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Why do some lineages radiate while others do not? Perspectives for future research on adaptive radiations

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Abstract

Understanding the processes that drive phenotypic diversification and underpin speciation is key to elucidating how biodiversity has evolved. Although these processes have been studied across a wide array of clades, adaptive radiations, which are systems with multiple closely related species and broad phenotypic diversity, have been particularly fruitful for teasing apart the factors that drive and constrain diversification. As such, adaptive radiations have become popular candidate study systems for determining the extent to which ecological features, including aspects of organisms and the environment, and inter- and intraspecific interactions, led to evolutionary diversification. Despite substantial past empirical and theoretical work, understanding mechanistically how adaptive radiations evolve remains a major challenge. Here, we highlight a number of understudied components of the environment and of lineages themselves, which may help further our understanding of speciation and adaptive radiation. We also outline some substantial remaining challenges to achieving a detailed understanding of adaptation, speciation, and the role of ecology in these processes. These major challenges include identifying factors that have a causative impact in promoting or constraining adaptive radiations, gaining a more holistic understanding of features of organisms and their environment that interact resulting in adaptation and speciation, and understanding whether the role of these organismal and environmental features varies throughout the radiation process. We conclude by providing perspectives on how future investigations into the adaptive radiation process can overcome these challenges, allowing us to glean mechanistic insights into adaptation and speciation.

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. It is not understood in all its appalling intricacy, but some understanding is in our grasp, and we may trust our own powers to obtain more. – G.G. Simpson, 1953

Background

Understanding the origin and persistence of phenotypic, ecological, and species diversity, and how this diversity changes through time, is a fundamental aim of evolutionary biology. To achieve this, researchers have undertaken both theoretical and empirical investigations in a variety of biological systems. Study systems with high phenotype and species diversity, including adaptive radiations (ARs), constitute particularly promising and popular focal study systems. ARs are groups of related species characterised by common ancestry, and correlated ecological and phenotypic variation that facilitates the exploitation of ecological variation (trait utility; Schluter 2000). Species within an AR originate via a series of, often rapid, speciation events that occur concurrently with the colonisation of various ecologically differentiated niches (Schluter 2000). Due to the explicit connections between phenotypic differentiation and the evolution of reproductive isolation in the AR process, ARs often provide unique opportunities to study the links between ecological variation and adaptation along multiple axes of variation, speciation, and the ways in which species-rich communities persist through time (Schluter 1996; Givnish and Sytsma 2000; Wellborn and Langerhans 2015; Stroud and Losos 2016). As a result, many ARs have become model systems for those wishing to disentangle the complex mechanisms underpinning phenotypic diversification, speciation, and species coexistence, with the aim of extending insights from these systems to better understand speciation as a whole (Martin and Richards 2019; Gillespie et al. 2020). To determine how evolution proceeds, many studies have aimed to pinpoint specific ecological factors that have either driven or constrained evolution and speciation within a given lineage (Grant 2017). Highlighting these features of organisms and their environment that drive or constrain evolution will help us understand the past evolution of clades, determine why some lineages radiate while others do not, and will also hint at the

predictability of evolution. Gaining a more mechanistic understanding of how and why some lineages undergo dramatic diversification and adaptation, and how adaptation and reproductive isolation are linked, will also provide insights into the future evolutionary trajectories of lineages, including, but not limited to, the response of lineages to climate and ecosystem change.

Researchers aiming to investigate factors that may drive AR often measure specific key aspects of the ecology across a clade, such as organism physiology, the environment, or interactions between organisms and their environment, and correlate these with the extent of species diversification within the clade. Significant positive associations between an axis of variation and diversification are then deemed representative of possible drivers of speciation and AR, and, likewise, significant negative associations are deemed representative of constraining factors (as in Wagner et al. 2012). ARs with independent instances of repeated diversification are particularly useful systems for undertaking such studies since they provide some degree of evolutionary replication and, depending on the types of ecosystems they span, can even act as natural experiments where biotic and abiotic conditions and traits vary between independent radiations (Salzburger et al. 2014). Studies that have linked specific organismal and environmental features with species diversity, have highlighted a number of potential drivers of AR, including genetic admixture and introgression between diverse lineages (Meier et al. 2017; De-Kayne et al. 2022), sexual selection (Wagner et al. 2012), gene duplication (Brawand et al. 2014), standing genetic variation (Choi et al. 2021), specific *de novo* mutations (Cerca et al. 2023), as well as broad-scale environmental biotic and abiotic features including energy (solar radiation or primary productivity), ecological opportunity (Wagner et al. 2012), and interactions between these and other environmental factors (Meier et al. 2019). However, despite these findings, and decades of research, robustly describing the role of these specific phenotypic features, the environment, and interactions between organisms and the environment, in the adaptation and speciation process during AR remains a challenge.

