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Opinion

Evolutionary genomics of oceanic island radiations

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A recurring feature of oceanic archipelagos is the presence of adaptive radiations that generate endemic, species-rich clades that can offer outstanding insight into the links between ecology and evolution. Recent developments in evolutionary genomics have contributed towards solving long-standing questions at this interface. Using a comprehensive literature search, we identify studies spanning 19 oceanic archipelagos and 110 putative adaptive radiations, but find that most of these radiations have not yet been investigated from an evolutionary genomics perspective. Our review reveals different gaps in knowledge related to the lack of implementation of genomic approaches, as well as undersampled taxonomic and geographic areas. Filling those gaps with the required data will help to deepen our understanding of adaptation, speciation, and other evolutionary processes.

Island adaptive radiations as windows into ecological and evolutionary processes

Oceanic islands and archipelagos have played a pivotal role in our understanding of evolutionary and ecological processes [1–9]. This is due to several characteristics of oceanic islands, including (i) their isolation, which limits the dispersal of terrestrial organisms and often results in **disharmonic communities** (see Glossary); (ii) specific ecological conditions, including geomorphological features, strong climatic variation across small geographic areas, discrete patches of habitats, and irregular cycles of disturbances, which play a role in the creation of ecological opportunity for diversification; (iii) the possibility to estimate their geological age, which offers a well-defined temporal framework for studying and modeling evolutionary processes; and (iv) their frequent occurrence in fragmented, spatial groups (archipelagos) which provide natural evolutionary 'experiments' with replicates [10–16].

Island evolutionary biologists have generally focused on two adaptive phenomena: the island syndrome and **adaptive radiation** [17,18]. The island syndrome describes the repeated and often extreme phenotypic changes which frequently involve predictable changes, such as cases of gigantism (e.g., *Birgus* coconut crabs) or miniaturization (e.g., *Stegodon* dwarf elephants), that might result from **ecological release** [19–21]. Adaptive radiation [22] broadly refers to the rapid diversification of a single evolutionary lineage into multiple descendant species that are notably ecologically differentiated [7,23]. Theory predicts a fundamental role of trait utility in adaptive radiation as well as a clear correlation between phenotypic traits and ecological niche space

Highlights

Oceanic islands have long inspired biogeographers, ecologists, and evolutionary biologists. A common feature of these islands is the occurrence of adaptive radiations, where a lineage quickly diversifies to occupy different ecological niches. Adaptive radiations offer a natural experiment to understand how ecology drives phenotypic and genomic evolution.

Recently, the 'genomics revolution' has made a major contribution to the field of evolutionary biology by uncovering patterns, processes, and mechanisms of genomic evolution.

Although progress is being made, we find that the application of genomic tools to understand the evolution of oceanic island organisms is still in its infancy. In response to this, we discuss fundamental questions that will help to integrate evolutionary genomics and island biology.

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occupation [24–26]. Adaptive radiations tend to occur on oceanic islands because they are located at the outer limit of the dispersal range of a given taxon [27]. Indeed, some of the most iconic examples of adaptive radiation are present on oceanic islands, such as the Hawaiian silversword radiation, which resulted in lianas, rosette plants, shrubs, cushion plants, and trees [28]. During the past ~3.5 million years they evolved outstanding variation in reproductive traits, floral architecture [28,29], and leaf morphology [29,30]. Equally prominent are the Galápagos finches, which collectively exploit many terrestrial habitats spanning from extremely arid, sun-exposed, coastal lava rock habitats to moist high-land *Scalesia* forests [31,32], and are renowned as a textbook example of adaptive radiation [33].

Advances in evolutionary genomics

The advent and development of high-throughput sequencing has transformed biology by opening new avenues of research that in turn provide new ways to tackle long-standing questions in evolution. These include resolving branches across the tree of life [34], uncovering the genetic basis of adaptation [35], and determining the evolution of genes and genomes across clades [36] (Box 1). In the context of adaptive radiation research, genomics has already contributed to the understanding of the genetic basis of adaptation and speciation [37], the role of hybridization in driving diversification [38,39], the genes underlying trait utility [40], and the genetic architecture of traits [41], among others.

Because some of the most celebrated adaptive radiations have occurred on oceanic islands, we set out to review evolutionary genomics on oceanic island adaptive radiations (Box 2) by asking what new insights have been gained by applying genomic sequencing to the study of speciation and diversification on oceanic islands. We found that there is currently both insufficient depth and diversity of genomic studies in the genomic studies of adaptive radiations on oceanic islands (Box 2 and Table S1 in the supplemental information online). Specifically, relatively few genomic studies have focused on understanding the fundamental factors that both promote and constrain adaptive radiations. We thus highlight the most substantial knowledge gaps regarding evolutionary genomics of adaptive radiations on islands through a set of outstanding questions (Box 3).

