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Letter

Anagenesis and Cladogenesis Are Useful Island Biogeography Terms

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When a species evolves as a unit into another, the progression is termed anagenesis. If a species splits into two (or more), the process is called cladogenesis. Emerson and Patiño [1] recently argued that these terms imply both 'trait change among species, and the mechanistic . . . basis of such change'. They suggest that 'the usage of anagenetic and cladogenetic speciation should be abandoned'. We claim that these propositions are false, confuse patterns with processes, mix speciation patterns with the geography of speciation, and call for abandonment of extremely valuable, straightforward, and widely used terms.

Searching Google for anagenesis and cladogenesis generates tens of thousands of hits, with those focusing on islands being a minority. Abandoning their use is akin to suggesting that, in island biogeography, we stop using terms such as population ecology, or peripatric speciation. Using new terms would confine island biogeography studies to a very specialized audience, causing research on islands to become overlooked, or misunderstood.

Emerson and Patiño suggest that inferring anagenesis on an island assumes that the 'source population is necessarily subject to evolutionary stasis'. Such an assumption is reasonable under some scenarios, for example when propagules arrive from the mainland and evolve quickly after reaching the novel insular environment [2]. It is likely, however, that both insular and mainland populations continue to evolve after the colonization event. The mainland populations, larger and hence responding more quickly to selection, may actually evolve faster [3,4]. The assumption of evolution only (or mainly) on the island is a 'straw man'. Almost no one makes it, and it is irrelevant to whether a cladogenetic or an anagenetic event took place.

Neither phenotypic evolution nor selection are necessary to define cladogenesis or anagenesis. If either the insular or mainland populations, or both, diverged enough, we define a cladogenetic event. Cryptic cladogenetic speciation, whereby no phenotypic traits differentiate island and mainland species, is also possible. Moreover, cladogenesis can result from neutral drift (especially in small, insular, populations).

Under peripatric speciation, possibly the most common geographic mode of speciation, when islands are colonized from elsewhere the source population becomes paraphyletic. Our trees, showing neat splits, will falsely suggest otherwise. For example, the wide ranging North American woodrat *Neotoma lepida* probably gave rise to multiple island species (e.g., *Neotoma martinensis, Neotoma anthonyi* [5]). We are likely to name the mainland species first, because it is more widespread, and mainland habitats are easier to reach [6,7]. Because islands are more often colonized from the mainland than the other way around [8,9], we can assume that the insular woodrat species evolved from *N. lepida* – in the sense that the ancestral, mainland population is a continuously evolving entity with internal genetic exchange. It does emphatically not have to mean, as Emerson and Patiño [1] suggest, that the mainland species is in stasis.

Some confusion may arise when discussing within-island speciation, as Emerson and Patiño [1] suggest. If a population colonized an island, and subsequently attained specific status, than it is a case of cladogenesis. Within the island, however, the population may have evolved anagenetically without further splits. The fossil record is replete with examples of anagenetic speciation (e.g. *Myotragus* in the Balearics). If we are interested in within-island speciation we need be wary when defining the insular speciation as anagenetic, because it is not true in the global context. We agree with Emerson and Patiño [1] that, when discussing the evolution of single island endemics and within-island diversification, we need to choose terms carefully. But there is no reason to throw the baby out with the bath water.

Emerson and Patiño propose replacing the terms anagenesis and cladogenesis by regional allopatric speciation and regional sympatric speciation, respectively. These new, cumbersome, terms wrongly confound the phylogenetic pattern of speciation (the imprint on the phylogenetic tree), with the geographic process behind it. Both cladogenetic and anagenetic patterns can be observed, in principle, both allopatrically and simpatrically.

We conclude that the terms anagenesis and cladogenesis are neutral with respect to trait change or selection, and are independent of the geographic setting that originate speciation. We think that the bugbears leading Emerson and Patiño to suggest replacing these terms originate from the erection of straw men based on irrelevant and seldom-made assumptions. We posit that the terms anagenesis and cladogenesis are useful and well defined, and should stay in use in both evolutionary biology as a whole, and in evolutionary studies of insular taxa.

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