Outstanding challenges

Correlating specific organismal traits, and biotic and abiotic factors of the environment with rates of diversification, or the establishment of reproductive isolation, is often insufficient to comprehensively identify the factors associated with diversification or to determine the mechanistic role of associated factors in the adaptation and speciation process. Studies that investigate only a small number of traits and environmental characteristics often oversimplify the many different interconnected axes of ecological variation that are important for species evolution and persistence and the processes that are involved in the evolution of new species. For example, without a comprehensive understanding of organismal and environmental variation it is difficult to distinguish whether factors associated with diversification contribute towards, or are essential for, lineage diversification, whether they play a key role but act in concert with other key factors, or whether they are simply indirectly associated with other causative factors that drive AR. Aiming to separate causal factors from factors which are spuriously correlated with diversification should be a major priority for future research on speciation biology. Making this goal of understanding the role of specific factors in AR even more challenging is the fact that many aspects of organisms and the environment are ecologically and evolutionarily intertwined. These links include different traits that co-vary within an organism, and environmental variables that are correlated with one another. Additionally, organismal traits vary in their degree of environmental-dependent expression and their expected responses to different selective agents (Felmy et al. 2022). To better understand the AR process we must therefore investigate organisms and their environment less simplistically and aim to demonstrate causality in the links between trait variation and fitness. This will involve moving away from selecting and measuring only a handful of individual organism and environmental features, and instead trying to tease apart the ecological interactions that facilitate the evolution of diverse ARs, especially by considering understudied and complex aspects of organismal and environmental variation. It will also be important to better understand which aspects of organisms and their environment are linked to avoid the pitfalls that these associations pose for correlative studies of diversification. We must also try to include assessments of the multitude of key ecological interactions and feedbacks present which undoubtedly moderate adaptation and, in the case of ARs, may eventually drive or facilitate speciation.

Approaches that correlate organismal and environmental traits with speciation rate or the establishment of reproductive isolation also fail to account for both stochastic and non-linear relationships between differentiation and organismal or environmental features. To address this, it will be critical to identify when during the AR process factors associated with diversification play a mechanistic role, and if their contribution to diversification is consistent through time. Resolving the temporal importance of these factors will be important for determining how ARs proceed. Investigations that only associate contemporary trait variation and contemporary metrics of diversification may be particularly vulnerable to finding both false positive and false negative associations between specific factors and speciation. This challenge is particularly well-represented by the difficulty of determining whether ecological differentiation precedes or follows the establishment of reproductive isolation. Despite many narratives and proposed examples of ecological speciation, where ecological differentiation seems to precede speciation, the opposite, i.e., where ecological differentiation is thought to have developed after reproductive isolation and speciation is not uncommon. For instance, in Darwin's finches, character displacement and ecological differentiation occurred only after a degree of reproductive isolation had already accumulated (Lack 1983). Additionally, an increasing number of examples of strongly reproductively isolated species groups that show only weak ecological niche differentiation have been noted, suggesting that speciation and ecological divergence are sometimes decoupled processes (McPeck and Gavrillets 2006; Rundell and Price 2009; Svensson 2012, 2018; Cotoras et al. 2018; Czekanski-Moir and Rundell 2019). These challenges linked to our fundamental understanding of whether ecological differentiation promotes, constrains, or is neutral with respect to diversification are also shared with linking almost any intrinsic or extrinsic factor with speciation, and must be addressed to establish a deeper understanding of adaptive radiations and the speciation process more broadly.

