

# THE ROLE OF DIVERSITY IN THE ENERGETICS OF PLANT COMMUNITIES<sup>1</sup>

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## ABSTRACT

Community organization, which is determined in an environmental matrix that varies in space, time, and resource quality, is an important determinant of fitnesses of constituent populations. In addition, the fitnesses of individual populations are important determinants of community properties. Changes in species richness and equitability during plant succession indicate that comparative fitnesses of co-occurring populations, as measured by their abilities to contribute to energy flow, become more similar as succession proceeds. The rate of species invasion diminishes with greater diversity, and a smaller proportion of the flora is subject to extinction in a given time period. Community diversity, population fitness, environmental heterogeneity, and population and community stability are members of a complex feedback loop which couples each to the others.

The theme of this symposium is "Energetics and Fitness", therefore much of the emphasis is upon the energetic properties of individuals which influence their ability to contribute genes to the next generation. To the extent that energy constitutes a limiting resource, or reflects the ability of an individual to utilize other limiting resources, the ability of a genotype to contribute offspring to the next generation must be influenced by its ability to exploit energy sources. Fitness, of course, is not determined in a uniform resource field, but in a system of resources which vary in space, time, and quality. In addition, fitness is not expressed in a biological vacuum, but is influenced by interactions among organisms at the same, and at different trophic levels. Fitness may, for instance, be determined by the extent to which a parental tree facilitates the escape of its offspring from predators, either in space or in time (Janzen 1967, 1969, 1970).

Successional communities, in which there is sequential replacement of certain populations by others, reflect time-dependent changes in the relative fitnesses of different populations on a given site. Certain species appear on a site, persist for a time, and then are replaced by populations of other species. Since there often are orderly and predictable patterns of species replacements on similar sites, fitnesses of invading populations are determined to a significant extent by the effect that resident populations have upon site properties influencing the invasion potential of subsequent occupants.

My objective is to examine the energetic properties of populations in complex mixtures of co-occurring species in ecological communities, to gain insight into the fitness of populations when they are a part of a complex community. The contribution of a population to community energy flow can be taken as an index of the relative fitness of populations in a community and I will use fitness in this rather restricted way. Specifically, I address three principal questions: 1. What are patterns of energy partitioning among populations in communities where the colonization process is modifying community diversity? 2. What mechanisms produce the patterns of energy partitioning? 3. Why have such mechanisms evolved? All of the data presented are from studies of old field succession in upstate New York where population abundances were estimated from net above-ground productivities measured by the short-term harvest method (Odum, 1960), and so represent energetic comparisons of populations. More complete data on successional trends are given elsewhere (Hurd *et al.*, 1971, Mellinger and McNaughton, in press) because my principal objective is to examine energy partitioning among populations in the context of "Energetics and Fitness."

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*Energetics, Diversity, and Resource Partitioning.* On the old field communities studied, above-ground net primary productivity was constant with time, except for a slight decline from the 5- to 6-year-old communities (table 1). At the same

TABLE 1  
*Patterns of change in net energy flow (total above-ground net primary productivity) and its partitioning among plant populations during old field succession in upstate New York.*

Field age (yrs.)	Net prod. (g/m <sup>2</sup> /day)	Diversity (H')	Richness (S)	Equitability (J)
5	11.174	1.909	22.0	0.619
6	9.37	2.001	20.8	0.660
16	7.82	2.406	31.0	0.700
17	7.64	2.722	31.0	0.793
36	9.18	2.817	39.8	0.766
F <sub>1,21</sub>	3.881	61.246	119.356	16.622
P	<0.10	<0.005	<0.005	<0.005

time, diversity ( $H' = -\sum p_i \log p_i$ ) of the communities increased consistently with succession. This diversity increase (Shannon and Weaver, 1949; MacArthur, 1955) was a consequence both of increasing numbers of species in the community(s), and increasing equitability ( $J = H'/\ln S$ ) of energy flow among populations (table 1). Several things are obvious about the relative abilities of different plant species to obtain resources in these ecosystems. First, the total energy flow through the plant community was constant, averaging about 9 g/m<sup>2</sup>/day over the growing season. Second, diversity increased consistently over the successional period considered. Third, the increase in diversity was a consequence both of increasing numbers of species, and of more even division of energy flow among the species. Therefore, the relative abilities of species to obtain resources became more similar as succession proceeded, and the number of different populations exploiting the resource pool increased.