What is the basis of genetic variation underlying adaptive radiations on oceanic islands?

The extent of ecological and phenotypic diversity on oceanic island radiations represents an apparent evolutionary paradox. A high level of genetic variation is usually necessary to diversify eco-morphologically to a great extent [42], but a species colonizing an oceanic archipelago will typically suffer from founder effects (Figure 1) and, in many taxa, also inbreeding, ultimately leading to low levels of genetic variation. For example, it has been estimated that the original colonizing population of Galápagos finches comprised only 30 to 100 individuals [43]. In addition, recurrent local population extinctions driven by small area and environmental change can lead to further reductions in genetic variation (**population genetic diversity debt** [44]).

Our survey uncovered that hybridization and introgression are prevalent denominators on oceanic island adaptive radiations, and often drastically increase the levels of standing genetic variation in a species or population upon which natural selection acts [10,45,46]. Hybridization could lead to an increase in genetic variation in recently established island populations that would otherwise have little variation [10,45,47], thus counteracting the common negative effects of small population sizes and inbreeding depression [16]. Through hybridization, new phenotypes (intermediate or transgressive) may be formed. An example of transgressive phenotypes is the emergence of leaf phenotypes outside the range of variation across the parental species through

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Box 1. Recent technical and methodological advances in genomics

As the field of genomics continues to change, progress is being made in terms of improving data quality and increasing the amount of data that can be obtained. These advances are made possible through improvements in sequencing machine chemistry, bioinformatic tools, and new theoretical models. Some recent and noteworthy advances in the field of genomics are given below.

Chromosome-resolved reference genomes

High-quality reference genomes are now becoming the standard of the field, and are obtained by combining long reads and contiguity-ligation sequencing. This has enabled the study of synteny, haplotype blocks, and rearrangements such as inversions and chromosomal fusions and fissions.

Detection and renewed interest in transposable elements (TEs)

TEs were previously difficult to study because they exist in high numbers along the genome and may comprise highly repeated regions. In practice, this meant that traditional sequencing approaches were unable to capture and reconstruct their extensive diversity, and early genomic methods would typically collapse TEs as high-coverage regions. The advent of high-quality long reads has allowed the identification and mapping of TEs, permitting reconstruction of their evolutionary history and impact on genome size and genes.

Determination of haplotype blocks and supergenes

Recent sequencing approaches and the development of methods to determine linkage between regions allow longer portions of the genome to be reconstructed, thus enabling detection of long portions of the genome that are inherited as a single block (**supergene**), which may have important evolutionary consequences.

Advances in the understanding of population genetics

The acquisition of a tremendous amount of genomic data has had an outstanding impact on population genomics because it has enabled the detection of **runs of homozygosity** along the genome, the inference of **ancestral recombination graphics**, the discovery of **barrier loci**, and distinction between introgression and incomplete lineage sorting.

Increased power to reconstruct phylogenies and the coalescence

Access to genomic data has spurred the development of new models to fully reconstruct relationships among species and populations. This includes genome-wide phylogenies and phylogenomic concordance factors [103].

Demographic histories

The use of genomic data to reconstruct demographic histories has enabled researchers to gain insight into population dynamics [104]. Recent advances in simulation models, which involves generating simulated data and comparing it to observed data, provide a powerful tool for understanding which factors may have played a significant role in shaping the evolutionary history of a lineage. These simulations can be intricate, and, by comparing them to empirical data, researchers are able to infer the probability of various demographic scenarios such as hybridization, population size fluctuations, and time of coalescence.

hybridization in the silverswords alliance, which enabled the exploitation of unoccupied ecological niches [48]. Hybridization can also lead to the evolution of intermediates, as shown in the *Argyranthemum* daisy radiation (Asteraceae, Canary Islands) in which two **homoploid hybrid species** occupy separate but intermediate geographic ranges of the parent species, with segregated ecological niches [49–51]. Two other examples are homoploid hybrids in the Hawaiian *Scaevola* naupaka radiation that occupy habitats intermediate relative to the dry and wet habitats of the parental species [52,53]. Finally, a direct consequence of hybridization might be introgression of a particular trait from one lineage to another, as was the case with muricate flowers in Hawaiian lobeliads (genera *Brighamia*, *Clermontia*, *Cyanea*, *Delissea*, *Lobelia* sect. *Galeatella*, *Lobelia* sect. *Revolutella*, and *Trematolobelia*) [54]. In this scenario, the introgression of functional alleles that facilitate the occupation of a vacant niche could result in phenotypic diversification and speciation.

What is the genetic basis of repeated evolution within adaptive radiations?

The repeated evolution of phenotypes or traits associated with the occupation of ecological niches offers a powerful approach for studying recurrent and potentially deterministic outcomes.

