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Evolution: An Archipelago Replete with Replicates

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Adaptive radiations, in which repeated bouts of diversification lead to phenotypically similar species, highlight the power of natural selection and predictability in evolution. A newly discovered radiation of stick spiders on Hawaii helps shed new light on this phenomenon.

Instances of adaptive radiation — that is, the evolution of a multitude of species from a common ancestor as a consequence of the adaptation to varying environments [1,2] — have long been recognized as important model systems to study organismal diversification. Two features of adaptive radiations in particular have attracted scientific attention, the rapid generation of phenotypic disparity (divergence) and the independent evolution of similar phenotypes (convergence) [3]. For example, the adaptive radiations of *Anolis* lizards have given rise to replicate sets of ecomorphs on different islands in the Caribbean, each containing forms adapted in body size and limb-length to live in the crown or on the trunk of trees, or in the bushes and grass beneath [4]. Similarly, threespine stickleback fish repeatedly diversified into benthic–limnetic species pairs in several

postglacial lakes [5]; and the adaptive radiations of cichlid fishes in the East African Great Lakes Victoria, Malawi and Tanganyika have not only produced what are the most species-rich endemic faunas in vertebrates [6] but brought forth arrays of convergent species pairs between [7] and within [8] lakes. Whether or not the occurrence of convergent forms as known from these iconic examples is a general feature of adaptive radiations, or if it is a rare phenomenon intriguing to researchers by the virtue of providing ‘natural replicates’ to study, is not entirely clear.

In a new study, Rosemary Gillespie and colleagues [9] report a hitherto overlooked adaptive radiation in stick spiders (Theridiidae, genus *Ariamnes*) on the Hawaiian archipelago, which is characterized by both divergence and convergence. More than a dozen of *Ariamnes* species have evolved on the

archipelago within the last two million years from a common ancestor that invaded the emerging archipelago from Asia. While in their original range *Ariamnes* species are known to steal prey from other spider’s webs — a strategy known as ‘kleptoparasitism’ — or even prey upon the net-building spiders themselves, the Hawaiian *Ariamnes* exhibit a free-living lifestyle; only a few species occasionally steal from endemic *Orsonwelles* spiders [10]. Hawaiian *Ariamnes* hunt at night in the native forest habitat and rest on vegetation during the day, which is when they are exposed to the risk of being eaten themselves by birds. Here, different types of body coloration confer crypsis on the specific substrates the individuals rest upon, impeding their detection by visual predators. Three quite distinct color morphs have evolved in the Hawaiian stick spiders: the most common ‘golden’ morph





Figure 1. Distribution of color morphs of *Ariamnes* stick spiders across the Hawaiian archipelago.

Multiples of the same color morph on an island belong to different species. Three examples are shown for comparison ('matte white' morph: *A. corniger*, East Maui; 'golden' morph: *A. uwepa*, Oahu; 'dark' morph: *A. sp.*, Kauai). Images by George K. Roderick.

matches the color of the undersides of leaves; the less frequent 'dark' morph is better concealed on dead ferns or in rocky crevices; whereas a third morph – 'matte white' – resembles the coloration of lichens covering tree trunks (Figure 1). Despite the stark differences in coloration between the morphs, it is possible that only minor metabolic or genetic changes are needed to create one instead of the other: Deposition of guanine crystals below the cuticle forms a white or reflective background, while pigments on top of this layer can add the hue, for example gold or red; if the guanine layer is not produced the midgut is not concealed and the spider appears dark in color.

The dated phylogeny presented by Gillespie *et al.* [9], which is based on one mitochondrial and two nuclear gene segments, reflects the time course of island formation, starting from around two million years ago when the islands Kauai and Oahu were already present. The reconstruction of the evolution of coloration in Hawaiian stick spiders based on the molecular phylogenetic hypothesis and data on the extant species' phenotypes revealed that the 'dark' and the 'matte white' ecomorphs are likely to have evolved from 'golden' ancestors several times in the history of the clade. Apparently, the radiation of *Ariamnes* on Hawaii was thus influenced by both rare dispersal of species and the resulting

geographic isolation between islands as well as replicated ecological divergence into ecomorphs within islands. This replication is also seen in another free-living spider radiation, but not in its web-building sister clade, possibly because free-living species are less constrained when choosing a resting place. Selection for camouflage in similar environments to protect from a limited set of predators might then result in identical evolutionary adaptations, especially given that the spiders' coloration is determined by few simple components that are presumably controlled by only a few genes.

