for small and dispersed patches requires different tactics from competition in continuous vegetation, but it should not be any less severe unless the stress is accompanied by physical disturbance.

The above discussion focused on some points along a continuous productivity gradient. The transition between these communities with different kinds of trophic dynamics should indeed be gradual. In the fringes of the mountain area where patches of vegetation are larger and closer to each other, grazers can be expected to be present as extremely sparse populations or as moderately frequent visitors, having still only marginal impact on the life of plants. With increased primary productivity, natural grazing pressure should gradually become more intense, culminating when the grazer stock at the grazer-plant equilibrium reaches the level at which predators can prevent further increase of population density.

In order to label ecosystems with different trophic dynamics, we can call them three-link, two-link, and one-link systems in accordance with Fretwell (1977). An appropriate definition for an n -link ecosystem in this context is that an ecosystem has n -link dynamic structure if the n th trophic level is the highest at which the dominating populations strongly influence their resources. Such terms can only represent coarse and somewhat arbitrary divisions of a continuous gradient of shifting trophic dynamics (see Fretwell 1987). Moreover, the terms have little to do with the number of trophic levels actually present in the area. Where the vegetation is barely productive enough to allow the persistence of a very sparse grazer population, the food-chain length in terms of OFAN is one link, since the impact of such a grazer population on the vegetation is marginal. Yet, two trophic levels are predicted, and even the presence of the third one is very likely. Every resource-limited grazer population produces easy prey (old, injured, and starving animals) that can be profitably harvested, even from a sparse population, by predators with appropriate adaptations. The two-link systems in OFAN can also

be periodically invaded even by "real" predators, because the grazer-plant equilibrium should often be locally unstable, generating periodic outbreaks of herbivore populations. Thus, Pimm's (1982) observation about the presence of predators and herbivores in almost all ecosystems does not conflict with the prediction in OFAN that the highest dynamically interesting trophic level shifts from predators to herbivores and eventually to plants in clines of decreasing primary productivity.

The perspective in OFAN removes the strongest arguments that could be leveled against HSS. The resource limitation of the caribous of Canadian arctic islands (Thomas and Edmonds 1983) and the lemmings at Barrow (Batzli et al. 1980) are no longer anomalies but pieces of corroborative evidence. Also, the shifting views of Sinclair (1977, 1985 a,b) about the importance of resource competition and predation for ungulates of East African savannas (and his current position that both processes are important) are readily understandable in the framework in OFAN. These savanna ecosystems include habitats on both sides of the predicted productivity threshold (about 700 g of dry matter per square meter per year; see McNaughton 1985). Consequently, the importance of predation and resource competition should vary, depending on where the study is performed and whether it is performed during moist or dry years.

I have consistently used the word "grazer" and avoided the word "herbivore." There is a good reason for this choice of terminology. The approach in OFAN depends critically on the assumption that the consumers experience their environment in a fine-grained manner both in time and in space (consumers move around at least within a habitat patch and are active throughout the year or suffer high costs of dormancy). For small arthropods that experience the environment as coarse-grained in time and space (i.e., herbivore and predator populations can live on a single plant and they complete their life cycles when the plant is green), the original HSS hypothesis should apply regardless of the productivity of the habitat. Thus, the ecological applicability of OFAN is limited for animals, but its ecological implications for plants are nevertheless profound. Recall that in the domestication experiment in the western Palearctic, three species of grazing vertebrates were sufficient to keep the vegetation scanty and to eliminate the grazing-sensitive plants. The native grazer fauna of relatively unproductive ecosystems usually includes more vertebrate species, and in arid environments, it is also supplemented by arthropods with vertebrate-like habitat utilization and long life cycles (e.g., grasshoppers).

At this point, I hope that I have remedied all communication problems that the jargon of n -link ecosystems and the intrinsic difficulty of the three-dimensional exploitation model have created. (The problem with the exploitation model was aggravated because the legend for all of fig. 2 in OFAN was included under fig. 2a.) What remains to be shown is that the critical predictions, created by OFAN not by HSS, are realistic. The biomass predictions have already been tested with corroborating results (Oksanen 1983). A still more critical prediction remains: in the absence of grazers, the vegetation of the tundras and steppes must be replaced by radically different kinds of plants.