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Box 2. Adaptive radiations on oceanic islands

To evaluate the existence of broad patterns across studies of adaptive radiations on oceanic islands, we conducted a literature survey of >300 scientific articles (see supplemental information online). This search uncovered studies spanning 109 putative oceanic island adaptive radiations (see Figure 1 in main text and Table S1; a comprehensive set of criteria on how we classified the radiations is given in the supplemental information online). Across the oceanic island adaptive radiations identified, we found that specific taxonomic groups were substantially overrepresented, encompassing 55 different plant and 39 arthropod radiations. From these, Asteraceae/Compositae (asters, 17 radiations), Carabidae (ground beetles, six radiations), and Lamiaceae (mints, five radiations) had the highest reported number of oceanic island adaptive radiations (see Figure 2 in main text). Although some of these are among the most diverse lineages on continents, these organism groups are also particularly successful on islands. In terms of geography (Figure I), the largest number of radiations are reported for Hawai'i (38 radiations), Canary Islands (21), and Galápagos (10).

Notably, most of the studied radiations have received little attention, and 51 of 109 radiations were investigated in a single paper, 38 in two to four papers, 12 in five to nine papers, and only eight in ≥ten papers. With 48 articles, the Galápagos finches were the most studied oceanic island adaptive radiation and accounted for ~15% of the literature surveyed (see Table S1 in the supplemental information online). The majority of the studies used DNA sequence data of single markers (131 articles), some form of morphological data (99 articles), or ecological data (81 articles). Only 48 (~15% of the entire set) studies employed some form of genomic-level data (e.g., RADseq, whole-genome resequencing, transcriptome, genome assemblies; see Table S1 in the supplemental information online).

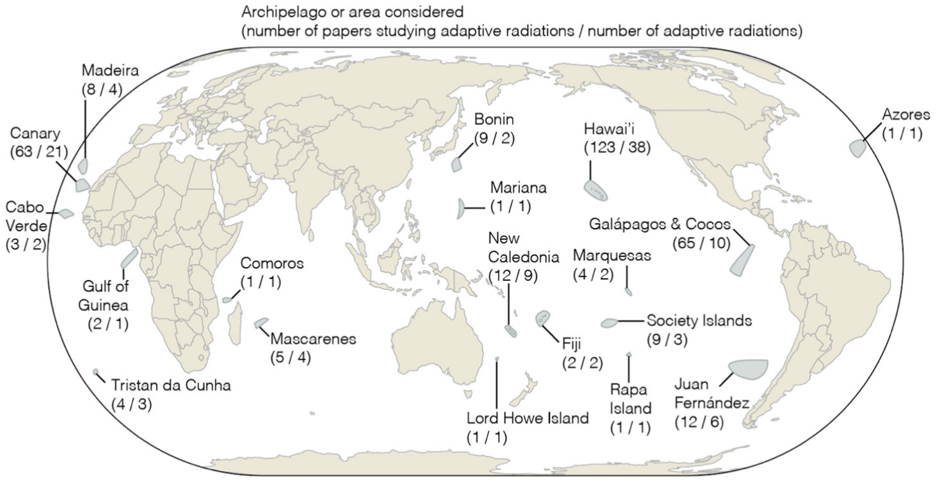

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Figure I. A global view of the number and distribution of adaptive radiations on islands. Numbers in parentheses give the number of articles studying adaptive radiation (left) and the number of adaptive radiations studied (right). The full dataset and criteria for establishing archipelagos are found in Table S1 in the supplemental information online. We retained New Caledonia because this continental island has been submerged, and therefore evolutionary and ecological processes occurred in a similar way to oceanic islands.

An important feature of oceanic island adaptive radiations is that species are, by definition, closely related, such that a common genomic and phenotypic background is likely, thus elevating prospects for the basis of repeated evolution. In addition, the diverse, discrete, and mosaic distribution of ecosystems on some islands can foster instances of repeated evolution of phenotypic traits and ecological occupation [55], thereby providing natural experiments to understand the genomic and ecological basis of traits associated with niche usage. Several studies identified in our literature search provided evidence of repeated evolution, including the Galápagos *Scalesia* radiation in which lobed-leaf morphologies evolved at least three times on different islands as a putative adaptive trait to arid conditions, whereas the tree habit evolved twice [56]. Similarly, evolutionary shifts to arid (xerophytes), humid (hygrophytes), and transition habitats (mesophytes)

Glossary

Adaptive radiation: the process in which multiple lineages diversify rapidly from a single ancestral lineage into a multitude of ecologically distinct forms.

Allopolyploid species: species with more than two haploid sets of chromosomes that are dissimilar and derived from different species.

Ancestral recombination graph: model used to represent coalescence and recombination events on a genome.

Barrier loci: loci that resist homogenization when gene flow occurs.