Already when coining the term 'adaptive radiation' more than one hundred years ago, Henry Fairfield Osborn [11] introduced the concept of 'local adaptive radiation' for the occurrence of diversification into similar forms repeatedly across space and time. However, for a long time, the phenomenon of convergent (or replicate) evolution was difficult to study, because phylogenetic relatedness could only be inferred from morphological characters. This has changed rapidly with the rise of molecular phylogenetics, allowing researchers to interpret a species' morphology in the light of their relatedness inferred from independent molecular characters. By doing so, numerous previously unknown cases of convergence were discovered and often interpreted to result from similar

selection pressures acting on similar genetic backgrounds. Analogous to experimental replicates in the laboratory, those cases can be viewed and scrutinized as 'natural replicates', explaining their particular scientific appeal. However, although there is a strong interest in such 'natural replicates', most studies focus on one particular study system only, and comparisons across adaptive radiations are scarce [12].

The new study by Gillespie and colleagues [9] on the Hawaiian stick spider radiation paves the way for more broad-scaled comparative studies into the topic for two main reasons: first, Hawaii, as a very isolated archipelago with unique biota, is an especially promising location for a comparison between adaptive radiations in different groups of organisms that, nevertheless, have progressed side by side (e.g. silversword plants [13], honeycreeper birds [14], fruit flies [15], or stretch spiders [16]); second, most case studies of adaptive radiations in animals focus on vertebrates, whereas arthropods are poorly investigated in this respect. A phylogenetic breadth can potentially be key to reveal the underlying causes of adaptive radiation and evolutionary replication, as Gillespie *et al.* [9] demonstrate by comparing replicated Hawaiian spider and Caribbean *Anolis* radiations to their respective non-replicate-producing sister clades. In both systems evolutionary replicates are produced in the sparse adaptive landscapes of insular environments in which camouflage in a particular microhabitat confers protection from the small set of predators that is typical for islands. The sister clades in those cases experience either more multifarious predation (mainland *Anolis*) or are constricted in their microhabitat choice (web-building spiders), possibly explaining the lack of replicated ecomorphs.

In addition to describing more cases of adaptive radiation from more evolutionary lineages, it will be equally important to examine these cases in sufficient detail and in an integrative manner. Increased sequencing power and lower costs per base pair now allow re-sequencing of whole genomes from a large number, or even all, species of an adaptive radiation [17–19]. Previously intractable questions about the extent of gene flow during adaptive radiation or the genetic basis of

key adaptive traits can thus be studied and compared within and across radiations [3]. While it is again the iconic adaptive radiations, such as Darwin's finches or the East African cichlids that have taken the lead here, there are also examples from emerging study systems [20]. Precise phenotypic and ecological data are needed as well. Modern imaging tools, such as computed tomography scanning, can deliver detailed phenotypic data covering a vast number of traits in a non-destructive way. The ecology of species can be assessed in a standardized manner by stable isotope ratio mass spectrometry [8]. Studies of extant adaptive radiations should also be complemented with fossil data, which would allow to more accurately reconstruct phenotypic evolution through time. The latest paleogenomic methods even allow sequencing of samples that are thousands of years old. In principle, this time range should allow sequencing individuals from the very early stages of some young, extant adaptive radiations.

In their new study, Gillespie and colleagues [9] have introduced an intriguing study system with replicate ecotype formation in an adaptive radiation and offered a potential mechanism for its evolution. When compared to other cases of adaptive radiations on islands, such as that of Caribbean anole lizards, the Hawaiian stick spiders highlight how very distantly related clades can show common patterns in their diversification. A suite of improved methods has now become available to further investigate precisely how such similarities arise.

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Left–Right Asymmetry: Myosin 1D at the Center

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While a ciliated organizer generates vertebrate left–right asymmetry, most invertebrates lack an organizer and instead utilize a myosin-based mechanism. A recent study now reveals that this myosin mechanism is conserved in the vertebrate organizer and functions to regulate cilia.

From snails to humans, asymmetry across the left and right side of the body is essential for life, and even love. Just ask Jeremy the Lonely Snail who was born with a rare body axis defect — a reverse-coiled shell [1]. Recently, Jeremy became

a media sensation as researchers made a public plea to help him find a lover, as he was unable to mate with normal-coiled snails. Luckily, all the media exposure did lead to a happy ending — several reverse-coiled partners were found for Jeremy