Here, we highlight a number of complex aspects of ecology, including variation in organismal traits and environmental characteristics, which may play a role in the adaptive radiation process, and as such, warrant more detailed future investigations. Despite being challenging to investigate, a better

understanding of these complex components of ecology may help address the key outstanding questions relating to how adaptive radiations proceed that are posed in Box 1. We conclude by providing perspectives on how future investigations into adaptive radiations can address the challenges outlined above, with the aim of revealing how radiations evolve through time and the features of organisms and their environment that are important throughout the AR process.

Box 1 – Key questions for investigating adaptive radiations.

The environment:

- Do specific key abiotic or biotic factors drive or constrain AR?
- Is the presence or absence of these factors important or is the breadth or variation in the factor important?
- Does the multidimensional niche occupied by a lineage, rather than specific abiotic or biotic environmental conditions, impact the propensity for a lineage to radiate?
- Does the capacity for the abiotic and biotic environment to be modified by organisms in a lineage impact the propensity for the lineage to radiate?
- Does variation in abiotic or biotic conditions through time play a role in driving or constraining AR?
- Is ecological niche stability necessary for AR?

The organism:

- Do specific organismal features drive or constrain adaptive radiation?
- Is the presence and absence of specific key innovations important in facilitating AR or is it the breadth and variability of traits?
- Does variation in reproductive strategies across a lineage affect the likelihood adaptive radiation will occur?
- Does developmental variation play a role in AR?

The Environment

The niche and ecological speciation

The fundamental ecological niche describes the set of conditions in which a species can persist and is a central concept in ecology. Species within ARs are typically described as being adapted to different niches and, as such, understanding niche differentiation is key to understanding species diversification and species persistence during ARs. As an AR unfolds, there is an increase in overall occupied niche space by the radiating clade, either resulting from the broadening of the niche of an ancestral lineage followed by niche partitioning, or the budding off and subsequent colonisation of novel niche space by daughter species. Ecological speciation, the divergence of populations resulting from divergent selection along ecological axes, has been demonstrated to underpin diversification in many ARs (Schluter 2000; Nosil 2012; Matsubayashi and Yamaguchi 2022). As a result, understanding links between niche differentiation and AR is critical to determining the mechanistic role of ecological diversification in the adaptive radiation process. The emergence of intrinsic barriers to gene flow as a result of niche differentiation is largely thought to require differentiation across multiple ecological axes, rather than just one. This has been demonstrated in plants, such as in teosinte where species are differentiated across both temperature and soil chemistry (Aguirre-Liguori et al. 2019) and in animals, including Alpine whitefish which are differentiated across both water depth and diet (Doenz et al. 2018). Sequential diversification across multiple different axes of differentiation including habitat, feeding morphology, and patterning, has also been proposed as the foundation for particularly dramatic levels of diversification in some ARs of cichlid fishes (Kocher 2004). Theory also suggests that intrinsic barriers to gene flow may evolve more easily when divergence occurs across multiple axes of variation (Chevin et al. 2014). As a result, accurately delineating the components that make up the multidimensional ecological niche occupied by different species within the radiation and determining how differentiation across each of these axes evolved will be critical to understanding the AR process (also see chapter by Germain et al., this volume).

In contrast, the expansion of the niche and ecological differentiation during AR may only occur after the establishment of reproductive isolation (Losos and Ricklefs 2009; Gillespie et al. 2020). A recent comparative study on sister species in vertebrates suggested that ecological speciation through niche

divergence was much less common (<10% of trait sets) than non-ecological speciation where incipient species occupy similar niches (Anderson and Weir 2022), indicating that the importance and broader prevalence of ecological speciation in diversification may have been somewhat overstated (Rundell and Price 2009; Czekanski-Moir and Rundell 2019). Since empirical data has implicated such ‘isolation first’ diversification in ARs (Cotoras et al. 2018), more tests of this hypothesis across different ARs are needed. Identifying recent speciation events and assessing the degree of niche overlap between the resulting species might allow us to identify whether new species within ARs arise by occupying different niches, or whether this is achieved only after reproductive barriers have been established. Additionally, comparing closely related repeated cases of ecological divergence and measuring both niche occupancy of radiating lineages and levels of reproductive isolation may help disentangle the directionality, predictability, and mechanisms of divergence.