Convergent evolution: the evolution of similar and derived phenotypes from dissimilar ancestral phenotypes.

Diploidization: the process in which a polyploid genome reverts to a diploid condition.

Disharmonic communities: communities that have an uneven composition and distribution of taxonomic groups compared to a mainland source.

Ecological release: population-level niche expansions and shifts when a constraining interspecific interaction is reduced or removed.

Ecological versatility: the ability to occupy a set of disparate environments.

Homoploid hybrid speciation: when two species of the same ploidy level give rise to a hybrid species with the same ploidy level.

Parallel evolution: the evolution of similar and derived phenotypes from similar ancestral phenotypes.

Population genetic diversity debt: the genetic variation that will be lost following drift and/or natural selection.

Runs of homozygosity: contiguous regions of the genome in which an individual is homozygous across all sites.

Shared ancestral polymorphism: the ancestral genetic variation available in the genome.

Supergene: a group of genes that are inherited as a single genomic region and which jointly encode complex phenotypes.

Synteny: physical colocalization of genetic loci on the same chromosome within an individual or species.

Box 3. Study design for investigating the genomics of oceanic island adaptive radiations

One of the biggest advances brought by the 'genomics revolution' has been the convergence and integration of fields that relied on genetic data but have been traditionally distant, including phylogenetic systematics, population genetics, and functional genetics. Below we describe the ideal design for each of the questions identified.

What is the basis of genetic variation underlying adaptive radiations on oceanic islands?

To fully understand the origins, maintenance, and evolution of genetic variation, an ideal study design will include closely related outgroups such that phylogenetic reconstructions can be rooted and alleles can be polarized to find their ancestral state. The design will also benefit from a broad and geographically representative sampling of insular populations to fully identify and understand divergence and differentiation among populations. The characterization and quantification of unique genetic variation can be achieved by decomposing genetic variation, studying population structure, exploring changes of allelic frequencies along the genome, scans of selection, selective sweeps, and reconstructing the ancestral recombination graphic. Introgression can be determined by establishing excess allele-sharing (e.g., Paterson's D or ABBA-BABA) and by demographic simulations that explicitly take hybridization into account.

What is the genetic basis of repeated evolution within adaptive radiations?

Lee and Coop [105] put together a comprehensive set of recommendations to distinguish the contribution of the three sources of repeated variation, namely *de novo* mutation, standing genetic variation, and introgression. Their recommendations involve the determination of long haplotypes and patterns of coalescence [105], and an experimental design will benefit from high-coverage data so that linkage can be estimated with confidence.

What is the genetic basis of repeated evolution across adaptive radiations?

The advent of chromosome-resolved genomes allows mapping of conserved (syntenic) and non-conserved regions of the genomes. By sequencing multiple genomes, and aligning and comparing them, one is able to understand which areas of the genome encompass broad genetic variation. Specifically, comparative genomic approaches permit the identification of general trends across large taxonomic lineages such as gene-family expansions (e.g., gene duplications) and contractions (gene losses), evidence of selection (dN/dS ratios), and mapping of gene features (synteny of genes, and TE locations). By functionally annotating genes using databases and model organism inferences, we are able to develop clear hypotheses about the causal links between features of the genome and their functions. These links should ideally be experimentally validated with functional genetic tools such as CRISPR and transcriptomic experiments. By determining sets of closely related genes in multiple genomes ('gene families') and studying their relatedness (the phylogeny of the gene family), one is able to understand expansions and contractions, and to determine the divergence of subgroups within the family.

When did the alleles underlying trait utility in adaptive radiations evolve?

Time-calibrated phylogenetic reconstructions allow an estimate of the divergence between lineages (species) to be obtained. If the allele of interest is present in a pair of species, it can be generally inferred that it pre-dates the divergence (speciation) event. The design benefits from including multiple outgroups to exclude scenarios of loss of a particular allele in a single outgroup. Determination of mutation rates, and simulations of the coalescent accounting for selective pressures and hybridization, can be used to obtain estimates for given alleles and haplotypes (Box 1).

What is the role of broad-scale genetic variation on oceanic island adaptive radiations?

Large-scale variation can be studied by comparing genomes from outgroups and radiations and by comparing lineages within radiations. Large-scale variation can also be putatively linked to ecological changes in some designs, although experiments such as CRISPR functional validation should be employed. Among-taxon comparisons can provide a window to conserved versus non-conserved genomic regions, whereas population-level whole-genome sequencing will complement this by informing on non-recombining blocks and on areas of the genome with excessive genomic divergence or differentiation. Novel techniques such as haplotagging hold great promise in determining large blocks under linkage at an affordable cost [106].

What is the prevalence of combinatorial effects on oceanic island adaptive radiations?

