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## WHEN IS IT COEVOLUTION?

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'Coevolution' may be usefully defined as an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first. 'Diffuse coevolution' occurs when either or both populations in the above definition are represented by an array of populations that generate a selective pressure as a group. Ehrlich and Raven's (1964) classic paper on the interactions of butterflies and plants was the first essay explicitly focused on coevolution. However, they did not define coevolution, and butterflies were neither stated nor implied to have been the single populations or array of herbivores that have generated the plant traits that they discuss as causing butterfly distributions on host plants. I believe that the lack of an original definition of 'coevolution,' the inapplicability of the example chosen by the original advocates of the use of the term, and the obvious commonplace nature of coevolutionary events in the history of plant-animal interactions have led to misleading uses of the term in contemporary evolutionary thought and studies. Here, I wish to call for more careful attention to the use of 'coevolution' as a word and concept.

There are three conspicuous misuses at present:

1) It is commonly assumed that a pair of species whose traits are mutualistically congruent have coevolved. For example, it is quite possible that the fruit traits of a mammal-dispersed seed coevolved with the mammal's dietary needs. However, it is also quite possible that the mammal entered the plant's habitat with its dietary preferences already established and simply began feeding on the fruits of the

species that fulfilled them. When this occurs, it is those species that are most exactly congruent which will appear most coevolved yet are likely to be the least coevolved. Are the hard seeds of those aridland trees dispersed by passage through a contemporary mammal gut coevolved with the mammal? Not necessarily.

2) In similar manner, a herbivore parasitic on a plant is often thought of as coevolved with the defense timing, chemistry, morphology, etc. However, when a parasite arrives in a new habitat, it will feed on those species whose defense traits it can circumvent because of the abilities it carries at the time. Such a parasite cannot be distinguished from one that evolved the ability to circumvent a defense while in trophic contact with its host.

3) When other evidence makes it clear that a parasite has evolved traits to circumvent the defenses of its host, it is frequently automatically assumed that coevolution has occurred. However, it is not necessary to conclude that the defense trait circumvented was evolutionarily produced in response to the parasite in question. In fact, it is likely that many defense traits of plants were produced through coevolution with animals no longer present in their habitat or no longer parasitizing them if present. Strongly coevolved parasite-host systems probably as often proceed to ecological independence of the participants as to relatively benign parasitism.

In summary, I plead for the retention of the usefulness of 'coevolution' by removing it from synonymy of usage with 'interaction,' 'symbiosis,' 'mutualism,' and 'animal-plant interaction.' A bee is not necessarily coevolved with the flower it pollinates, a caterpillar is not necessarily