Despite the central role of niche theory in the AR literature, several challenges have prevented a more comprehensive integration of ecological niche theory with mechanistic evolutionary models of diversification. One challenge is that producing representative and comparative niche descriptions of organisms inhabiting complex environments is challenging, which may result in oversimplified characterizations of environmental variation, such as only characterising the trophic niche of species as either herbivorous or carnivorous, or the habitat use of fish as simply limnetic or benthic. Rather than capturing the multidimensionality of niches, such simplified descriptors often exclude other, key, aspects of ecology relevant to the persistence of species, including the range of abiotic and biotic conditions over which species can survive (Schluter 2000). Although more sophisticated ways of representing multidimensional niche space have been developed (e.g., the “*N*-dimensional hypervolume”; Blonder et al. 2018, which builds on foundational work by Hutchinson (1957)), the level of abstraction of these metrics, and the empirical data required to accurately implement these methods, makes them impractical as well as difficult to interpret. As a result, an intermediate approach, where continuous ecological data is used to provide a more detailed and comprehensive overview of niche quantification rather than categorical descriptor, may be a solution. Intermediate approaches avoid the need for overly abstract metrics that aim to capture all variation (see chapter by

Germain et al., this volume) but are still sensitive to the possibility that multiple interacting factors may be important for diversification. Without developing this kind of nuanced approach and aiming to understand niche variation more comprehensively, and how it might change over the course of an AR (Harmon et al. 2019), it will remain challenging to draw comparisons across systems and to highlight components of the niche critical to the AR process.

The frequent lack of knowledge on the temporal consistency of niche divergence (or lack thereof) also poses challenges for assessing its contribution to the divergence process. Although some aspects of the biotic and abiotic environment may remain relatively consistent through time, facilitating species divergence and persistence, other aspects of the environment vary. Such fluctuations likely result in dynamic selection pressures which vary over time. These potential changes pose a significant challenge for estimating links between niche variation in organisms estimated at a single contemporary time point, and metrics of diversification. For instance, the irregular cycles of disturbances in oceanic archipelagos can both create and remove niche space and ecological opportunity (Whittaker 1995; and even result in species extinction - discussed in more detail below) but these dramatic historical changes are not necessarily reflected by contemporary patterns of organismal and environmental characteristics. Furthermore, cases of putative multidimensional adaptation and ecological speciation are known to proceed in non-linear ways, with populations varying through time in their degree of adaptation to a given environment as well as the strength of reproductive isolation. For example, barriers to gene flow between species can become both stronger and weaker over time in response to a number of different factors including organismal and environmental changes. This has been demonstrated by extreme cases, where reverse speciation has occurred between previously ecologically differentiated and reproductively isolated species, which may be caused by rapidly changing abiotic and biotic environmental conditions. For example, anthropogenically-induced eutrophication of lakes led to the breakdown of ecological niches and subsequently ecological distinctiveness and reproductive isolation between Alpine whitefish species, which were previously more genetically differentiated (Vonlanthen et al. 2012; Frei et al. 2022). Radiating species themselves likely have a feedback effect on ecosystems, and as such can also play a

role in changing the ecological landscape (Matthews et al. 2016). Early in the radiation process species that evolve may modify existing features of the environment resulting in the alteration, creation, or even loss of niches, resulting in substantial effects on ecological differentiation and speciation. For example, the co-occurrence of green ecomorphs in *Tetragnatha* spiders has been suggested as a potential trigger of ecomorph diversification through competition (Cotoras et al. 2018). This temporal variation makes it particularly challenging to determine which features drive AR, particularly based on inference from the most common forms of data, that of single timepoints. Better utilising both ecological and evolutionary time-series data, including the ever-growing feasibility of sequencing historical specimens (as used in Frei et al. 2022), investigating the fossil or sediment record (for those species which readily fossilise or are preserved in sediment deposits; Ngoepe et al. 2023), or undertaking chronosequence-based approaches that involve sampling across successional landscapes such as volcanic islands or areas of glacier retreat, will be key to disentangling the temporal components of niche differentiation during ARs. Data from multiple timepoints or timepoint-equivalents would allow us to investigate both contemporary patterns of niche differentiation and the historical trajectory of change.