Combinatorial effects involve understanding whether hybridization and population divergence has catalyzed speciation and adaptation. The experimental design involves sequencing multiple individuals from different populations, testing for excess allele-sharing and genomic divergence, and performing demographic simulations with scenarios of where hybridization occurs.

have occurred repeatedly in Cape Verdean wall-rockets (*Diplotaxis*) [57,58]. In animals, several lineages of Hawaiian spiders show independent and repeated evolutionary origins of ecomorphs, notably stick spiders (genus *Ariamnes*) [59] and long-jawed spiders (genus *Tetragnatha*) [60]; in

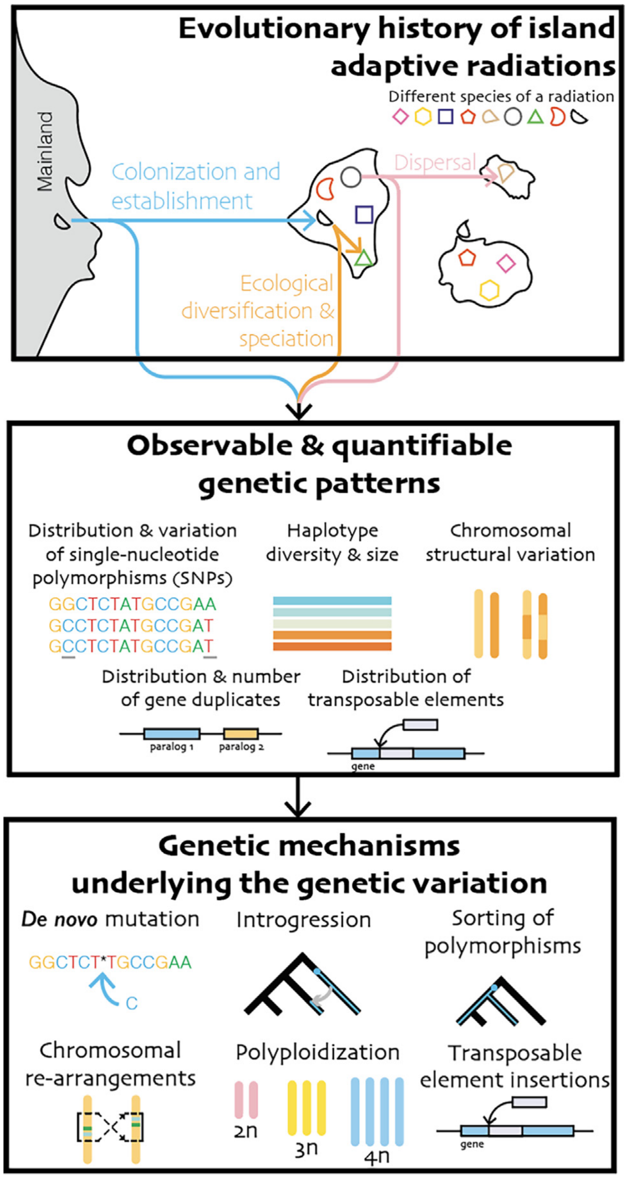

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Figure 1. Evolutionary history, observable genomic patterns, and mechanisms of an adaptive radiation. The top panel shows a graphical representation of one possible trajectory of an adaptive radiation involving colonization, establishment, *in situ* speciation and ecological diversification, and subsequent dispersal. The middle panel displays some possible types of genetic patterns that can be observed and quantified to disentangle the contributions and impacts of the different processes (SNPs, haplotype diversity and size, chromosomal variation, distribution and number of gene duplicates and transposable elements). The bottom panel highlights possible genomic mechanisms that can be inferred from the genomic patterns from the intermediate box (mutation, hybridization, ancestral polymorphism, rearrangements, polyploidization, transposable element insertions).

both lineages, taxa with similar niche and phenotype have evolved from different ancestors within the radiation.

Three mechanisms have been suggested to underlie repeated evolution, **parallel evolution,** or **convergent evolution** during radiations of oceanic island biota: hybridization (introgression), **shared ancestral polymorphism**, and *de novo* mutation [61,62]. Vizueta *et al.* [63] found identical amino acid shifts in different lineages of *Dysdera* spiders (Canary Islands), suggesting *de novo* evolution of dietal phenotypes. In Galápagos *Hogna* wolf spiders, introgression underlies parallel evolution [64,65]. In the woody Hawaiian *Metrosideros*, a rich pool of ancestral genetic variation and the reassortment of this variation have likely fueled the radiation [66]. Despite these important insights, the prevalence and relative importance of these mechanisms remain mostly unexplored.

What is the genetic basis of repeated evolution across adaptive radiations?

