

Forum

Anagenesis, cladogenesis and speciation on islands

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Abstract

Anagenesis and cladogenesis are fundamental evolutionary concepts, but are increasingly being adopted as speciation models in the field of island biogeography. We review the origin of the terms anagenetic and cladogenetic speciation, critique their utility, and finally suggest alternative terminology that better describes the geographic relationships of insular sister species.

The Evolution of Cladogenetic and Anagenetic Concepts in Island Biogeography

Cladogenesis (from the Greek *clados*, “branch”) describes the branching of evolutionary lineages, whereby an ancestral species can give rise to two or more descendant species. Anagenesis (from the Greek *ana*, “up”, referring to directional change) describes evolutionary change of a feature within a lineage over time. The geography of cladogenesis and the drivers of anagenesis are two underpinnings of island biogeography. Cladogenesis and anagenesis are different processes, but are inherently interconnected, as speciation is the joint action of divergence (cladogenesis) and change (anagenesis). It has recently been pointed out that usage of the terms cladogenesis and anagenesis is inconsistent and vague across disciplines, leading to the suggestion that they be altogether abandoned [1]. In particular the terms have been rebranded within the field of island biogeography as anagenetic and cladogenetic speciation [2], and in doing so their original meaning [3] has been changed. Cladogenetic speciation has been defined as involving anagenetic change in both lineages that arise from a cladogenetic event [2]. It thus describes speciation where both descendant species undergo character divergence from an ancestral type (Figure 1). The term anacladogenesis was subsequently coined [4] to describe when anagenetic change occurs in only one of the sister taxa, with the other subject to character stasis with regard to the ancestral type (Figure 1), and has subsequently been replaced with the term anagenetic speciation [2].

Cladogenetic speciation (Figure 2a) has been associated with speciation events that occur within a single island, but has also been used in reference to speciation at the archipelago scale [2,4,5]. Anagenetic speciation has been primarily used to describe island colonisation [2,4,6], where source species are inferred to retain the ancestral type (evolutionary stasis), while species derived from colonisation events diverge from the ancestral type (Figure 2b). Anagenetic speciation has also been suggested to likely occur within an island if the most recent common ancestor (MRCA) of two descendant species colonised the island [4]. The argument put forward is that stable environments will favour character stasis [4, p. 339], such that character state of the MRCA will remain relatively unchanged in one of the descendant species, assuming that similar habitats are colonised between islands [4, p. 341] (Figure 2c).

Practitioners of island biogeography are increasingly using the terms cladogenetic and anagenetic speciation to describe the geography of species relationships [e.g. 5,7–9], and as convenient

terms for emerging theory [e.g. 10–12]. Cladogenetic speciation has become synonymous with speciation within islands, and anagenetic speciation has become equivalent to speciation events involving the colonisation of a new island. However, because both terms also infer how anagenetic change is distributed between descendant species (Figure 1), and exclude other plausible evolutionary scenarios (Figure 2), we argue that the terms anagenetic and cladogenetic speciation should not be used, but instead replaced with evolutionarily impartial terms. The anagenetic and cladogenetic speciation models yield an incomplete and biased framework for insular biogeographic investigation. This bias manifests itself as: (i) overestimation of the importance of evolutionary stasis in insular systems; and (ii) an assumed positive association between radiation (diversification) history and adaptive change. Below we support our argument by addressing the logic and assumptions that underlie the cladogenetic and anagenetic speciation models. We conclude by proposing alternative terminology to describe the geography of sister species relationships.

Are Source Species of Single Island Endemics Subject to Evolutionary Stasis?

Implicit within the concept of anagenetic speciation [2] is that it explains the evolution of lineages represented by single endemic species within an island, assuming that they have not become single island endemic (SIE) species due to the extinction of populations on other islands. That a founding population on a new island might undergo anagenetic change on the path to become a SIE is a reasonable assumption. What is less reasonable to assume, however, is that subsequent to the colonisation of a new island, a source population is necessarily subject to evolutionary stasis, as proposed in [4]. Such an assumption, taken together with a model of island age-based colonisation (e.g. the progression rule) invokes increasing evolutionary stasis, across island communities with island age (Figure 2d–e). While this might be an interesting hypothesis, no evidence-based support is provided by studies using the anagenetic speciation concept. To infer character state evolution and ancestral character states requires historical information, either directly from fossils, or indirectly through character mapping onto a robust phylogeny. Instead, the evolutionary history of character state change has been inferred based on the present day geographical distribution of character states [e.g. 2, 4–6]. There is an inherent circularity to the conclusion of stasis in source species, as that is essentially an unsupported starting assumption. Thus, the general importance of evolutionary stasis within a source island subsequent to colonisation of a new island remains unknown, and its generality as an assumption is unfounded.