Biotic interactions

One of the most complex and challenging barriers to better understanding the ecology of organisms and links between ecology and adaptive radiation is the fact that individuals, populations, and species rarely persist in isolation. In addition to the interactions between organisms and their environment (discussed above), biotic interactions both within and between species are key features of ecosystems, impacting adaptation and speciation. However, the complexity and temporal variation in biotic interactions poses a challenge to quantifying and fully integrating their role into our understanding of the AR process. Biotic interactions play a significant role in the evolution and maintenance of ecological communities, shaping the fitness, abundances, spatial ranges, and, ultimately, the evolutionary trajectories of species (Weber et al. 2017). Five main types of biotic interactions have been described - competition, predation, herbivory, parasitism, and mutualism (Krebs 1985). Each of these may constitute a cause and, or, consequence of phenotypic divergence and speciation, and

different types of interaction may impact different stages of the AR process. Many biotic interactions have negative effects on organismal fitness. As a result, biotic interactions may impose or alter selection pressures and reduce the likelihood of diversification due to directional selection. Alternatively, biotic interactions can sometimes promote diversification by causing divergent natural selection (Nosil 2012).

Competition can be a powerful agent of character displacement and divergent natural selection, and has been described as underpinning some of the most iconic ARs, including Darwin's finches, where food competition and changes to song drove divergence in beak size and shape (Huber and Podos 2006; Grant 2017). While this process may not directly establish barriers to gene flow between populations (and in many cases reproductive isolation may have already built up), competition can cause organisms to switch to new niches which might have indirect, but important, implications for ecological speciation (discussed above; Brown and Wilson 1956). However, despite being frequently invoked as a driving force for niche differentiation, few studies have demonstrated its existence and, more importantly, its intensity. While the existence of competition is typically demonstrated or inferred using various proxies such as measuring feeding traits, recording foraging place or time, gut content analysis, or field observations, an explicit characterization of its intensity is challenging and, as a result, rarely reported. Since a limitation on resource availability is often the selective force that drives niche differentiation, a better understanding of competition will be key for understanding the AR process.

Although comparatively less well studied, the roles of other biotic interactions including herbivory and parasitism in driving AR have also been investigated. The links between herbivory and diversification have mostly been studied from a macroevolutionary perspective (Wheat et al. 2007). For example, there has been substantial interest in whether diversification is associated with an expansion in novel chemical defences in different plant species, making them distasteful or toxic to some herbivores (e.g., in Burseraceae; Bécerra et al. 2009), or whether declines in chemical defences have facilitated diversification (e.g., in *Asclepias*/milkweeds; Agrawal et al. 2009). Parasitism has also

been noted in ARs (also see chapter by Vanhove et al., this volume), with some stickleback populations being less resistant to parasites than others, suggesting that selection against migrants and parasite-mediated post-mating isolation may drive divergence (El Nagar and MacColl 2016).

Many biological interactions shape the selective pressures that diverging lineages are exposed to, and while many types of interactions might result in lower fitness, they may have varying impacts on AR. Although competition for resources may favour diversification, predation might have the opposite effect, hindering diversification (McGee et al. 2020; Chaparro-Pedraza et al. 2022). However, mutualism is also prevalent across ARs, and by their nature, interactions of this kind drive diversification by facilitating the occupation of new niche space and leading directly to reproductive isolation (e.g., reinforcement; Hopkins 2013). For instance, plant-pollinator mutualisms have been shown to play a key role in diversification in several plant clades. Orchids of the genus *Disa* are pollinated by nearly all major groups of pollinating insects, with evidence of repeated adaptation to similar pollinators (Johnson et al. 1998). Moreover, in the bee orchid (*Ophrys*) radiation, divergence in floral scent and flower morphology presumably to attract different bee species may underlie speciation through pollinator shifts (Baguette et al. 2020). As with many interactions, mutualistic interactions are not always static in their nature through time, and the breakdown of mutualistic interactions into parasitic interactions have also been indicated as fuelling AR (e.g., in the *Yucca* moths; Pellmyr and Leebens-Mack 2000). Determining whether the presence or absence of certain biotic interactions is a cause or consequence of AR is challenging, not least because the effect of these interactions on diversification may not be consistent across taxonomic groups or through the radiation process. Radiations thought to be catalysed by competitive interactions, for example, may undergo an early burst of diversification, but this rate may decrease over time (Martin and Richards 2019). This change in the extent and strength of biotic interactions over time represents eco-evo feedbacks where the evolution of lineages occupying new niches has an impact on the selective pressures that other organisms experience (directly or indirectly).

