COMMUNITY STRUCTURE, POPULATION CONTROL, AND COMPETITION

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The methods whereby natural populations are limited in size have been debated with vigor during three decades, particularly during the last few years (see papers by Nicholson, Birch, Andrewartha, Milne, Reynoldson, and Hutchinson, and ensuing discussions in the Cold Spring Harbor Symposium, 1957). Few ecologists will deny the importance of the subject, since the method of regulation of populations must be known before we can understand nature and predict its behavior. Although discussion of the subject has usually been confined to single species populations, it is equally important in situations where two or more species are involved.

The purpose of this note is to demonstrate a pattern of population control in many communities which derives easily from a series of general, widely accepted observations. The logic used is not easily refuted. Furthermore, the pattern reconciles conflicting interpretations by showing that populations in different trophic levels are expected to differ in their methods of control.

Our first observation is that the accumulation of fossil fuels occurs at a rate that is negligible when compared with the rate of energy fixation through photosynthesis in the biosphere. Apparent exceptions to this observation, such as bogs and ponds, are successional stages, in which the failure of decomposition hastens the termination of the stage. The rate of accumulation when compared with that of photosynthesis has also been shown to be negligible over geologic time (Hutchinson, 1948).

If virtually all of the energy fixed in photosynthesis does indeed flow through the biosphere, it must follow that all organisms taken together are limited by the amount of energy fixed. In particular, the decomposers as a group must be food-limited, since by definition they comprise the trophic level which degrades organic debris. There is no a priori reason why predators, behavior, physiological changes induced by high densities, etc., could not limit decomposer populations. In fact, some decomposer populations may be limited in such ways. If so, however, others must consume the "left-over" food, so that the group as a whole remains food limited; otherwise fossil fuel would accumulate rapidly.

Any population which is not resource-limited must, of course, be limited to a level *below* that set by its resources.

Our next three observations are interrelated. They apply primarily to terrestrial communities. The first of these is that cases of obvious depletion of green plants by herbivores are exceptions to the general picture, in which

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the plants are abundant and largely intact. Moreover, cases of obvious mass destruction by meteorological catastrophes are exceptional in most areas. Taken together, these two observations mean that producers are neither herbivore-limited nor catastrophe-limited, and must therefore be limited by their own exhaustion of a resource. In many areas, the limiting resource is obviously light, but in arid regions water may be the critical factor, and there are spectacular cases of limitation through the exhaustion of a critical mineral. The final observation in this group is that there are temporary exceptions to the general lack of depletion of green plants by herbivores. This occurs when herbivores are protected either by man or natural events, and it indicates that the herbivores are able to deplete the vegetation whenever they become numerous enough, as in the cases of the Kaibab deer herd, rodent plagues, and many insect outbreaks. It therefore follows that the usual condition is for populations of herbivores *not* to be limited by their food supply.

The vagaries of weather have been suggested as an adequate method of control for herbivore populations. The best factual clues related to this argument are to be found in the analysis of the exceptional cases where terrestrial herbivores have become numerous enough to deplete the vegetation. This often occurs with introduced rather than native species. It is most difficult to suppose that a species had been unable to adapt so as to escape control by the weather to which it was exposed, and at the same time by sheer chance to be able to escape this control from weather to which it had not been previously exposed. This assumption is especially difficult when mutual invasions by different herbivores between two countries may in both cases result in pests. Even more difficult to accept, however, is the implication regarding the native herbivores. The assumption that the hundreds or thousands of species native to a forest have failed to escape from control by the weather despite long exposure and much selection, when an invader is able to defoliate without this past history, implies that "pre-adaptation" is more likely than ordinary adaptation. This we cannot accept.

The remaining general method of herbivore control is predation (in its broadest sense, including parasitism, etc.). It is important to note that this hypothesis is not denied by the presence of introduced pests, since it is necessary only to suppose that either their natural predators have been left behind, or that while the herbivore is able to exist in the new climate, its enemies are not. There are, furthermore, numerous examples of the direct effect of predator removal. The history of the Kaibab deer is the best known example, although deer across the northern portions of the country are in repeated danger of winter starvation as a result of protection and predator removal. Several rodent plagues have been attributed to the local destruction of predators. More recently, the extensive spraying of forests to kill caterpillars has resulted in outbreaks of scale insects. The latter are protected from the spray, while their beetle predators and other insect enemies are not.

