

The genomics of organismal diversification illuminated by adaptive radiations

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Adaptive radiation is the rapid and extensive ecological diversification of an organismal lineage to generate both phenotypic disparity (divergence) and similarity (convergence). Demonstrating particularly clear evidence of the power of natural selection, adaptive radiations serve as outstanding systems for studying the mechanisms of evolution. We review how the first wave of genomic investigation across major archetypal adaptive radiations has started to shed light on the molecular basis of adaptive diversification. Notably, these efforts have not yet identified consistent features of genomic architecture that promote diversification. However, access to a pool of ancient adaptive variation via genetic exchange emerges as an important driver of adaptive radiation. We conclude by highlighting avenues for future research on adaptive radiations, including the discovery of ‘adaptation genes’ based on genome scans using replicate convergent populations.

Outbursts of life

In adaptive radiation and in every part of the whole, wonderful history of life, all the modes and all the factors of evolution are inextricably interwoven. The total process cannot be made simple, but it can be analyzed in part. (G.G. Simpson, 1953 [1])

The history of life is a cumulative story of evolutionary radiations (see [Glossary](#)); such outbursts of unprecedented forms are thought to be responsible for much of the extant and extinct organismal diversity on Earth [1–4]. For example, all cellular life has radiated out of such a simple – by way of comparison – beginning as the primordial self-replicating molecules [5]; all major animal phyla were in place by the fading of the Cambrian evolutionary radiation (commonly known as ‘Cambrian explosion’) [1,5]; and about every 20th extant fish species is the product of the ongoing explosive radiations of cichlids in the East African Great Lakes that, together, cover as little as ~0.031% of the total and ~0.044% of the water surface of our planet

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[6]. Evolutionary radiations are termed adaptive radiations (ARs) if new lifeforms emerge rapidly through the extensive ecological diversification of an organismal lineage [2,3]. Archetypal examples of ARs include Darwin’s finches on the Galapagos archipelago [7]; spiders [8] and silversword plants [9] on Hawaii; anole lizards on the islands of the Caribbean [10]; threespine stickleback fish in north temperate waters [11]; and the above-mentioned cichlid fishes in the East Africa Great Lakes and in various tropical crater lakes [12]. ARs have inspired generations of naturalists and have for decades served as essential model systems in evolutionary biology. With the recent proliferation of new tools for genomic investigation and their application to ARs, an overview of the opportunities and challenges that ARs provide in understanding the genomic basis of organismal diversification seems timely. We open this review by discussing the major features of ARs, describe the biological questions that genomic investigation

Glossary

Divergence mapping: marker-based search for genome regions exhibiting exceptionally strong differentiation (typically quantified by the fixation index F_{ST}) between ecologically-different populations as a consequence of divergent natural selection on specific loci.

dN/dS ratio: index combining the frequency of non-synonymous (i.e., amino acid changing) and synonymous (i.e., not amino acid changing) nucleotide substitutions across a gene to explore the type of selection that has acted on the gene.

Ecological niche: sum of all environmental conditions (e.g., resources, antagonists) relevant to the lifestyle of an organism.

Ecological opportunity: availability of novel or under-exploited ecological niches, resulting from the colonization of a novel habitat, the extinction of antagonists, or evolutionary innovation.

Ecomorph: distinct phenotype tightly associated with a specific ecological niche.

Evolutionary radiation: increase in taxonomic diversity; in other words, in the number of phenotypically distinct populations or species, within an organismal lineage.

Genome architecture: here this term is used to subsume global characteristics of a genome, such as overall genome size, gene counts, or the number of transposable elements.

Haplotype: stretch of DNA on a chromatid, inherited as a single unit.

Historical contingency: accumulation of stochastic events in the course of the evolution of a lineage.

Introgressive hybridization: hybridization between populations that causes the exchange of genetic material (gene flow) in some regions of the genome.

Lineage: evolutionary line of descendants, independent of its taxonomic status.

Mosaic genome: a genome heterogeneous in ancestry, emerging from introgressive hybridization, lateral gene transfer, or retention of ancestral polymorphism.

Syndrome selection: selection on a combination of traits (e.g., body and jaw morphology and coloration in cichlid fish [18,27]) in a given environment.

Box 1. Common features of adaptive radiations

Bouts of diversification commonly considered ARs have several characteristics in common:

- (i) *Extensive divergent evolution*. Diversification results in the generation of phenotypic disparity [1–3].
- (ii) *Divergent natural selection*. Diversification entails performance trade-offs such that the radiating taxa perform well in their specific ecological niche but relatively poorly in the niches of other members of the radiation [1,2].
- (iii) *Common ancestry*. Diversification starts from a delimited founder population [2]. Because diversification occurring within a confined area is particularly likely to meet this criterion, organisms radiating on islands or within isolated water bodies have always figured among the iconic examples of AR.
- (iv) *Rapid evolution*. Diversification occurs on a relatively short time scale [83,84]. Consequently, the products of AR generally still exhibit intrinsic genetic compatibility, facilitating genetic investigation (e.g., using artificial crosses).
- (v) *Speciation*. Diversification is accompanied by some degree of reproductive isolation. Restricted gene flow results directly from adaptive divergence because this implies the inferiority of hybrids and migrants between ecologically specialized populations [85–87], but many other reproductive barriers may operate (e.g., sexual isolation).
- (vi) *Convergent evolution*. Diversification results in similar phenotypes in multiple independent but ecologically-similar habitats [3,88]. This phenotypic similarity often comprises a diverse suite of traits as a consequence of ‘syndrome selection’.
- (vii) *Evolutionary (key) innovation*. The evolution within a lineage of a phenotype of particular significance to AR because it creates access to hitherto underutilized habitats, thus triggering

the subsequent diversification to different ecological niches within these habitats [1,2].

Several of these features arguably contain a subjective flavor. For instance, the extent and speed of diversification varies dramatically among ARs: only 14 species of ground and tree finches have emerged in the Galápagos archipelago within hundred thousands of generations [7]. By contrast, the younger radiations of cichlids in lakes Malawi or Victoria have each produced hundreds of endemic species [6], and white fish and sticklebacks have produced countless convergent ecomorphs within a few thousand generations [11,17,89–91]. Another ambiguity concerns the position of an AR along the speciation continuum. For example, the strength of reproductive isolation within the stickleback AR is variable, with genetic differentiation between diverging populations in close contact ranging all the way from negligible to very high ([89,92], see also [64,93] for cichlids). We thus avoid drawing a line between populations, ecomorphs, or species as the outcome of AR. Finally, many aspects of AR remain untested. For instance, performance trade-offs among divergent populations within ARs have only rarely been demonstrated, and their association to specific phenotypes often remains unclear (but see [94–97]). In particular, the concept of key innovations is controversial because tests permitting such demonstration are difficult to conceive [2].

Nevertheless, the fundamental commonality and beauty of ARs is that they highlight the power of natural selection in driving diversity in ecological function among a group of closely related organisms. Emphasis should not be placed on whether or not diversifying organismal systems qualify as AR, but instead on how such systems can be exploited to illuminate the mechanisms underlying biological diversification.

in AR can address, and highlight avenues for future research.

Key elements of ARs

AR is defined as the rapid diversification of an organismal lineage into an array of closely related species as a consequence of adaptation to different ecological niches [1–3] (a more comprehensive characterization is provided in Box 1). Closer inspection of such bouts of diversification reveals two important elements. The first is the generation of unique, distinct phenotypes specialized to different ecological niches – divergent evolution. This aspect of diversification is epitomized by Darwin’s finches, which have evolved distinct beak morphologies facilitating the exploitation of distinct food resources [7]. The second element of AR concerns the repeated generation of similar phenotypes in geographically independent but ecologically similar habitats – convergent evolution. Indeed, most of the well-known ARs exhibit both divergence and convergence. For instance, *Anolis* lizards on the Greater Antilles have diverged into an array of ecomorphs adapted to specific foraging niches but, across several islands, specific niches are predictably inhabited by phenotypically similar ecomorphs [13,14] (Figure 1). Similarly striking examples of convergence nested within divergence include wing-color mimetics in passion vine butterflies (*Heliconius* [15,16]), trophic ecomorphs of white fish and threespine stickleback in northern temperate freshwaters [11,17], and cichlid fishes that have evolved extraordinary similarity in color and in body and mouth shape among several East African lakes [18], and even within single lakes [19].

The occurrence of extensive divergence and convergence in ARs offers rich opportunities for genomic explorations of

two important issues in evolution. The first concerns why phenotypic divergence is vast and rapid in some lineages but not in others. Can the study of AR identify genomic or population genetic determinants of diversification rates? Second, convergent evolution represents outstanding evidence of the deterministic action of natural selection [20,21]. Molecular studies of ARs may therefore provide particularly strong insights into the genomic underpinnings and consequences of adaptation. In the following we elaborate on these two major themes.

Genomic determinants of AR

It has long been recognized that the question why some groups of organisms diversify more extensively than others is tightly connected to the pivotal concept of ecological opportunity: ARs are triggered by access to novel or hitherto under-utilized ecological niches [1,2,12], sometimes in combination with sexual selection [22]. The answer to the question about the determinants of organismal diversification is thus partly ecological and also includes historical contingency [14,23], but will remain incomplete without information from a genomic angle because exploiting ecological opportunity requires that genomes can relatively rapidly generate phenotypic modifications and innovations.

Early on, the profuse diversity displayed by some ARs already spurred speculations that the genomes of the emerging species may exhibit unusual features conducive to rapid phenotypic divergence [24–26]. The rise of next-generation sequencing technologies further fueled the expectation that such peculiarities in the genomes of radiating clades can be identified, if they exist [20,27]. To date, the quest for a genomic basis of adaptive radiation is still in its infancy. One reason is that typically only a single

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