LETTERS TO THE EDITORS

ECOSYSTEM CONVERGENCE

The fine line between ecological theory and tautology, explained so effectively by Peters (1976), has long been a source of uneasiness among theoretical ecologists. Faced with the prospect of untestable "theories," a number of workers have been drawn to the concept of ecosystem convergence (Cody 1974*a*; Mooney 1974). If one wishes to test the generality of a theoretical construct involving adaptation in a particular natural system, all that is necessary is to find in a similar climatic zone an ecosystem composed of species which evolved in isolation from the first group, or so the argument goes. The attraction of this approach has been wide, spawning considerable research activity as well as many papers and several books (e.g., DiCastri and Mooney 1973; Goodall 1976; Mooney 1974, 1977; Orians and Solbrig 1977).

That the attraction of the convergence concept can be powerfully seductive is suggested in a paper by Went (1971), who observed a series of situations where strong parallel evolution had occurred in a restricted area without similar patterns developing in climatically homologous regions elsewhere. So unsatisfactory did Went find this that without additional evidence he postulated a new genetic mechanism involving viral transport of gene complexes between phylogenetically distant angiosperm species.

While Went did not do so, it is important to differentiate between parallel and convergent evolution. Parallel evolution refers to two or more ecologically similar species evolving in much the same way in response to similar selective pressures. In contrast, convergence occurs when different sorts of organisms evolve such that they come to resemble each other, usually as a consequence of occupying similar habitats. It is not the purpose of the present communication to discredit Went's hypothesis. Rather, the argument will be presented that separate cases of parallel evolution in climatically similar but biogeographically isolated areas can sometimes produce divergent results. Convergence should not automatically be expected. Emphasis will be placed on dominant plant species with the suggestion that physiognomic divergence will be paralleled by other biologic components.

Given a new set of environmental conditions, it is usual to expect convergent evolution toward an optimal (*sensu* Cody 1974*a*) adaptive solution. Such

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evolution frequently results in numerous ecologically similar but phylogenetically distant species occupying the same habitat. Numerous examples exist of such assemblages of closely convergent species; mangrove shrubs, tropical rain-forest trees, and Mediterranean-climate sclerophyll shrubs are some of the best known. Given such a set of convergent, coevolved species occupying a habitat undergoing environmental change, parallel evolution toward some new optimal adaptive solution should be expected.

Stebbins (1974) suggests that several different evolutionary solutions are possible for any selective pressure. What then determines which potential strategy is likely to be realized and where convergence is to be expected? I suggest that historical factors play a much more important evolutionary role than is generally recognized.

The adaptive peak realized by the evolutionary process will depend to a large extent on the phenotypes originally present and the nature of past climatic variation. (The present climate of a particular region does not necessarily reflect the prior climatic history.) The resulting parallel evolution can be explained by an ecological equivalent of Stebbins's (1974) evolutionary canalization principle. According to Stebbins (1974), "Evolutionary canalization can be defined as the tendency for populations to respond adaptively to new environments in ways that are determined by characteristics acquired as a result of previous adaptative radiation" (p. 23). While Stebbins was referring to genetic processes, the same definition can be applied to "ecological canalization" with the substitution of species for populations. Similarly, two supporting propositions offered by Stebbins apply. The first is selective inertia: the degree of selection needed for new adaptations is many times greater than that needed for modifying existing adaptations. Second, adaptive modification will generally occur along lines of least resistance. These two propositions strongly support my contention that different selective solutions to environmental conditions will be reached reflecting the selective pressures to which the species have been subjected. Convergence in isolated systems should not necessarily be expected.

Following Carlquist's (1974) discussion of island biogeography and evolution, we can assume that most invaders to an isolated system will be generalists. Unless the system is young and few specialized species have evolved or colonized, invasion of new species into established communities on the island will occur only rarely.

Assume the case of an island with a recently altered environment such that many diverse species are undergoing evolution toward some adaptive solution with somewhat less adaptive value than a different strategy achieved elsewhere in the world. In such a situation, competitive pressure from the species already present would likely prevent evolution of the more highly adaptive forms because of the selective disadvantage to which intermediates would be subjected. This suggests that the only mechanism through which species of the more highly adaptive peak can enter the system is introduction from outside. As more highly specialized (K-selected) species are less vagile than generalists (r-selected), such introductions would not be expected for isolated systems.

Proximity to other source areas will increase the rate of successful colonization by species evolved outside the system (MacArthur and Wilson 1967). It follows that the more isolated a system, the less likely the eventual adaptive solution to an environmental situation will resemble that found in other parts of the world. Went (1971) observed that "the more geographically isolated a floral area is, the more pronounced the cases of [distinctive] parallel development are" (p. 198). This observation fits exactly with expectations based on colonization potential. (He later suggests, "... no evolutionary theory can be general without accounting for this type of [geographically restricted] parallel development" [p. 220]. Would Went expect viral transport to be influenced by the degree of isolation?) It is, therefore, not surprising that vagile groups such as birds (Cody 1974*b*) show greater convergence than more sedentary groups like lizards (Pianka 1975) and plants (Went 1971).

The preceding argument does not deny the importance of convergence at the local level (here lumped with the concept of parallel evolution), but rather emphasizes it. What is denied is that the same adaptive solution will always be found for a certain set of environmental conditions. An example is found in the growth forms of desert plants. As described by Beard (1976), different desert floras have evolved different plant growth forms and especially different types of succulence. In the deserts of the southwestern United States, stem succulents (Cactaceae) are important and provide a classic example of convergence when compared with stem succulents of northern African deserts (Euphorbiaceae). In south Africa leaf succulence is dominant instead. In northwest Brazil and the Andean Puna regions, leaf-succulent rosette plants (Bromeliaceae) are important. In the deserts of Australia, succulence is relatively unimportant. The existence of different types of succulence suggests that different routes exist to achievement of the same adaptive end. The small number of succulents in the Australian deserts does not imply that they are nonadaptive, but that an alternative adaptive solution to the desert environment evolved first in this highly isolated system. That succulents can be successful in Australia is suggested by the explosive growth of opuntia after its introduction. The impact of high rates of colonization found in continental desert regions is suggested by the very high diversity of growth forms in the Sonoran desert (Whittaker 1972; Givnish 1975) relative to Australia (Beard 1976) and smaller island systems.

A wealth of additional botanical examples of geographically restricted parallel evolution can be found in Went (1971). Investigation of the adaptive significance of these cases will doubtless continue for many years. One example is the prevalence of shrubs with thorns derived from branches in the central Mexican thorn scrub as contrasted with the large percentage of species with thorny leaves in the equivalent Australian system. Clearly, Went was correct in asserting that this could not result from chance alone. Perhaps the explanation will be found in their respective development in areas of immature, nutrient-rich soils and ancient, nutrient-poor soils. The lack of deciduous forms in the Australian area can be attributed to nutrient deficiencies (see Monk 1966; Walter 1973), and the low levels of phosphorous have been suggested to lead physiologically to thick, coriaceous leaves (Beadle 1966). In the Mexican

system, conservation of leaves has not been as critical, and the deciduous habit may well have been an intermediate step. In such a case, leaves are less likely to have been sufficiently tough to form effective thorns. An equally plausible theory could be constructed on the basis of long-term exposure to different groups of browsing animals.

Tests of ecological theory using isolated ecosystems with similar climatic regions will continue. The preceding discussion only emphasizes that such tests must be viewed as one-sided and that failure to observe convergence will not be a readily interpretable result.

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