Are Founding Species Subject to Evolutionary Stasis if They Speciate?

It has been argued that if a founding species undergoes speciation within the founding island, then only one of the two descendant species is likely to undergo anagenetic change, with the other subject to evolutionary stasis [4] (Figure 2c). The provided rationale is that “progenitor” species (ancestral

character states) will persist in the colonised island, most likely due to environmental similarity [4, p. 339]. This argument is logically inconsistent with that of the preceding section, which argues that founding species are subject to anagenetic change (Figure 2b). Despite this inconsistency, this argument has been adopted as an assumption for character state evolution within oceanic insular systems [2,4] biasing toward inferences of evolutionary stasis when applied to the interpretation of insular species distribution data. This is because, for any pair of endemic species that are assumed to have evolved from a single colonising species, the assumption is that one of the species has been subject to evolutionary stasis (Figure 2f). As highlighted within the previous section, in the absence of robust phylogeny for character mapping, such inferences of character evolution are unsupported.

Does Population Genetic Process Differ between Radiated and Non-Radiated Endemic Lineages?

Species evolve and diverge from one another by both adaptive and non-adaptive evolutionary change. The relative importance of both types of change within an evolving species is a complex temporal dynamic involving the adaptive landscape and species traits (e.g. genetic variation, niche, dispersal), both of which will change over time. The concepts of anagenetic and cladogenetic speciation have been further developed to suggest that speciation within islands (cladogenetic speciation) is driven by adaptive evolutionary process, while evolutionary change after a colonisation event (anagenetic speciation), particularly on islands with limited environmental complexity, is largely explained by neutral population genetic processes [2,6]. Thus, the terms anagenesis and cladogenesis, in the field of island biogeography, now describe both evolutionary change and evolutionary process to be a function of the geography of sister species relationships inferred from species distributions. Cladogenetic speciation is limited to speciation events occurring within the same island [4], with the implication being that these are largely driven by adaptive evolutionary change within both species [2,6]. Anagenetic speciation is primarily associated with newly founded populations on an island, with the implication that evolutionary change is largely non-adaptive [2,6]. While both scenarios are reasonable models for the evolutionary origins of species, they exclude many alternative speciation models (e.g. allopatric speciation via drift, cryptic speciation, convergent evolution). These cladogenetic and anagenetic speciation models are thus hypotheses to be tested, not assumptions to be imposed.

Concluding Remarks

Previous studies that have labelled species as either anagenetic or cladogenetic to primarily describe or infer the geography of their sister species relationships, whether intentional or not, also carry inferences about both the distribution of trait change among species, and the mechanistic (adaptive or neutral) basis of such change. However, as we have demonstrated, the interpretation of these terms should not extend to inferences of evolutionary change within species. Therefore, we propose that: (i)

the usage of anagenetic and cladogenetic speciation should be abandoned; and (ii) the terms anagenetic and cladogenetic species can be replaced with regional allopatric and regional sympatric species. The epithet of regional can then be replaced depending on the nature of the study by, for instance, *island* in insular biogeographic studies. These terms make no assumptions about evolutionary process, and should not be confused with the terms allopatric and sympatric speciation. They describe only the geography of sister species relationships, whereby an *island allopatric species* is inferred to have its closest relative on another island or continental region, while an *island sympatric species* is inferred to have its closest relative on the same island.