Our literature review revealed that particular taxonomic groups have repeatedly and extensively radiated across multiple archipelagos, but that not much research has been done to compare the genetic basis of repeated phenotypic evolution across radiations (Figure 2). The repeated occurrence of adaptive radiations in taxa from the same higher taxonomic group offers a powerful approach for understanding to what extent intrinsic factors facilitate radiations. Among intrinsic factors, we consider both the underlying genomic basis and the phenotypic traits themselves. Noticeably, the groups radiating frequently on islands are not always from taxa that are the most globally diverse. For example, Orchidaceae is one of the most species-rich plant families, but orchids are underrepresented as adaptive radiations on remote islands, likely because their dependence on mycorrhiza and specialized floral biology limits establishment [67,68]. The tendency of some groups to adaptively radiate on islands could indicate that particular families have an appropriate set of traits to disperse, establish, and speciate in relatively isolated environments [7,10,62], and that members of these families have capabilities to quickly adapt and fill ecological niches. As an example, the basis of **ecological versatility** for Curculionidae (snout weevils) is associated with their capacity to feed on different plant hosts [69–72], whereas a 'weedy' life history might benefit radiation in the Asteraceae. The high potential for particular traits

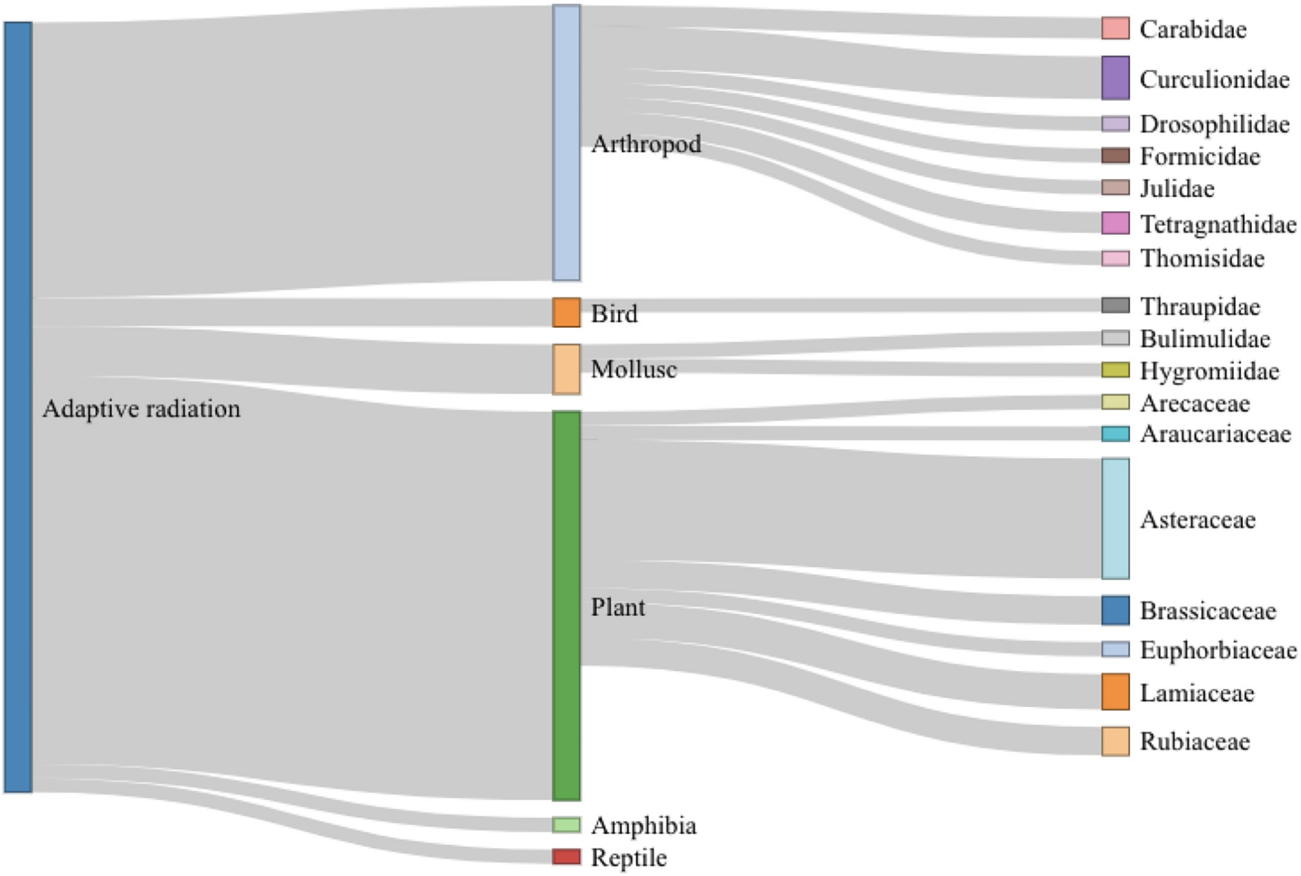

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Figure 2. Overall number of hypothetical adaptive radiations presented by taxon. The 109 adaptive radiations identified in our review of the literature (bar to the left) are organized by major taxa (bars in the middle). On the right we display families in which two or more adaptive radiations were found. The size of the bar indicates the number of radiations within each. The supplemental information online provides details of how we scored the hypothetical radiations. Specifically, the dataset collected is found in Table S1 and a thorough description on scoring the adaptive radiations is provided in the supplemental information.

to repeatedly evolve [55], such as variation in beak morphology in birds, seems to be commonplace in multiple radiations.