GRAZER ENCLOSURES AND GRAZER-FREE ISLANDS IN MODERATELY UNPRODUCTIVE ENVIRONMENTS

The most critical predictions in OFAN, differentiating it both from HSS and from hypotheses emphasizing the ability of plants to defend themselves against grazers, are related to moderately unproductive ecosystems (productivity interval of about 40–700 g/m²/yr; see Oksanen et al. 1981), that is, temperate steppes, arid tropical grasslands, thorn scrublands, and arctic-alpine tundras. OFAN predicts that these plant communities as we know them are strongly dependent on grazers. Their removal should result in an increase in the plant biomass: rapid and pronounced on the upper end of this productivity interval, slower and smaller on the lower end. In addition, the species composition of the vegetation should change as relatively prostrate grazing-tolerant plants become replaced by plants better adapted to compete for space in the absence of grazers.

Enclosure experiments have been performed in two ecosystems with appropriate primary productivities: the arid plains of the Serengeti, Tanzania, and the lowland tundra at Barrow, Alaska. The case of the Serengeti plains is especially critical, since it represents the uppermost end of the productivity interval, at which two-link dynamics should prevail (McNaughton 1985). The changes in the enclosures should thus be both pronounced and rapid. They have been indeed. Within about a decade, the dominating grass species of the plains has completely disappeared from grazer enclosures, and tallgrasses that are normally abundant only in moister parts of the Serengeti have taken over (McNaughton 1979*a,b*).

The lowland tundra at Barrow, with productivities of about 200–280 g/m²/yr (Miller et al. 1980) belongs to the lower half of the predicted interval with two-link trophic dynamics. The enclosures, run since the early 1950s, have nevertheless produced clear vegetational changes. At well-drained sites, mosses and lichens have built up thick carpets, and the previously dominating tundra graminoids occur only as scattered shoots. In the wettest sites, the enclosures are dominated by tall graminoids and characterized by copious accumulations of standing dead material (Batzli 1975; Batzli et al. 1980), a condition similar to that of the Serengeti enclosures.

The Fennoscandian tundra International Biological Programme (IBP) did not include corresponding enclosure experiments. The tundra communities seem to represent the whole productivity range of two-link ecosystems, with only the most luxuriant willow thickets being too productive and the most extreme snow beds being too barren (Wielgolaski 1975). Since 1977, I have run enclosure experiments in three Fennoscandian tundra habitats: a rather productive meadow, a much less productive lichen heath, and a still more barren dwarf willow snow bed, with three enclosures and seven open sample plots in each habitat (Oksanen and Oksanen 1981). The plots, harvested in 1985, were censused annually by a modified point-frequency method. In all habitats, pronounced changes in the vegetation occurred from 1977 to 1985. Except for larger woody plants that were recovering from major vole damage on all plots in 1974–1975, enclosures and open plots clearly differed (table 2). The meadow enclosures were characterized by an increase in

