

References and Notes

1. Work up to the end of the 1969 field season is summarized by R. E. Leakey, A. K. Behrensmeyer, F. J. Fitch, J. A. Miller, and M. D. Leakey [*Nature* 226, 223 (1970)].
2. Under the leadership of R. E. Leakey, expeditions have undertaken exploration and research over three field seasons (1968-1970). This has been done with the permission and cooperation of the Kenya Government and the trustees of the National Museum of Kenya. The National Geographic Society of Washington, D.C., has generously provided funds to cover the basic costs of the operation. A grant from the Wenner Gren Foundation, New York, made participation by G.L.I. possible. N. A. Mudoga, who was kindly seconded by the Kenya Government, J. Barthelme, who was supported by a training grant from the Ford Foundation, and P. A. Robins, assisted with survey and the supervision of excavations. Mrs. A. B. Isaac drew Figs. 2 and 3. Dr. M. D. Leakey gave advice in the field. K. Kimeu, M. Mangoka, and J. Kimengech were excavation foremen.
3. For information on hominid fossils, paleontology, and stratigraphy for the 1970 season, see R. E. F. Leakey, C. F. Vondra, G. Johnson, A. K. Behrensmeyer, B. E. Bowen, V. Maglio, *Nature* 231, 241 (1971).
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Stability and Diversity at Three Trophic Levels in Terrestrial Successional Ecosystems

Abstract. *An ecosystem perturbation experiment in which inorganic fertilizer was added to two successional old fields of different ages indicated that stability, expressed as resistance to modification by enrichment, increased during succession only at the primary trophic level. The perturbation was propagated throughout the arthropod herbivores and carnivores. Both herbivores and carnivores were less stable in the older field. In contrast to current ecological theory, greater diversity at a trophic level was accompanied by lower stability at the next higher level.*

Ecosystem stability and its relationship to other ecosystem properties are among the most widely discussed ecological concepts (1). The origin of this discussion can be traced at least to MacArthur's (2) assertion that food-web diversity should stabilize a community by providing alternate channels for energy flow. Definitions of stability have ranged from convergent points in an n -dimensional field (3) to turnover time, the ratio of biomass to net productivity (4). We here use a definition derived from thermodynamics: stability is the ability of a system to maintain or return to its ground state after an external perturbation (5). The degree of stability is characterized by (i) the amplitude of the deflection from the ground state, (ii) the rapidity of response to the perturbation, and (iii) the rate at which any deflection is damped. We report here experiments designed to determine the stability of net productivity and species richness of successional abandoned hayfields after an experimental nutrient input to the

primary producers. We believe this is the first experimental treatment of current ideas that relate stability to diversity and ecosystem age (6).

We studied two adjacent abandoned hayfields in central New York, one 1.15 hectares (2.84 acres) and the other 1.11 hectares (2.75 acres), which had not been agriculturally employed for 7 and 16 years, respectively. Microclimate and soil series are identical (7). Each field was divided into two control and two treatment plots. A 10-10-10 (N, P, K) pebble fertilizer was applied to the treatment plots with a commercial lawn spreader at a rate of 560 kg/ha (555 lb/acre) on 1 May 1970 (8). Since enrichment has a destabilizing effect upon competitive systems (9), this would seem to be a particularly efficacious test of the relationship between stability and other ecosystem properties.

Producers were sampled monthly by the harvest method (10) from two quadrants (1.0 × 0.5 m) per plot randomized on a grid system (11). Sam-

ples were dried at 90°C for 20 hours and weighed. Producer biomass increased linearly with time to peak biomass in September. The best fit regression lines were determined by least squares (12), and net productivity, exclusive of herbivore consumption, was expressed in grams per square meter per day from the slopes of these lines. Species diversity for the producers and consumers was assessed as the number of species recorded at peak biomass (13). Arthropod consumers were sampled at regular intervals with a power vacuum sampler covering a 0.093-m² (1-square-foot) circular area (14). These sample positions were also randomized on the grid system. Samples were dried at 70°C for 48 hours and weighed. There were two arthropod biomass peaks, one in late May and the other in late July or early August. Net productivity of the arthropod herbivores and carnivores, in milligrams per square meter per day, was determined by summing the positive slopes of the biomass curves.

Net producer productivity in both control and treatment plots was significantly greater in the young field (7 years from last cultivation) than in the old field (16 years from last cultivation) (Table 1). Producer productivity was significantly greater in treatment plots than in control plots, in both fields. There was a significant interaction between age of the field and response to treatment. Simple effects analysis (15) indicated that the old field ($F_{1,12} = 307.4$, $P < .01$) responded less than the young field ($F_{1,12} = 1610.0$, $P < .01$). Although the number of species was significantly greater on the old field, there was no diversity response to fertilization. It might be argued that one growing season is insufficient time for additional plant species to invade. Catastrophic perturbations which open multiple niches, however, are followed by rapid appearance of several previously absent species over periods of just a few weeks (16), and it is well known that soils typically contain a reservoir of viable seeds of many species that do not occur in the community itself (17).