We gain some insight into the dynamics of species diversity on these fields by applying MacArthur and Wilson's (1963, 1967) colonization model. They pointed out that the number of species present in an ecosystem at any one time is a consequence of the integration of immigration ( $I$ ) and extinction ( $E$ ) rates, such that

$$S_t = \int_0^t (I - E) dt$$

where immigration and extinction rates are integrated over time  $dt$ . According to their model, the difference between immigration and extinction rates should decline exponentially with time until balanced and a steady state of species richness is approached. Such a pattern did hold on the old fields (fig. 1), with a sig-

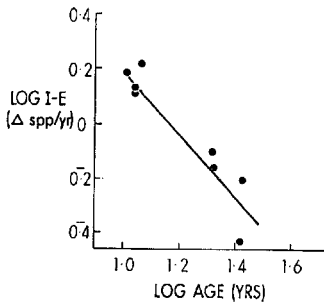


FIGURE 1. Decline of the species colonization rate as successional fields in upstate New York aged.  $I$  is the immigration rate, and  $E$  is the extinction rate.

nificant ( $r = -0.933$ ,  $df = 6$ ,  $P < 0.001$ ) inverse relationship between colonization rate and successional age. An examination of the relationship of colonization rate to its two components, immigration and extinction, revealed that they did not contribute equally to the observed pattern. While there was a significant positive relationship between immigration and colonization rates ( $r = 0.922$ ,  $d.f. = 6$ ,  $P < 0.01$ ), there was no significant relationship between extinction and colonization rates ( $r = -0.186$ ,  $d.f. = 6$ ,  $P = n.s.$ ), with extinction rate averaging  $0.4 \pm 0.16$  (0.95 confidence interval) species per year. This indicates that the primary factor controlling species diversity on the old fields was the immigration potential of the site, rather than the extinction process. Similar results, indicating a control of richness by immigration rate, were obtained in studies of protozoan succession (Cairns *et al.*, 1969).

If diversity of communities is controlled by the ability of new species to invade, what controls invasion potential? This problem is essentially resource partitioning on a site, which is increasingly fine and equitable through succession, as indicated by richness and equitability in the plant communities. Ability of a species to invade must depend upon its ability to obtain resources at a given time and place with a greater competitive efficiency than the present occupant being displaced. Since species extinction was not an important contributor to increasing diversity on these fields, it seems likely that there was only partial rather than complete displacement of resident species from the portion of the resource pool they previously exploited. Such a partial displacement would, of course, account for the increase in equitability that accompanies invasion.

One of the most thoroughly studied systems of co-occurring species from the standpoint of mechanisms of resource partitioning is the grazing unguulate community of Eastern Africa. These studies reveal that co-occurrence is a nominal characteristic only, with the species partitioning resources in space, time and quality (Vesey-Fitzgerald, 1960; Lamprey, 1963; Bell, 1969). The extensive migrations of animal populations, both on a seasonal and on a more restricted temporal basis, tend to divide renewable resources in time, with different herbivore species utilizing the same plant species at different times in the same place. Similarly, different herbivore populations occupying the same place simultaneously tend to have different preferred plant species (Stewart and Stewart, 1971), or take different portions of the same species (Gwynne and Bell, 1968). This leads to evolution of digestive patterns to optimize resource yield from the forage-type exploited (Bell, 1971). Similar evidence of resource partitioning in space, time, and kind of food taken concerns co-occurring bird populations (MacArthur, 1958; Root, 1967).