TABLE 2

CHANGES IN THE ABUNDANCE SCORES OF DIFFERENT PLANT GROUPS ON THE STUDY PLOTS ON
FINNMARKSVIDDA FROM 1977 TO 1985

HABITAT, PLANT GROUP	NO. OF CASES						NET CHANGE (%)	
	Open Plots			Exclosures			Open Plots	Exclosures
	—	0	+	—	0	+		
MEADOW								
Semishrubs	0	1(5)	1	0	1(1)	1	+ 106	+ 119
Dwarf shrubs								
Broad-leaved	0	4(2)	1	0	1(1)	1	— 3	+ 59
Ericoid	0	1(5)	1	1	0(2)	0	+ 136	— 75
Herbs								
10 cm < fh < 15 cm	0	2(3)	2	1	1(1)	0	+ 53	— 52
5 cm < fh < 10 cm	0	6	1	3	0	0	+ 1	— 70
fh < 5 cm	0	4(2)	1	0	2(1)	0	— 1	— 29
Graminoids								
15 cm < fh	0	2(5)	0	0	1	2	+ 47	+ 364
5 cm < fh < 15 cm	0	0(1)	6	0	1	2	+ 141	+ 127
fh < 5 cm	0	0(2)	5	0	0(3)	0	+ 261	0
HEATH								
Semishrubs	0	2(3)	2	0	1(1)	1	+ 37	+ 59
Dwarf shrubs								
Broad-leaved	0	3	4	0	0	3	+ 52	+ 198
Ericoid	0	6(1)	0	0	1(1)	1	+ 23	+ 36
Graminoids	0	6(1)	0	0	1(2)	0	+ 37	+ 59
SNOW BED								
Dwarf shrubs								
Broad-leaved	4	3	0	0	0	2	— 24	+ 40
Ericoid	0	2(5)	0	0	0(2)	0	— 5	— 100
Herbs								
5 cm < fh < 10 cm	0	3(4)	0	0	2	0	— 10	+ 38
fh < 5 cm	0	4(3)	0	1	1	0	— 4	— 92
Graminoids								
5 cm < fh < 10 cm	0	5(2)	0	0	0	2	+ 34	+ 314
fh < 5 cm	0	3(1)	3	0	0(2)	0	+ 122	—

NOTE.—Number of cases gives the number of sample plots on which, according to two-tailed χ^2 test, the change was significantly positive ($P < 0.05$) (+), not significant (0), or significantly negative (—). The numbers in parentheses in column "0" refer to cases in which a decrease would have been impossible to detect, because of the smallness in the score (<5) for 1977. The net change from 1977 to 1985 is given as a percentage of the 1977 score. fh, mean foliage height of a well-developed shoot in a habitat typical for the species.

the abundance of tallgrasses. (Their biomass remained rather modest, but copious amounts of standing dead shoots accumulated.) Medium-sized herbs and ericoid dwarf shrubs were heading for extinction, apparently because of the heavy cover of grass litter that shaded them and prevented generative reproduction. In the heath exclosures, broad-leaved dwarf shrubs increased strongly, whereas a corresponding increase on open plots was much weaker. In the snow-bed exclosures, the strongest absolute increases were scored by broad-leaved dwarf shrubs (which declined on open plots), and the greatest proportional gains were obtained by

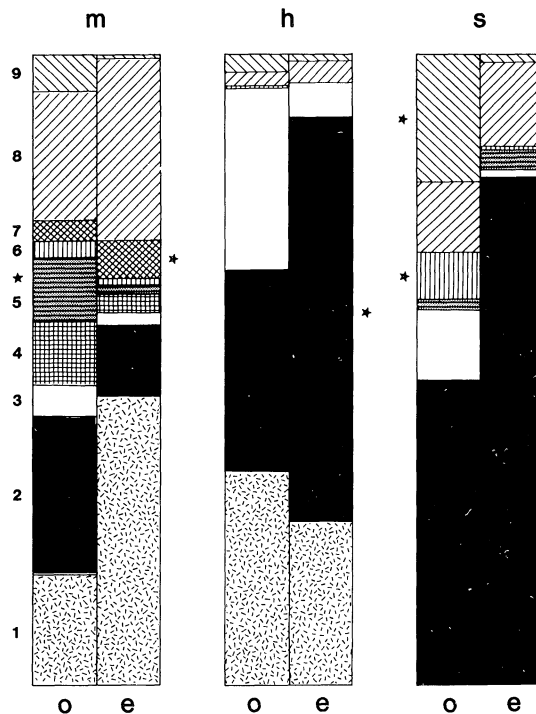


FIG. 1.—Composition of the field layer in percentages of biomass (oven-dried wt) on open plots (o) and within exclosures (e) in three low-arctic habitats: meadow (m), heath (h), and snow bed (s) on Finnmarksvidda. 1, semishrubs (= *Betula nana*); 2, broad-leaved dwarf shrubs; 3, ericoid dwarf shrubs; 4, moderately tall herbs (10 cm < foliage height < 15 cm); 5, low herbs (5 cm < fh < 10 cm); 6, prostrate herbs (fh < 5 cm); 7, tall graminoids (fh > 15 cm); 8, medium-sized graminoids (5 cm < fh < 15 cm); 9, prostrate graminoids (fh < 5 cm). Star, the aboveground biomass of the plant group in question is significantly greater than it is in the other treatment (Mann-Whitney *U*-test, $P < 0.05$). On the snow bed, where the third exclosure failed, $P = 0.056$ (the highest possible level of confidence) was regarded as significant.

relatively tall graminoids. Low herbs that held their ground on open plots became virtually extinct in exclosures. The biomass data (fig. 1) carry largely the same message, although emphasizing the initially abundant plant groups and giving less clear results for the heterogeneous meadow vegetation.

