

A COMPARATIVE ANALYSIS OF HERBIVORY AND AMNIOTE DIVERSIFICATION IN MODERN TERRESTRIAL ECOSYSTEMS

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The comparative methodology proposed by Brooks and McLennan (1993) to study the process of adaptive radiation is employed to examine the hypothesis that the origin of herbivory has been a causal factor in the proliferation of amniote diversity in modern terrestrial ecosystems. An exhaustive search of the primary systematic literature provided sufficient phylogenetic information to allow the inclusion of 83% (10 of 12) of all known modern terrestrial amniote groups in which herbivory has evolved. In every group examined, the following comparative criteria were satisfied: (1) herbivory was determined to be an apomorphic feeding preference, (2) each herbivorous group was significantly more species-rich than its faunivorous sister group, (3) the high diversity of each speciose clade was determined to be an apomorphic condition, (4) herbivory (and its associated attributes) is proposed as the key innovation that conveys an ecological advantage to its possessors and has the potential to accelerate diversification rates by promoting speciation and reducing extinction.

Herbivory in modern terrestrial amniotes has been variously manifested as folivory (consumption of leaves, shoots, roots and other cellulose-rich vegetative plant structures), general herbivory (consumption of buds, flowers, seeds, nuts and other cellulose-poor plant structures), and frugivory (consumption of fruit). Sister-group comparison revealed that herbivorous clades were, on average, 16.8 times more diverse than their respective faunivorous sister taxa. The various forms of herbivory were found to be correlated with differential average increases in species diversity: folivory, 34.6 fold increase; general herbivory, 5.5 fold increase; and frugivory, 2.6 fold increase. The plesiomorphic feeding habit from which herbivory arose could be determined unambiguously for eight of the ten study groups; insectivory was the plesiomorphic feeding preference in seven groups, whereas carnivory was plesiomorphic in only one. Within two herbivorous clades, faunivory arose secondarily, suggesting that the evolution of herbivory is not an irreversible phenomenon.

Although provisional, the findings of this study provide compelling evidence of a correlation between herbivory and accelerated faunal diversification. It is proposed that herbivory promotes diversification by allowing these groups to expand their geographic range and allow increased access to available resources. The evolutionary scenario in which herbivory originated (and the manner in which it is maintained) in modern terrestrial amniotes is considered. The findings of this study suggest strongly that herbivory represents a pervasive force in the evolution of modern terrestrial biodiversity.

BROOKS, D.R., AND D.A. MCLENNAN. 1993. Comparative study of adaptive radiations with an example using parasitic flatworms (Platyhelminthes: Cercomeria). *American Naturalist*, 142: 755-778.