Studies of coexistence in animal populations suggest that co-occurrence of species populations is a consequence of coevolution among the populations, resulting in resource specializations which restrict niche overlap. We may ask whether similar mechanisms of resource partitioning apply to the successional plant communities. To approach this problem, the proportion of the total flora ubiquitous in space, or with a seasonal temporal frequency greater than 80% was examined in the successional communities. If mechanisms of resource partitioning in space and time documented for co-occurring animal populations also apply to these plant communities, there should have been a decline in spatial and temporal frequency of species as succession proceeded and diversity increased. Such patterns were observed (table 2), and data reveal that more species were restricted in space, and in seasonal time, as succession proceeded and diversity increased. Increasing diversity in these communities is coupled with increasing specialization among the co-occurring populations, with species more and more restricted in the space and time matrix which they exploit. These patterns suggest that fitness is expressed in a contracting framework of space and time as diversity increases. Similarly we may deduce from studies of soil nitrogen partitioning between nitrate and ammonium ions that as succession proceeds (Rice

TABLE 2

*Proportion of the total flora that was ubiquitous in space or had a temporal frequency over the growing season of greater than 80% in successional communities of different ages.*

Field age (yrs.)	Resource partitioning	
	spatial	seasonal
5	0.325	0.556
6	0.386	0.531
16	0.291	0.356
17	0.360	0.518
36	0.280	0.432
F <sub>1,21</sub>	8.863	9.278
P	<0.01	<0.01

and Pancholy, 1972), there may be resource partitioning through the exploitation of different resource states in plants just as in animal populations.

MacArthur and coworkers (1964, 1965) examined the possible similarity of co-occurring species and concluded that this limiting similarity may be influenced by specialization and by resource thresholds, supply, utilization ability, and temporal variability. To the extent that different populations "co-occur" through spatial resource partitioning, we can add spatial variability of resources to the list. Since both richness and equitability increase through the successional sequence studied, with constant total energy flow, invasion may be accompanied by convergence of resource flow and fitness among all populations, or there may be preferential displacement of dominant species. We can gain additional insight into the mechanisms of niche partitioning in these communities by examining productivities of dominant and rare species, since these represent extremes of the resource flow spectrum. Such an examination revealed a constant lower limit of resource flow over the period studied, while ability of dominant species to obtain resources diminished as diversity increased (table 3). This indicates that the lower threshold of fitness in these communities is remarkably constant, probably representing a minimum population size that can be maintained. Invasion occurs

TABLE 3

*Patterns of change in productivity of the most abundant and least abundant species during old field succession.*

Field age (yrs.)	Net productivity (g/m <sup>2</sup> /day)	
	Dominant species	Rarest species
5	4.28	0.16
6	3.20	.003
16	2.05	.003
17	1.30	.004
36	1.92	.005
F <sub>1,21</sub>	29.485	0.712
P	<0.005	n.s.

through preferential displacement of dominant species from the portion of resources they occupied in earlier and less diverse stages. It seems that invasion depends upon invading species finding "resource holes" in the ecosystem to exploit more efficiently than present occupants (MacArthur and Levins, 1964; MacArthur, 1965). Decline in productivity of dominants, while the lower productivity limit remains constant, indicates that resource holes are more available in the resource matrices exploited by dominants than in those exploited by rare species. Generalist species were replaced by specialists as succession proceeded, which was further supported by increasing temporal and spatial restrictions of populations as diversity increased.

*Diversity, Fitness and Energy Flow.* Several patterns have been revealed by our data analyses. First, energy flow was partitioned among more species, and more equitably among the species present, as succession proceeded on the old fields. Second, the diversity increase was primarily a result of species immigration which restricted resource flow into more abundant species in the community. Third, temporal and spatial specialization of resource demand within invading species were important mechanisms of invasion and resource partitioning. The basic assumption of a discussion of "Energetics and Fitness", which several symposium participants have challenged and examined, is that fitness may be dependent upon energetic efficiency. Rather than questioning this basic assumption, I have modified it in the preceding discussion by assuming that although energy may not be the principal factor limiting fitness, it still can be used as an index of the ability to obtain resources and, thereby, may reflect fitness. It is apparent that the average ability of a population to obtain resources declined on fields as diversity increased and, in fact (fig. 2), there was a significant negative