In extreme cases, biotic interactions and abiotic environmental change may impact fitness or demography so severely that populations or species go extinct (Frei et al. 2022). The link between extinction and AR is likely situation-dependent, and the specific consequences of extinction may depend on the specific species or populations that go extinct and the rate and amount of extinction, i.e., local extinction or total species loss (Losos 2010). Extinction may have a range of effects, including the reduction or altering of the network of biotic interactions within an ecosystem. While extinction may lead to the vacancy of niches, translating into novel opportunities for surviving lineages, it may also lead to the collapse of niche space, for example through trophic cascades or indirect interactions. Although it has been suggested that high turn-over rates of species on islands are expected to promote AR (Gillespie et al. 2020), associating divergence with extinction is challenging because many lineages have gone extinct without tangible evidence. Whether it is possible to infer extinction rates from phylogenetic data alone is controversial and it remains a challenge to accurately determine the frequency of extinction (Stadler 2011). Understanding the link between speciation and extinction may be particularly important, and difficult, if species are often ‘ephemeral’, with speciation occurring readily but most species failing to persist through time (Rosenblum et al. 2012). This ultimately limits our understanding on whether extinction and the changes to biotic interactions that follow (as well as subsequent abiotic changes) have a net positive or negative effect on diversification, speciation, and specifically, AR.

The organism

Life history

The role of specific, key, organismal traits in underpinning AR has been the focus of the many investigations. This focus stems from the tight links between trait utility, where a given trait confers a fitness advantage in a given environment, and diversification across ARs. As a result, many have aimed to identify whether specific traits, or variance in traits, might make lineages more likely to undergo ecological diversification and/or facilitate the establishment and maintenance of reproductive isolation. Due to the tight link between adaptation and the establishment of reproductive isolation across ARs, traits that impact both the number and size of offspring, and how organisms interact with

their environment may play important roles in driving AR. One such aspect of organismal trait diversity is variation in life history strategies, which relates to the consequences of reproductive strategies and their role in organismal diversification (Stearns 1992). These life history traits include age and size at maturity, the size and number of offspring, lifespan, and body size. Since these traits may directly contribute to the occupation of a given niche or vary because they are associated with traits under direct selection, life history variation across a given clade may play an important role in diversification and coexistence of radiating species during AR. Many ARs are associated with substantial interspecific differences in life history traits (Schluter 2000), although, as with much interspecific variation, determining whether this variation drove speciation or emerged following speciation is challenging. One of the most well-studied ARs that exhibit life history variation is the radiation of lungless salamanders of the family Plethodontidae (Weaver et al. 2020). While some species within the family exhibit little phenotypic variation and have been the subject of studies focussing on non-adaptive radiations (Kozak et al. 2006; Rundell and Price 2009; Czekanski-Moir and Rundell 2019), other members of this species-rich radiation (which includes around 500 species) exhibit complex life cycles and differ greatly in their ontogenetic development (with or without larval stages), body sizes, and their age at first reproduction (Bruce 1996; Mueller et al. 2004). Another example relates to the cichlid fishes in Lake Tanganyika, in which about 250 ecologically, morphologically, and behaviourally distinct species evolved from a common ancestor in ~10 MY (Ronco et al. 2021), offspring numbers per clutch range between 5 and >10,000 (Konings 2015; Ronco et al. 2019) and egg sizes vary from ~1-8 mm (Kuwamura 1986; Konings 2015). While it has been shown that several trait-complexes such as body shape and mouth and jaw morphology show a strong phenotype-environment correlation in the Tanganyika cichlid radiation (Ronco et al. 2021), the causal links between the evolution of life history traits, ecology, and AR are unknown, despite an amazing variance in strategies.