Arthropod consumers responded to the perturbation somewhat differently than the producers did. Herbivore productivity at the first biomass peak was significantly greater in the fertilized plots (Table 1). However, simple effects analysis indicated that nutrient

input to the producer level affected herbivore productivity in the old field significantly more ($F_{1,76} = 117.3$, $P < .01$) than in the young field ($F_{1,76} = 8.1$, $P < .01$). In agreement with the plants, the first peak herbivore diversity was greater in the old field. In addition, however, species diversity was greater in the treatment plots, and the magnitude of the diversity increase was greater in the old field ($F_{1,76} = 50.5$, $P < .01$) than in the young field ($F_{1,76} = 9.4$, $P < .01$). In the control plots, the young field herbivore productivity at the first peak was greater, but species diversity was less, indicating higher productivity per species in the young field.

Herbivore productivity response at the second peak was similar to the first peak (Table 1). Simple effects analysis indicated that the major treatment effect was contributed again by the old field ($F_{1,76} = 298.1$, $P < .01$), not the young field ($F_{1,76} = 1.6$, $P > .10$). While herbivore diversity at the second peak increased in the control plots with successional age, it decreased on the treatment plots with age. Simple effects analysis indicated a significant increase in species diversity in the treatment part of the young field ($F_{1,76} = 35.1$, $P < .01$) but no significant difference between treatment and control plots in the old field ($F_{1,76} = 2.0$, $P > .10$). Herbivore productivity per species decreased seasonally in the control and treatment plots in the young field, while in the old field herbivore productivity per species decreased in the control and increased in the treatment plots.

Carnivore productivity at the first peak (Table 1) was enhanced more in the old field ($F_{1,76} = 7.3$, $P < .01$) than in the young field ($F_{1,76} = 0.2$, $P > .10$). Fertilizer treatment increased species diversity in both fields. Productivity per species in the young field decreased with treatment but increased slightly with treatment in the old field. There were no significant treatment or age differences in carnivore productivity at the late season peak (Table 1). Species diversity was greater in the old field, but there was no treatment effect upon late season carnivore diversity.

Current theory (6) states that stability and diversity increase while productivity decreases during succession. Our results support this theory completely only at the producer trophic level. For the producers the old field is more diverse, less productive, and more stable than the young field. Since producer

Table 1. Net productivity and diversity in control and treatment plots of two successional fields. Values are means in each case. Net productivity for the producers is in grams per square meter per day, and for the herbivores and carnivores, in milligrams per square meter per day. Diversity for the producers is number of species per 0.5-m² area; for the herbivores and carnivores, per 0.093-m² area. F values were derived from a 2×2 factorial design analysis of variance. F_A , age effect; F_T , treatment effect; F_{AT} , interaction effect. Producer F values were with 1,12 degrees of freedom; herbivore and carnivore F values were with 1,76 degrees of freedom.

	Producers		Herbivores				Carnivores			
			Early		Late		Early		Late	
	6- year field	17- year field	6- year field	17- year field	6- year field	17- year field	6- year field	17- year field	6- year field	17- year field
	<i>Net productivity</i>									
Control	4.46	2.68	6.06	3.56	4.17	3.77	4.75	2.43	1.61	1.01
Treatment	8.76	4.56	7.92	10.71	4.77	11.85	4.45	5.05	1.17	1.36
F_A	1549.7*		0.2		100.9*		3.6		0.6	
F_T	1662.0*		93.6*		172.0*		6.8†		0.0	
F_{AT}	255.2*		31.8*		127.8*		10.6*		2.4	
<i>Diversity</i>										
Control	10.25	17.50	3.40	3.65	3.35	4.95	1.85	1.75	1.50	2.50
Treatment	9.50	18.00	4.20	5.50	5.45	4.45	2.35	3.05	1.30	2.05
F_A	46.0*		17.7*		1.4		3.4		17.3*	
F_T	0.0		51.8*		10.2*		31.0*		0.4	
F_{AT}	0.3		8.1*		26.9*		6.1†		0.4	

* $P < .01$. † $P < .05$.

diversity does not increase upon perturbation and productivity does, additional productivity is not a result of adding more plant species. In fact, in successional time, net productivity within both control and treatment plots is an inverse function of species richness at the producer level. Patten's (18) studies of plankton populations indicated that environmental effects were damped temporally in the plankton. Our studies indicate that this damping property of the ecosystem's biotic component increases with successional time. The average fertilizer stimulation of net primary productivity was 97 percent in the 7-year-old field and 71 percent in the 16-year-old field ($t = 4.17$; $P < .01$; d.f. = 6).

Productivity of both herbivores and carnivores in the control plots declined with successional time. Consumer diversity increased in the control plots with successional time except for the first carnivore peak. Both of these observations also support current successional theory.

The primary departure from current theory is that stability decreased with successional time, and with species diversity, at the consumer trophic levels. This is particularly apparent at the herbivore level. Old field herbivore populations were much more responsive, either proportionately or absolutely, to the experimental treatment than young field populations at both biomass peaks. Since the species composition is

mainly annual arthropods, it seems likely that reduced mortality, rather than increased fecundity, generated the effect. In addition, there may have been immigration in response to the increased food supply. The ability of the fertilizer to enhance herbivore productivity contradicts the hypothesis of Hairston *et al.* (19) and the data of Pulliam *et al.* (20), both indicating that herbivores are not food limited. In fact, only a relatively small proportion of total plant biomass actually may be available to the herbivores (21), so that enhancement of producer productivity may have a substantial effect in increasing the amount of food available to the consumers.