The tendency to radiate may involve a combination of ecological, phenotypic, and genomic factors. For now, the paucity of comparative genomic studies (Box 2) revealed by our literature search makes it difficult to identify the underlying genetic basis that is responsible for the diversification, although this remains a central aspect of understanding the process of radiation. The combination of high-quality genomes and comparative genomics will likely provide answers to this question and open new avenues of research.

When did the alleles underlying trait utility in adaptive radiations evolve?

Trait utility, together with common ancestry, rapid speciation, and phenotype–environment correlation, is one of the four criteria outlined to diagnose the adaptive nature of a radiation, and it characterizes trait performance or fitness in different environments [22]. Some phenotypic variation of particular traits, such as leaves in plants and beaks in birds, seem to underlie repeated changes across oceanic island adaptive radiations, and this may be facilitated by particular genomic architectures [41]. Genomic data allow the age of genetic variants to be estimated, and there is accumulating evidence for the role of 'ancestral genetic variation' in producing new phenotypes [38,66,73]. For instance, there is a 240 000 bp long haplotype encompassing the *ALX1* homeobox gene in Galápagos finches. This gene is associated with beak morphology, which finches use to feed on different seeds (trait utility), and the variation within the haplotype pre-dates the origin of the radiation [40,73–75].

What is the role of broad-scale genetic variation on oceanic island adaptive radiations?

Because of its convenience and power, the field of population genomics has traditionally focused on understanding how the frequencies of SNPs vary between populations and over time. However, our understanding of phenotypic traits and local adaptation remains incomplete until we are able to make sense of the broad-scale variation thatis increasingly being uncovered as novel technologies emerge (Box 1). We found evidence that the following five types of broad-scale genetic variation have contributed to oceanic adaptive radiations.

(i) Transposable elements (TEs): these are DNA sequences that proliferate along the genome, thus having an impact on genome size and cell economy, and can directly interfere with genes [76,77]. When TEs jump within a genic region they can lead to frameshifts, to the creation of a pseudogene, or to the movement of genes. Instability caused by founder events, inbreeding, and environmental stresses typical of oceanic island adaptive radiations could suppress TE regulation (i.e., the genome shock hypothesis) [78]. This could lead to an upsurge of TE insertions, especially when combined with low effective population sizes which decrease the efficacy of selection in purging deleterious mutations [78]. The adaptive radiation of Caribbean *Anolis* lizards (in a mixture of continental and oceanic islands) has an unusual accumulation of TEs within *HOX* clusters [79,80], which is hypothesized to be associated with increased phenotypic variation [80]. However, compared to closely related lineages, the Hawaiian *Tetragnatha kauaiensis* [81], the Macaronesian *Dysdera silvatica* [82,83], and the Galápagos *Scalesia atractyloides* [84] show no evidence of TE proliferation.

(ii) Gene duplication: this can lead to the formation of new phenotypes – one of the copies could acquire novel functions (neofunctionalization) or both copies can become specialized, resulting in two separate genes contributing to the function of the original ancestral gene (subfunctionalization) [79]. All these phenomena also take place in the continent, although they appear to act faster on islands. As an example, evidence from the silverswords shows that the floral genes *ASAP1* and *ASAP3* are duplicates, likely resulting from allopolyploidization (**allopolyploid species**) [85]. In addition, the genomes of the spiders *T. kauaiensis* (Hawaiʻi) and *D. silvatica* (Macaronesia) contain evidence for gene-family expansions associated with sensory perception of taste, chemosensory ability, and metabolism [81,82].

(iii) Haplotype blocks: these are non-recombining portions of the genome that are inherited together [86,87] and function as blueprints for complex phenotypes [86]. They are being identified in an increasing number of organisms with the help of genomic data, which enable reconstruction of linkage along the genome. The only evidence of haplotype blocks we are aware of on oceanic adaptive radiations comes from the Galápagos finches, in which beak development genes are suggested to be overrepresented in these blocks [75].