To better determine the role of life history variation in facilitating or constraining ARs, and to avoid the pitfall of mistakenly highlighting all variables that correlate in some way with life history variation, it will be important to investigate study systems that have varying degrees of diversity but

with minimal trait variation outside of life history variation, ecological differentiation, and reproductive isolation. Future research should also identify whether a propensity to radiate is impacted by the variance in specific life history traits or in the presence or absence of specific key innovations. This could be achieved by assessing whether radiating lineages exhibit a wide range of age at maturity, body size at maturity, number and size of offspring, and by determining whether this variation is an emergent property and axis of early variation during AR. Ideally, replicated study systems of varying ages could also be used to determine whether life history variation is important throughout the AR process or whether it plays a more prominent role in facilitating divergence early, or late, in the AR process.

Eco-evo-devo

The challenge of mechanistically understanding how ARs evolve is made even more complicated by the fact that variation within an organism's lifetime can also have considerable impacts on evolution. Although key traits are often measured on adult organisms, the multitude of phenotypic changes that occur throughout an organism's development represent important aspects of variation which can easily be overlooked. Capturing developmental variation may be critical for understanding both how speciation generally proceeds, and specifically how ARs evolve, because this variation can have significant impacts on key lineage characteristics, including demographic rates, reproductive rates, and interactions with other organisms. For example, body size, which plays a substantial role in underpinning metabolic processes and ecological interactions (Woodward et al. 2005; Eklöf et al. 2013), can increase four orders of magnitude throughout the lifetime of many fish species (Werner and Gilliam 1984), resulting in large, rapid, changes in the composition of populations and communities, and potentially contributing to the speciation process (Persson and de Roos 2013; Rudolf and Rasmussen 2013; Chaparro-Pedraza and de Roos 2020). Variation of this kind can, in turn, have substantial knock-on effects to population dynamics and biotic interactions. For example, an increase in the mortality rates of juveniles relative to adults could strengthen intraspecific competition, induce frequency-dependent selection, and potentially culminate in adaptive diversification (Chaparro-Pedraza 2022).

As a result, developmental variation has been studied across multiple ARs. This work has successfully highlighted a strong link between developmental variation, ecological opportunity, and ontogenetic shifts in habitats, diets, and resource requirements across ARs (Schluter 2000). Developmental changes occur across a variety of traits, meaning that over the course of their development and maturity individual organisms can vary widely in the ecological niches they occupy. For instance, predatory species that emerge from ARs and subsequently feed on other AR members have been described in various systems, including the African Lake cichlid radiations (Seehausen 2006), the Bahamas *Cyprinodon* pupfish radiations (Martin and Wainwright 2011), and the Lake Baikal amphipod radiation (Naumenko et al. 2017). Yet, because predators usually require an advantage in body size over their prey species (between 0.5 and 4 orders of magnitude; Heckmann et al. 2012), this ecological niche is typically only accessible for larger, older individuals.

In addition to modulating traits throughout an organism's lifetime, developmental variation can play a key role in differentiating species that result from AR and underpinning key innovations. A number of studies have investigated key morphological innovations that facilitate niche expansion during AR (summarised in Miller et al. 2023). Developmental variation that impacts how organisms interact with their specialised niche has been demonstrated in Darwin's finches, where beak height, a key axis of ecological variation and a trait involved in the establishment of reproductive isolation via its impact on song (Huber and Podos 2006), is related to the expression of the *BMP4* gene during development (Abzhanov et al. 2004). Similarly, in the Hawaiian spiny-legs, individuals of the species *Tetragnatha polychromata* change their colour and subsequently their trophic niche during development (Brewer et al. 2015). It is therefore likely that different selective pressures affect these species throughout their lifetime. Trying to determine the role of ontogenetic trait and niche shifts in facilitating AR will involve characterising organismal traits across ontogenetic stages and constitutes a challenging, but essential, avenue of future research.