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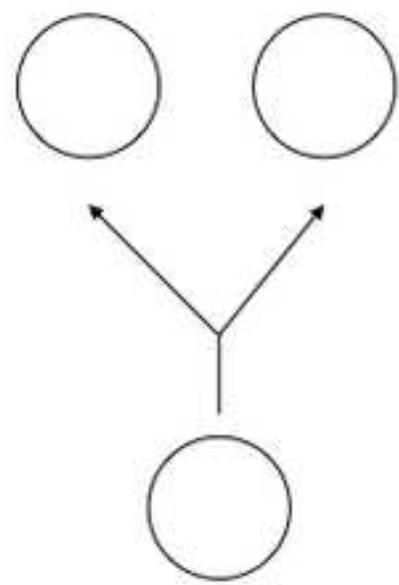
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Figure 1. Anagenesis and Cladogenesis in Island Biogeography. Anagenesis describes trait change through time (A changes to B) between ancestor and descendant. Cladogenesis describes the origin of sister species from an ancestral species, but makes no inference about character state change. Island biogeographic cladogenesis (or cladogenetic speciation) describes the origin of sister species from an ancestral species, with the added caveat that both descendant species have undergone ancestral character state change. Anacladogenesis (or anagenetic speciation) describes the origin of sister species from an ancestral species where only one descendant species has undergone ancestral character state change. Modified from [4].

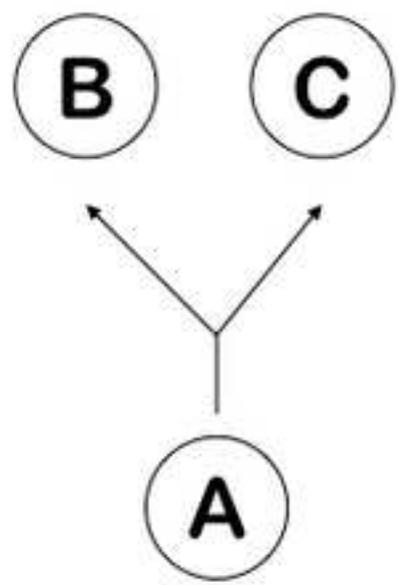
Figure 2. Examples of How, in the Absence of Ancestral Character State Information, Island Biogeographic Inferences Can Incorrectly Infer Trait Change. A hypothetical ancestral species is depicted in geographic, genomic and morphological trait space. Geographic (source island, colonised island), phylogenetic (genomic divergence), and trait (morphology) change through time are shown with solid lines for two hypothetical descendant species. (a) The cladogenetic speciation model describes trait divergence in two descendant species from their most recent common ancestor (MRCA), and is suggested to explain most speciation events within an island [2,4]. (b-c) The anagenetic speciation model infers trait divergence from the MRCA in only one descendant species. It is suggested to explain trait change in only the founding lineage when a new island is colonised (b), or in one of the descendant lineages within an island if the MRCA was a colonising species (c), assuming a founding habitat that is sufficiently similar to the source island habitat [4]. (d-g) Dotted lines and grey islands represent inferences of morphological change under the anagenetic and cladogenetic models of speciation. (d) Assuming anagenetic speciation incorrectly infers the source island species to have undergone evolutionary stasis, with the extent of anagenetic change exaggerated in the colonised island species. (e) Assuming anagenetic speciation incorrectly infers the source island species to have evolved under evolutionary stasis with the colonised island species incorrectly inferred to have undergone anagenetic change. (f) Assuming anagenetic speciation on a colonised island (i.e. character state of the colonising species remains relatively unchanged in one of the descendant species [2,4]) incorrectly infers that one of the species (in this case brown) has evolved under evolutionary stasis and overestimates anagenetic change in the other species. (g) Assuming cladogenetic speciation on a source island (i.e. the ancestor is not a colonising species) incorrectly infers that the brown species has undergone anagenetic change and underestimates anagenetic change in the blue species.



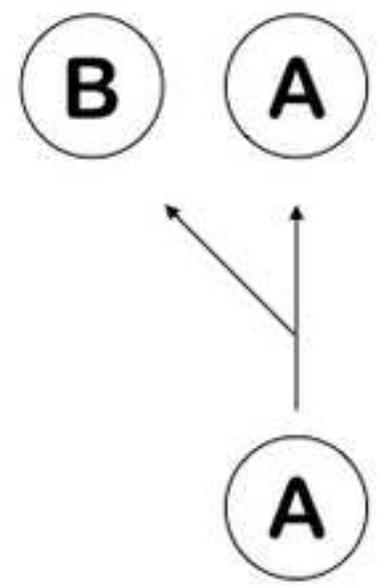
Anagenesis



Cladogenesis



**Island biogeographic
cladogenesis**



Anacladogenesis