Since the critical variable in OFAN is the average productivity of the area utilized by an herbivore, even an abrupt border between a productive ecosystem and a totally barren one can be regarded as a productivity gradient if there is a grazer that spends time in both habitats. Exclosure experiments have recently been performed in a case of this type, the border between a subalpine meadow and talus at Gothic, Colorado (Huntly 1987). During the first years, all plants responded positively to the exclusion of vertebrate grazers (pikas). After a couple of years, however, tall herbs and woody plants started to take over, and the abundance of low herbs started to decline.

In spite of showing pronounced vegetational changes, the enclosure experiments discussed above did not demonstrate that arid grasslands and arctic-alpine tundras would change into radically different types of vegetation in the absence of grazers. Small grasses, herbs, and ericoids generally suffered, but taller and broader-leaved ones were favored. Thus, the vegetation within the enclosures was only a modification of the original plant community. This is indeed an inevitable outcome of the experimental designs and their relatively short durations. Even if some *Acacia* shrubs would be the potential dominants of the Serengeti enclosures and mountain birches were able to grow in the enclosures of Finnmarksvidda, it is very unlikely that their seedlings would spontaneously become established within a decade. Even if such an unlikely event occurred, the growth of shrubs and the consequent replacement of tallgrasses could require much time. In order to obtain more-profound changes, more-imaginative experimental designs (e.g., combinations of fencing and seeding or planting) should be used or a very long period should be available.

Fortunately, natural long-term grazer-exclusion experiments are available in arctic and arid climates. Two islands of the Norwegian Arctic, Jan Mayen and Björnöya, have been essentially free from grazing vertebrates and accessible to plants during several millennia. (Geese regularly visit Björnöya and are occasionally observed on Jan Mayen, and rock ptarmigans have been observed on Björnöya, but mammalian grazers are absent; see Bird and Bird 1935; Lövenskiöld 1964.) According to the available verbal descriptions and semi-quantitative data (Summerhayes and Elton 1923; Russell and Wellington 1940; Wilson 1952; Lid 1964; Engelskjön and Schweitzer 1970), the most wind-exposed parts of these islands are covered with various types of polar deserts with rosette and cushion plants. Sites that are somewhat more sheltered harbor copious moss banks, and the most favorable sites are dominated by broad-leaved herbs. Normal grass-sedge tundra vegetation is totally absent, although there are grassy patches in sites disturbed by birds and on sandy beaches. On volcanic Jan Mayen Island, with its steep topography, unstable soils, and consequently strong solifluction (Wilson 1952), typical arctic-alpine sedges (and horsetails) are widespread but not abundant (table 3; Lid 1964). On the geologically stable Björnöya, sedges are floristic rarities. Arctic grasses (*Dupontia fisherii* sensu lato; *Arctophila fulva*) are somewhat more widespread but play a negligible role in the vegetation (Engelskjön and Schweitzer 1970).

The moss banks of Jan Mayen and Björnöya islands represent a natural continuation of the trend observed in the enclosure experiments at Barrow. The herb meadows of more-favorable sites can be related to the snow-bed enclosures in Finnmarksvidda, where the greatest winners were the tallest herbaceous plants. Actually, the two trends manifest a single phenomenon: low graminoids give way to plants better adapted to monopolize space. In protected sites, elevated foliage is an optimal technical device for control over space, whereas on windy and chilly sites where trapping air warmed by direct solar radiation is overridingly important, cushion morphology is favored.