Thus, although rigorous proof that herbivores are generally controlled by predation is lacking, supporting evidence is available, and the alternate hypothesis of control by weather leads to false or untenable implications.

The foregoing conclusion has an important implication in the mechanism of control of the predator populations. The predators and parasites, in controlling the populations of herbivores, must thereby limit their own resources, and as a group they must be food-limited. Although the populations of some carnivores are obviously limited by territoriality, this kind of internal check cannot operate for all carnivores taken together. If it did, the herbivores would normally expand to the point of depletion of the vegetation, as they do in the absence of their normal predators and parasites.

There thus exists either direct proof or a great preponderance of factual evidence that in terrestrial communities decomposers, producers, and predators, as whole trophic levels, are resource-limited in the classical density-dependent fashion. Each of these three can and does expand toward the limit of the appropriate resource. We may now examine the reasons why this is a frequent situation in nature.

Whatever the resource for which a set of terrestrial plant species compete, the competition ultimately expresses itself as competition for space. A community in which this space is frequently emptied through depletion by herbivores would run the continual risk of replacement by another assemblage of species in which the herbivores are held down in numbers by predation below the level at which they damage the vegetation. That space once held by a group of terrestrial plant species is not readily given up is shown by the cases where relict stands exist under climates no longer suitable for their return following deliberate or accidental destruction. Hence, the community in which herbivores are held down in numbers, and in which the producers are resource-limited will be the most persistent. The development of this pattern is less likely where high producer mortalities are inevitable. In lakes, for example, algal populations are prone to crash whether grazed or not. In the same environment, grazing depletion is much more common than in communities where the major producers are rooted plants.

A second general conclusion follows from the resource limitation of the species of three trophic levels. This conclusion is that if more than one species exists in one of these levels, they may avoid competition only if each species is limited by factors completely unutilized by any of the other species. It is a fact, of course, that many species occupy each level in most communities. It is also a fact that they are not sufficiently segregated in their needs to escape competition. Although isolated cases of non-overlap have been described, this has never been observed for an entire assemblage. Therefore, interspecific competition for resources exists among producers, among carnivores, and among decomposers.

It is satisfying to note the number of observations that fall into line with the foregoing deductions. Interspecific competition is a powerful selective force, and we should expect to find evidence of its operation. Moreover, the evidence should be most conclusive in trophic levels where it is neces-

sarily present. Among decomposers we find the most obvious specific mechanisms for reducing populations of competitors. The abundance of antibiotic substances attests to the frequency with which these mechanisms have been developed in the trophic level in which interspecific competition is inevitable. The producer species are the next most likely to reveal evidence of competition, and here we find such phenomena as crowding, shading, and vegetational zonation.

Among the carnivores, however, obvious adaptations for interspecific competition are less common. Active competition in the form of mutual habitat-exclusion has been noted in the cases of flatworms (Beauchamp and Ullyott, 1932) and salamanders (Hairston, 1951). The commonest situation takes the form of niche diversification as the result of interspecific competition. This has been noted in birds (Lack, 1945; MacArthur, 1958), salamanders (Hairston, 1949), and other groups of carnivores. Quite likely, host specificity in parasites and parasitoid insects is at least partly due to the influence of interspecific competition.

Of equal significance is the frequent occurrence among herbivores of apparent exceptions to the influence of density-dependent factors. The grasshoppers described by Birch (1957) and the thrips described by Davidson and Andrewartha (1948) are well known examples. Moreover, it is among herbivores that we find cited examples of coexistence without evidence of competition for resources, such as the leafhoppers reported by Ross (1957), and the psocids described by Broadhead (1958). It should be pointed out that in these latter cases coexistence applies primarily to an identity of food and place, and other aspects of the niches of these organisms are not known to be identical.

SUMMARY

In summary, then, our general conclusions are: (1) Populations of producers, carnivores, and decomposers are limited by their respective resources in the classical density-dependent fashion. (2) Interspecific competition must necessarily exist among the members of each of these three trophic levels. (3) Herbivores are seldom food-limited, appear most often to be predator-limited, and therefore are not likely to compete for common resources.

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