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J. Baird Callicott and Robert Frodeman, Editors in Chief

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Kurt Jax

IV. DIVERSITY-STABILITY HYPOTHESIS

The idea that biological diversity enhances ecological stability has inspired a huge body of scientific research. It has also played an important role in environmental ethics, especially in Aldo Leopold's land ethic. According to Leopold, biodiversity is essential for "a food chain aimed to harmonize the wild and the tame in the joint interest of stability, productivity, and beauty" (1949, p. 199). Potential links between diversity and stability have helped to spur conservation efforts.

Nevertheless, ecologists have at times shown what Samuel McNaughton called a "marked instability of attitudes regarding diversity-stability relationships." He attributed this to a "low diversity of empirical tests of the hypothesis" (1977, p. 523). In this respect scientists are now in a much better position to assess the diversity-stability hypothesis (henceforth merely "the hypothesis"), with more than forty direct experimental trials on the books and more in progress. But another reason for changing attitudes has been that stability is a multivocal concept, and evidence suggests that not all types of it vary positively with biodiversity. Thus, the plausibility of the hypothesis has varied as different kinds of ecological stability have come into vogue.

Three interrelated trajectories have been discernible in the years since World War II. First, scientists' confidence in the hypothesis plummeted in the early 1970s; but then it steadily rose again, beginning in the mid-1990s. Two other trends help to explain this recovery: Emphasis has shifted from the stability of individual populations to that of entire communities or ecosystems, and ecologists have come to focus on forms of stability that are both empirically measurable and theoretically tractable.

In the 1950s, three of the twentieth century's most influential ecologists argued that the hypothesis was plausible enough to warrant further study (Odum 1953, MacArthur 1955, Elton 1958). They reasoned that if a given species preys on several others, its population size will fluctuate less in response to environmental variations affecting one of its prey than it would if the species in question ate fewer prey species. Similarly, if a species has many predators, its population will vary less in response to exogenous changes in one predator's population size. As empirical support for these ideas, Eugene Odum and Charles Elton cited the dramatic oscillations experienced by many populations in the Arctic but not in the far more species-rich tropics; they further noted the tendency for pest populations to undergo more frequent and severe "outbreaks" in simplified agricultural systems than in complex natural systems. Although MacArthur's paper was more conceptual than empirical, he also conceived the hypothesis in terms of population stability.

The few empirical studies of diversity-stability relations conducted in the 1960s and early 1970s yielded a confusing mix of positive, negative, and ambiguous results (Goodman 1975). But the coup de grâce came from a purely theoretical exercise, on the basis of which May claimed that "simple mathematical models with many species are *in general* less stable than the corresponding simple mathematical models with few species" (1973, p. 49; italics added). This is not actually a general theoretical result, since it depends on *particular* and, indeed, quite debatable assumptions about whether and how certain other variables (e.g., the number and strength of interactions between species pairs) change as the number of species increases (McCann 2000). Nevertheless, the idea that diversity destabilizes ecological systems quickly became a "new paradigm" despite a continued dearth of empirical tests of the hypothesis (Loreau et al. 2002).