(iv) Chromosomal rearrangements: these include translocations, fusions, agmatoploidy, dysploidy, inversions, and fissions that might result in new genetic combinations by changing linkage patterns or by separating genes from their regulatory elements [86,88], and often underlie haplotype blocks. In animals, the most studied group comprises >100 species of subgenus *Drosophila* from Hawaiʻi and displays a strong pattern of inversion polymorphism. **Syntenic** analyses of the *S. atractyloides* genome revealed strong associations between gene-rich regions and inversions [84].

(v) Polyploidy: this phenomenon has been suggested as an important mechanism for ecological versatility and phenotypic evolution in plants [89]. We detected a high incidence of polyploidy in radiating plant lineages, in line with previous more comprehensive research showing that many endemic plants on islands are polyploids (80% of Hawaiian endemics [90] and >60% of Juan Fernández endemics [91]). It has been suggested that the colonizing ancestors of many of these lineages may already have been ancestral polyploids [92] and that elevated ploidy might act as a catalyst of ecological versatility through the 'two heads think better than one' analogy. Empowered by two (sub)genomes, the colonizing lineage has more genes and more alleles, which can translate into a potentially more efficient response to novel ecological conditions [85,92]. Although this is plausible, polyploidization could also have the opposite effect by inhibiting responses to selection if an advantageous allele is recessive and masked by the remaining alleles [93]. *S. atractyloides* is a tetraploid species, and it has been speculated that **diploidization** in this lineage slowed down as a result of insular adaptation [84].

What is the prevalence of combinatorial effects on oceanic island adaptive radiations?

The combinatorial synthesis postulates that when ancient genetic variation is brought together by hybridization, it might catalyze speciation processes [38]. This synthesis emerged from the growing recognition of the role of hybridization in increasing the genetic variability of lineages [38,73,94], which opposes the long-standing view that hybridization has a negative effect on biodiversity [4] and that hybrids are 'evolutionary noise' [95]. An important consideration of the combinatorial synthesis is the time-window wherein hybridization occurs: if the hybridizing species have diverged only minimally, hybridization might have no effect [96] or even lead to lineage fusion, as reported for the Galápagos tortoises [97], whereas with higher levels of species divergence introgression may not be possible or could result in sterile progeny owing to the build-up of reproductive barriers. Combinatorial events occur between these two periods, and it is likely that the temporal duration of this window is taxon- or lineage-specific.

Combinatorial effects may occur on oceanic islands through a combination of introgression and changes of allelic frequencies owing to genetic drift. Genetic drift has a potentially important role because the possibility of inter-island allopatric establishment and the regular cycles of disturbance and change within islands (e.g., volcanic, erosional, topographic) lead to population fragmentation with random changes in allelic frequencies. Fragmented and to some degree genetically diverged populations could become locally adapted, and secondary contact between these may catalyze combinatorial processes [10,98]. For example, in Hawaiʻi, ecosystems are fragmented by lava flows, creating mosaic ecosystem patches (kīpuka). Because ecological succession may take place across decades or centuries, kīpuka remain semi-isolated, and organisms with low dispersal abilities, such as arthropods or some plants, might be confined to particular kīpuka and undergo divergence [96,98]. On the island of Lanzarote in the Canary Islands, these same volcanically isolated patches are referred to as 'islotes'. In this same group of islands, climatic oscillations may change the ratio and the source of colonizing species, and thereby lead to cycles of secondary contact with continental species [44,99,100]. Some of the features and patterns recognized in the combinatorial synthesis are shared with the 'surfing syngameon hypothesis' [44,99], which postulates that secondary contact from the mainland or other islands followed by gene flow has generated genetic diversity in some regions in the Canary Islands. An integration of the combinatorial synthesis and the surfing syngameon may be warranted [101].

Concluding remarks: the future of genomic research on oceanic island adaptive radiations

The study of evolutionary genomics on oceanic island adaptive radiations is in its infancy, but has tremendous potential to inform us about ecology and evolution. The diversity and variation observed in these radiations can provide complementary insights to the outstanding body of work of adaptive radiation research, but which has been limited to a handful of biological systems. However, before this is possible, the gap between evolutionary genomics and island biology needs to be addressed. To this end, we have postulated a set of genomic questions that are connected to the evolution of island radiations (see Outstanding questions).

Considering the threats to island biotas, such as tourism, habitat loss, habitat fragmentation, introduced diseases, and invasive species [102], among many others, opportunities to study biodiversity on islands are likely to diminish rapidly unless current trends are reversed through accelerated conservation efforts.

Outstanding questions

What is the basis of genetic variation underlying adaptive radiations on oceanic islands?

What is the genetic basis of repeated evolution within adaptive radiations?

What is the genetic basis of repeated evolution across adaptive radiations?

When did the alleles underlying trait utility in adaptive radiations evolve?

What is the role of broad-scale genetic variation on oceanic island adaptive radiations?

What is the prevalence of combinatorial effects on oceanic island adaptive radiations?

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Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

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