## ECOLOGICAL DIVERSIFICATION: INNOVATION AND INVASION AS INFERRED FROM PHYLOGENY IN SNAILS

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When, and under which conditions, do lineages enter habitats and take on modes of life not exploited by them previously? Answers to these questions offer insights into the environmental context of evolutionary innovation and diversification and for expansion of the biosphere. We used phylogenetic and stratigraphic data for Cenozoic rapanine muricid gastropods to extimate when, where, and how often lineages of low intertidal and sublittoral snails became specialized for life in the upper intertidal zone. High-shore specialization evolved at least six times in the Indo-Pacific and twice in tropical America, apparently during the latter half of the Miocene. No cases of invasion of the lower shore from above are known, and there are no examples of high-shore specialization by rapanines in the eastern Atlantic or the temperate zones. In a separate analysis, sister-group relationships at the genus level imply that drilling, a slow method of predation of shell-bearing prey, is the plesiomorphic condition in rapanines, and that faster means of subduing shelled prey as well as exploitation of other kinds of prey evolved at least ten times. Habitat shifts and predation-related innovations occurred mainly during the Miocene under circumstances of high diversity and abundant resources.