When islands are used as substitutes for long-term ecological experiments, ideally, two conditions should be satisfied. The islands should have controls in

TABLE 3

PERCENT COVER OF DIFFERENT PLANT TYPES IN FOUR HABITAT GROUPS OF JAN MAYEN'S VEGETATION

PLANT TYPE	VASCULAR COVER			
	INLAND			SEASHORE
	$\geq 70\%$	20%–69%	$< 20\%$	8%–66%
Characteristic species	<i>Oxyria digyna</i>	<i>Salix herbacea</i>	<i>Cerastium arcticum</i>	<i>Carex maritima</i>
Dwarf shrubs	3 ($\pm$ 4)	17 ($\pm$ 4)	+	+
Herbs				
Monolayer	60 ($\pm$ 11)	6 ($\pm$ 2)	3 ($\pm$ 1)	11 ($\pm$ 4)
Multilayer	+	+	+	+
Cushion	+	+	2 ($\pm$ 0.3)	+
Rosette	+	+	+	–
Graminoids				
Tall	2 ($\pm$ 2)	–	–	–
Rosette	+	+	+	–
Typical	+	8 ($\pm$ 4)	3 ($\pm$ 0.6)	21 ($\pm$ 10)
<i>Equisetum</i>	10 ($\pm$ 8)	+	–	+
Lower cryptogams				
Mosses	18 ($\pm$ 11)	45 ($\pm$ 6)	11 ($\pm$ 5)	+
Hepatics	+	3 ($\pm$ 3)	+	–
Lichens	+	4 ($\pm$ 1)	2 ($\pm$ 2)	+

NOTE.—Percentages were obtained by grouping Lid's (1964) material on the basis of the habitat (inland, shore) and total coverage by vascular plants. The method of calculation is explained in the Appendix. Coverages below 2% have been marked by +.

climatically similar areas with grazers. This is the case: Norwegian mountains are climatically similar to Jan Mayen, whereas Björnöya has close climatical counterparts in coastal arctic areas (Walter et al. 1975). There should also be evidence against the alternative interpretation that the vegetational peculiarities of the islands are attributable to floristic impoverishment, because propagules have failed to arrive. This condition is also satisfied. Representatives of arctic-alpine graminoids are present on both islands. Moreover, the most striking case of floristic impoverishment, the virtual absence of the sedge and cottongrass family from Björnöya, can hardly be attributed to geographic isolation, because distances to source areas are longer on Jan Mayen, where this family is much better represented. A more plausible assumption is that this floristic peculiarity is a consequence of high extinction rates of sedges and cottongrasses in the absence of grazing and profound physical disturbance.

The time scale of these natural experiments is ecological, not evolutionary. Except for minor qualitative changes (evolution of endemic, broad-leaved dandelions, also an apparently general increase in stature and leafiness of many herbs; see the drawings in Lid 1963, 1964), the plants are essentially a sample of the Atlantic-arctic flora, having coevolved with grazers over a long period and probably having acquired a large number of grazing-adapted features. In the time scale of a few million years, the plants should undergo radical changes as they become

adapted to the combination of cold climate and the absence of vertebrate grazers. In the herb fields, natural selection should favor taller plants with leaves elevated by erect shoots, petioles, or perennial stems. On sites that are colder or more exposed to the wind, where the advantages of trapping warm air by means of tightly packed shoots override the advantages of elevated foliage, the ultimate plant should be an extremely robust and tall cushion plant.

Subantarctic and antarctic islands and the mountains of New Zealand can be regarded as continuations of the Björnöya–Jan Mayen experiments in evolutionary time scale (New Zealand only in an imperfect way, because of the evolution of herbivorous birds). The available descriptions of the vegetation (Werth 1928; Mark 1955; Cockayne 1958; Billings and Mark 1961; Wace 1961; Walter 1968; Gimingham and Lewis Smith 1970; Bell 1973; Collins et al. 1975; Jenkin 1975; Lewis Smith and Walton 1975; Williams 1975) are in accordance with the evolutionary predictions in OFAN. On the mountains of New Zealand, woody vegetation often grades directly into communities dominated by robust cushion plants, without any alpine herb mats or graminoid swards in between. Where herb fields occur, the dominant plants have broad, roundish leaves elevated by tall petioles (e.g., *Stilbocarpa* spp.) or an erect, perennial, semiwoody stem (e.g., *Pringlea antiscorbutica*). Grasses prevail on sites disturbed by marine wildlife, salt spray, erosion, or fire. The morphology of these grasses is most unusual: huge perennial pedestals (1–2 m tall) from which robust leaves spread like the canopy of a palm tree. Moreover, the steppe areas of New Zealand with a temperate climate used to differ radically from their counterparts that supported grazing mammals. Before being burned by the Maori, the areas were mainly scrublands, with grasslands only in areas disturbed by shifting channels of streams. Even these were dominated by species with perennial pedestals (Connor 1965; Burrell 1975).