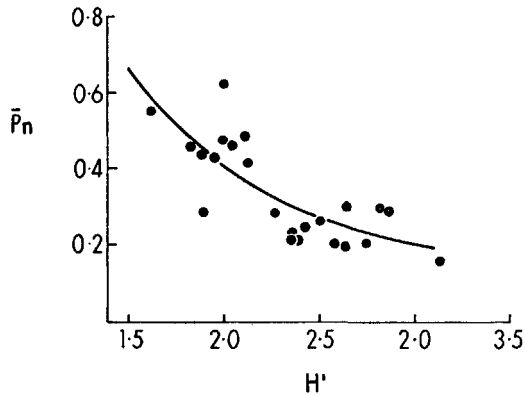


FIGURE 2. Inverse relationship between the average productivity of a species ( $\bar{P}_n$ ) and diversity ( $H'$ ).

relationship ( $r = -0.825$ ,  $p < 0.001$   $df = 21$ ) between mean productivity of populations and diversity, such that

$$\bar{P}_n = 1.319H'^{-1.705}$$

where  $\bar{P}_n$  is average net above-ground productivity per species. Insofar as net productivity of a population is an index of fitness, average fitness declined with diversity. There is direct evidence that net productivity of a population influenced fitness on these fields, since net productivities of species which became extinct were far below the mean. The mean net productivities of species which became

extinct were  $0.0342 \pm 0.005$  g/m<sup>2</sup>/day, a percentage of  $5.2 \pm 2.2$  of the mean productivity. Species with low fitness on the fields which went extinct, were species whose populations sustained an energy flow far below that of the average population.

There seem to be some basic contradictions apparent at this point. While the average energy flow through a population declined with succession, populations with low energy flow were more likely to go extinct on the site. The colonization data indicated that colonization probability declined with diversity and extinction probability was constant. Part of the explanation for this, I believe, is the increase in equitability of energy flow among populations as diversity increased. Since there is preferential invasion of the resources exploited by dominant species, the lower limit of resource availability remains relatively constant. With increasing equitability of resource flow, the proportion of the total species pool near the extinction threshold declines as diversity increases. Over the period studied, extinction rate declined from 1.40% of the flora per year in the 5-6-year-old field to 0.91%/yr in the 16-17-year-old field, for a significant ( $t=4.202$ ,  $P<0.05$ ,  $df=3$ ) decline in the proportional extinction rate. Therefore, increasing equitability, associated with invasion of resources exploited by the major species, resulted in a proportional increase in fitness among constituent populations.

In an experiment designed to determine the relationship between community diversity and stability of ecosystem function, an inorganic fertilizer (10-10-10, N-P-K) was applied to 6- and 17-year-old fields at a rate of 560 kg/ha (Hurd *et al.*, 1971). This experiment revealed that the 6-year-old community was much less stable than the 17-year-old community. Average energy flow per species on control sections was 0.453 g/m<sup>2</sup>/day on the young field and 0.325 g/m<sup>2</sup>/day on the old field, for no significant difference ( $F_{1,7}=2.263$ ). In fertilized sections, however, mean net productivity per species was 0.710 g/m<sup>2</sup>/day in the young field and 0.295 g/m<sup>2</sup>/day in the older field, for a significant difference ( $F_{1,7}=10.160$ ,  $P<0.025$ ). So, there was a significant interaction between field age and, hence, diversity: the younger and less diverse field was less stable to the experimental perturbation ( $F_{1,12}=16.401$ ,  $P=0.005$ ). No experimental effect on mean population productivity could be detected in the older and more diverse field ( $F_{1,7}=1.297$ ,  $P=n. s.$ ).