Similarly, the carnivores were much less stable in the old field during the first biomass peak. However, the perturbation effect was seasonally damped in this trophic level, and there was little response during the second biomass peak.

An important property of ecosystem succession is the attenuation, with time, of ecosystem output, that is, net productivity. This attenuation occurs at all three trophic levels in the fields we examined. It is clear, however, that this attenuation is accompanied by increased stability only at the producer level. Although arthropod consumer productivity declines with successional age, the disruptive effect of the perturbation increases with age. Perturbation effects are undoubtedly a func-

tion of the kind of perturbation employed and the species composition of the communities affected (22). The most responsive species will be those specialized for, and limited by, the niche parameters influenced by the environmental modification (13). Species with different critical niche dimensions will be affected less by the same modification.

Although MacArthur (2) argued that stability of a population should increase as the number of food species available to it increases, our results suggest that increased diversity at the plant and herbivore levels generates decreasing stability at the next higher trophic level. This is similar to Watt's (23) results from examining herbivorous insects. In our experiment, the only reasonable explanation of the lower stability in the old field consumers appears to be the possibility that fertilization preferentially enriched palatable food classes at the primary level. Documentation of such an enrichment would require careful determination of food preferences at the herbivore level, and the availability of these food classes within the plant communities.

The third aspect of stability, the long-term damping effect, is not reported here because such evidence will require several years to obtain and, at any rate, will not affect the interpretation of the first two components of the stability definition.

L. E. HURD, M. V. MELLINGER
L. L. WOLF, S. J. MCNAUGHTON
*Department of Biology,
Syracuse University,
Syracuse, New York 13210*

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pontine tegmentum not previously identified as components of the central taste pathway. The cells in this pontine taste area project to the thalamus, providing the basis for the thalamic and cortical representation of gustatory sensibility. In addition, this pontine taste area is potentially the first link in a polysynaptic pathway through which gustatory information could reach the limbic system areas associated with feeding and drinking behavior.

Gustatory information reaches the brain through the seventh, ninth, and tenth cranial nerves which synapse primarily in the nucleus of the solitary tract (NST) (2). In the thalamus, the projection area for the tongue is known to be localized in the medial third of the ventrobasal nucleus. Neurons responding to gustatory stimuli occupy the most medial portion of this lingual projection area (3). In 1923 Allen (4) described the ascending projections of the NST in the guinea pig as crossing to the contralateral medial lemniscus and distributing with this tract in the ventral and lateral thalamic nuclei. Stimulation of the chorda tympani [lingual branch of the facial nerve (VII)] or the glossopharyngeal nerve (IX), however, produces bilateral evoked potentials in the thalamus of rats, cats, and monkeys (5). The receptive fields of thalamic neurons responding to gustatory stimuli have been found to be ipsilateral on the tongue (6). We have now resolved this discrepancy between the anatomical and physiological evidence regarding the secondary pathways of the gustatory system by combining neural recording and degeneration techniques.

Rats anesthetized with pentobarbital were placed in a stereotaxic instrument fitted with blunt ear bars to avoid rupturing the tympanic membrane; the skull was trephined at a point 13 mm posterior to the bregma and 2 mm lateral to the midline. A fine wire electrode (67 μ m in diameter), introduced through the overlying cerebellum, recorded neural activity from the rostral medulla while the tongue was stimulated with 0.25M NaCl, water, and a fine paint brush. Light brushing of the incisors, lips, chin, cheek, and whiskers were also routinely used as stimuli (7). When a response to tongue stimulation was obtained, a permanent record was made with a resistor-capacitor integrator and several other gustatory stimuli were tested (8).

When testing was complete, a small

Taste Pathways in Rat Brainstem

Abstract. By means of a combination of electrophysiological and anatomical procedures, the projections of the anterior portion of the solitary nucleus were traced to the parabrachial nuclei in the pons, structures hitherto not considered to be included in the taste pathway. Responses to taste stimuli were recorded from this pontine area. Lesions in the pontine taste area resulted in degeneration of fibers reaching the lingual area in the thalamus.

The end point in any sequence of food-seeking behavior is either ingestion or rejection. Gustatory stimuli act as a final arbiter of the consummatory behavior. In addition, gustatory stimuli have innate hedonic value—they are either positively or negatively reinforcing. Despite the importance of gustatory sensibility to behavior, the neural substrate for taste has remained poorly understood compared to that of the

visual, auditory, or somatosensory systems. Neuroanatomy texts are hesitant about the central gustatory pathways, but nevertheless perpetuate the notion that the taste system joins the direct lemniscal pathways of the spinal and trigeminal somatosensory systems (1). We now have evidence that the taste pathways to the thalamus are neither direct nor lemniscal in the strict sense, but are mediated by cell groups in the