These natural evolutionary experiments can be criticized since they lack climatically equivalent controls, and floristic impoverishment cannot be ruled out a priori. However, the alternative explanations do not seem to match available empirical evidence. If the prevalence of weird types of plants depended on the failure of more-efficient competitors to arrive, the vegetation of the southern islands should be vulnerable to the introduction of exotics. As Cockayne (1958) pointed out, this is not the case. The native plants are vigorous competitors and aliens are successful only in areas strongly affected by introduced grazers. Troll (1960) and Walter (1968) attributed the vegetational peculiarities of the southern islands to their extremely maritime climate (Walter et al. 1975). This explanation leaves many unanswered questions. (Why should a climate with persistently chilly temperatures and frequent gale-force winds be favorable for tall and broad-leaved plants? If tall tussock morphology depends on maritime climate so much, why does the morphology occur in the dominating sedges of boreal creek-side marshes?) Moreover, the climatic explanation ignores the profound impact of introduced grazers on the vegetation of the southern islands.

The case of the Kerguelen archipelago is especially instructive. The German expedition provided detailed accounts of the vegetation at the turn of the century, only a few decades after the introduction of rabbits. The original dominants of lowland and upland sites (a rosette shrub, a giant cushion plant) had already been

eliminated from large parts of the main island, with only dead specimens, remnant stands, and the vegetation of adjacent rabbit-free islands testifying to their former prevalence (Werth 1928). The grazed sites were occupied by a trailing dicot, rather similar to the dominants of low-arctic maritime tundras of the Northern Hemisphere. After the introduction of reindeer, even this plant suffered and began to be replaced by alien rhizomatous grasses (Lesel and Derenne 1975; for corresponding data from South Georgia, see Leader-Williams et al. 1981; Vogel et al. 1984). Most of the current vegetation of the Kerguelen thus looks like the ordinary vegetation of tundra. A physiologically inclined plant ecologist, unaware of the history of the archipelago, would hardly have problems in interpreting the current vegetation as having been shaped by the adaptations of plants to the rigorous subantarctic climate.

The evidence reviewed above has some important gaps. The role of the absence of grazers on the islands could be tested more rigorously, for example, by introducing lemmings and root voles to Björnöya (to determine whether the island starts to resemble typical tundra areas if grazers are present) and by introducing subantarctic plants to Jan Mayen (to determine whether they can flourish in an arctic maritime climate in the absence of grazers). Studies in which grazer-exclosure experiments are complemented by seeding or planting would also be instructive. The available evidence is, however, supportive of OFAN, and it also demonstrates an essential difference between HSS and OFAN. HSS could have been used as an argument of plant ecologists for ignoring herbivorous animals and retaining plant ecology as a separate discipline. OFAN implied that the division of ecology to botanical and zoological branches is deeply unfortunate. Regardless of the trophic level in which one is primarily interested, due attention should be paid to interactions between populations on other trophic levels as well.

CONCLUSIONS

Proponents of the Odum school of systems ecology may have a case when they maintain that most evolutionary ecologists prefer not to think about ecosystems (Patten and Odum 1981). However, on the issue of how to think about ecosystems, good reasons exist for taking an approach that differs from theirs. In particular, trophic interactions need not become mutualistic in evolutionary time, and the presumed cybernetic constraints on ecosystem structure can be passed over lightly. The emergent properties of ecosystems can quite well arise by chance from unregulated Darwinian struggles between individual organisms and from interactions between populations ultimately deriving from such struggles. HSS managed to explain a great deal about the functioning of many ecosystems on the basis of this very assumption. OFAN removed the main shortcomings in HSS by considering what should follow from its assumption of exploitative trophic interactions in ecosystems with different primary productivities.