Although this experiment represents a positive perturbation, increasing energy flow to the populations, I think it can serve as a model for interpreting the increasing proportional protection of populations from extinction as diversity increased. There is a residue of populations in all communities near the extinction level as a consequence of low resource flow. Although the actual number of species in this pool does not change as diversity increases, the bulk of the species pool, as a result of increased equitability of resource flow is increasingly remote from this extinction threshold. The perturbation experiment revealed that populations in the less diverse community are more subject to resource flow modification as a result of modification of environmental characteristics. I assume that negative perturbations, which would tend to diminish resource flow, would be similarly stabilized by diversity. This stabilization undoubtedly arises as a result of increased specialization of resource exploitation modes, so that no species has a significant competitive advantage through dominating resource flow. This stabilization of community energy flow characteristics would tend to protect species from extinction, because environmental fluctuations would be less likely to increase the competitive ability of some species at the expense of others.

*Factors Driving Community Diversity.* The increases in diversity and equitability during succession indicate that comparative fitnesses of co-occurring populations, measured by their ability to contribute to resource flow, become more similar as more species invade the community. In addition, the rate at

which species invade also diminishes with greater diversity, and a smaller proportion of the flora is subject to extinction in a given time period. The principal mechanism of the increase in diversity is subdivision, by invading species which specialize in space and in time, of the resources utilized by dominant species. A cause for these patterns can be constructed from the literature on plant-environment relations.

It is known from community studies that modifications in soil properties are important components of successional trends (Keever, 1950; Crocker and Major, 1955). In addition, individual plants generate gradients of soil properties in their vicinities (Zinke, 1962). This production of resource gradients, and the resulting environmental heterogeneity, is probably a principal cause of increased diversity during succession (McNaughton and Wolf, 1973). The niches of co-occurring plant species can be defined by species distributions in relation to soil properties (Rogers and King, 1972). Therefore, colonization of a site results in an increasingly complex gradient of soil properties on a site. Superimposed on nutrient gradients are gradients of allelopathic chemicals (Wilson and Rice, 1968). Such increases in environmental heterogeneity will result in the creation of loci where individuals of invading species may become established and subdivide the niches of previous occupants, increasing equitability as richness increases. The more abundant species appear to be more vulnerable to displacement by this invasion process, indicating that there is a consistent replacement of species that exploit resources widely in space and time by species which are restricted in space and time.

Restriction of the resource exploitation pattern in space and time results in protection of the plant species from attack by herbivores. Root (1973), for instance, has shown that species in monoculture are more subject to herbivore attack by insects than those in more complex species mixtures. And, in an elegant investigation of the mechanisms of this protection, Tahvanainen and Root (1972) showed that olfactory cues to insects from host plants may be confounded by similar cues from non-host plant populations, providing protection directly attributable to growing in a complex species mixture.

The resistance of more complex species mixtures to disruption by environmental perturbations, documented here by the insensitivity of the more diverse community to nutrient perturbation, may provide a further increase in fitness among members of complex species mixture. Stabilization of energy flow patterns by increasing specialization will reduce the ability of co-occurring populations to affect each other's fitnesses through competitive restriction of resource flow. The regular patterns of species combination that occur in successional communities on similar sites indicate that coevolution of resource exploitation strategies is a fundamental component of species co-occurrence.

At this point, it seems important to indicate that I am not arguing for communities as super-organisms. Rather, I am arguing that community organization, in an environmental matrix that varies in space, time, and quality, is an important determinant of fitnesses of constituent populations. In addition, the fitnesses of individual populations determine community properties. Most science tends to deal with linear systems of cause and effect, where B is a result of A and a cause of C. In ecology such linear systems are rare enough to cause considerable frustration, if we attempt to model the ecosystems in such terms. Community diversity, population fitness, environmental heterogeneity, and population and community stability are members of a complex feedback loop which couples each to the other. Populations invading an ecosystem modify population fitness and community organization. It is impossible to disentangle cause and effect in such systems, but we can hope to trace functional interconnections to provide some insight into the interconnections among colonization, population fitness, and community organization.

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