Indeed, the model in OFAN is not a final product but only one step in a Darwinian research program about ecosystem structure. The stability analysis in OFAN has already been revised by including seasonality (L. Oksanen, T. Oksanen, and N. Stenseth, MS). Moreover, the model provides no predictions about

the quality of plants and animals in ecosystems with different trophic dynamics and ignores the possibility of a feedback relationship between the intensity of grazing and the productivity experienced by grazers. I am currently working on these issues. These limitations in OFAN do not argue against the underlying Darwinian approach. Each specific hypothesis consists of fundamental assumptions, concerning general principles, and of technical assumptions, which are frequently no more than guesses (usually in the form of initially choosing the most simple of the possible alternatives). Problems are a natural part of science, and perhaps the most serious error of Hairston et al. was to present their ideas initially as facts to be believed, not as a process to be joined.

SUMMARY

The ecosystem theories of the Odum school are based on the premise that the observed order in ecosystems is unlikely to arise by chance from Darwinian struggles for existence. However, Hairston et al. (1960; HSS) showed, a quarter of a century ago, that such emergence of order from exploitative interactions, guided by short-term maximization of individual fitness, is not at all unlikely. The original HSS hypothesis conflicts with well-documented cases of resource limitation in herbivorous populations and with the recurring strong impacts exerted by these populations on the vegetation. However, this conflict is only apparent. HSS explained why the world is green and why there can be an abundance of forage that is not consumed. This observation does not refer to steppe and tundra environments, which are green for only a few weeks and where there is an obvious shortage of forage during the unfavorable season. The limitation of grazers by resource depletion in such environments and the strong impacts of herbivory on the vegetation are, in fact, straightforward consequences of the exploitation view in HSS, applied to relatively unproductive ecosystems. The same reasoning, applied to still more barren environments, predicts that these should be passively harsh (in the sense of White 1978), with grazers being limited by resource shortage but having only marginal impact on the vegetation. This extension of the logic in HSS, preliminarily proposed by Fretwell (1977) and formally analyzed later (Oksanen et al. 1981), creates predictions that are in good agreement with the results of competition experiments and grazer-exclosure experiments and with the aberrant vegetation of grazer-free islands in cold regions.

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APPENDIX

TREATMENT OF LID'S (1964) DATA ON THE VEGETATION OF JAN MAYEN

The data consist of records of abundances of plants on sample plots of 1 square meter, representing the sites of various plants of the island. No written descriptions accompany these tables, which usually consist of 5 to 10 plots per *synedria* (habitat of a given plant species). The data are presented on the Scandinavian five-class scale.

The data were roughly converted to linear coverage estimates (in accordance with Oksanen 1976) as follows: 5→71%; 4→36%, 3→18%, 2→9%. The open coverage class 1, including coverages from trace to 6%, was arbitrarily converted to 1%. (The low value was chosen to prevent the occurrence of a great number of species in trace amounts from inflating the coverage estimates for the plant group in question.) For each *synedria*, I calculated the mean coverages of all plants and thereafter summed up the coverages of the different plant types represented in table 3. (Plants were assigned to different morphological types on the basis of Lid's figures.) The data obtained for vegetation structure were divided into four groups according to the total coverage of vascular plants and whether the habitat of the plant under study was restricted to the physically disturbed seashore. Within each of these groups, I calculated weighted mean coverages for each plant group, the weighting factor being the number of records for the plant whose habitat was under study (counted from Lid's distributional maps). The name of the plant with the greatest number of records is presented in the row "Characteristic species."

"Dwarf shrubs" are, in practice, equivalent to the broad-leaved, trailing willow *Salix herbacea*. "Monolayer herbs" consist mainly of *Oxyria digyna* and of endemic broad-leaved dandelions. "Cushion herbs" also include relatively loose, tuft-forming species (e.g., *Cerastium arcticum*). "Tall graminoids" consist solely of *Calamagrostis neglecta*. "Rosette graminoids" are *Luzula* species.

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