Despite the potential for ontogenetic niche shifts (heterochrony) to facilitate adaptive divergence, and play a role in the AR process, theoretical work has shown that developmental changes may, in fact, hinder the radiation process. For example, while piscivorous morphs attain the largest body size among the African Lake cichlid radiations (Seehausen 2006), and their distinct piscivore-specific morphologies have already developed at the larval stage, they do not realise these ecological niches until they are adults, with small-bodied juvenile cichlids of many different morphs still competing for similar resources (Singh et al. 2017). As a result, and despite the widespread nature of ontogenetic diet shifts in different animal lineages (Werner 1988), this increased competition at the larval stages can potentially hinder AR, even in the presence of extensive ecological opportunity (Ten Brink and Seehausen 2022).

Evo-devo studies have already provided evidence of developmental variation underpinning important aspects of variation across ARs, but the degree to which analogous developmental changes may play a key role in facilitating AR in different taxa is unclear. Instances of re-use and re-wiring of developmental networks and developmental variation being associated with evolutionary innovation appear to be especially widespread across ARs (e.g., the evolution of morphological novelty via the re-wiring of ancestral gene-regulatory networks in cichlid radiations; Mehta et al. 2021; Singh et al. 2021). One classic example of evolutionary innovation being associated with developmental variation is the functionally decoupled oral and pharyngeal jaws of cichlid fishes (Liem 1973). Recent work shows that varying levels of modularity between the two jaws in younger versus older cichlid radiations may play a role in their propensity to diversify (Conith and Albertson 2021). Evolutionary developmental mechanisms have also given rise to key innovations and AR in plants (Fernández-Mazuecos and Glover 2017), including the evolution of flowers, which enabled radiation through plant-pollinator interactions (Grimaldi 1999). Early-diverging lineages of the angiosperm radiation exhibited lower floral development specialisation and were species-poor, in contrast to the species-rich groups with highly specialised flowers such as orchids (Melzer and Theißen 2016).

Developmental changes in the floral tube and stigma have contributed to the AR of *Petunia* in South America, giving rise to 20 species in <3 MY (Reck-Kortmann et al. 2014). Ecological speciation in

Petunia spp. has been linked to molecular changes in the R2R3-MYB family of transcriptional regulators that modulate plant floral development (Yuan et al. 2013). In the iconic AR of Hawaiian silverswords, it has been found that diverse species of trees, shrubs, mats, and vines have evolved from ancestral tarweed with major shifts in body plans as a result of regulatory changes in developmental pathways in <6 MY (Purugganan and Robichaux 2005).

Future research focusing on identifying differences in development between radiating species will be important to understand how eco-evo-devo contributes to speciation and AR, as links between evo-devo variation and a mechanistic understanding of speciation and AR remain tenuous and largely species-specific. For example, frameworks such as West-Eberhard's flexible-stem hypothesis (2003), which suggests that ancestral developmental plasticity sets the stage for AR, have aimed to mechanistically link developmental variation and AR. However, evidence supporting this hypothesis is scarce, as founder populations of most ARs no longer exist and have usually not left a substantial fossil record from which developmental variation can be studied. This has made it particularly challenging to identify causative aspects of developmental variation that may be critical for lineages to radiate. Future studies investigating the link between developmental variation and adaptive radiation should also investigate the role of developmental plasticity, which has been thought of as an important precursor to the emergence of evolutionary innovations, a feature of ARs (West-Eberhard 1989; Moczek et al. 2011). The presence of developmental plasticity in a lineage may have a strong influence on the propensity for a lineage to radiate since it may act as an avenue for species to colonise previously unoccupied niches (Hunter 1998), provided that these changes become heritable (genetic assimilation).

Next steps – perspectives for future adaptive radiation research

In our pursuit of better understanding how ARs evolve and the role of different aspects of organisms and their environments in driving or constraining AR two broad barriers remain: 1) overcoming the limitations of studying the diversification process with data from only one, or a limited number of, timepoints; and 2) separating mechanistic links between, often simplified, ecological factors and

diversification from indirect, sporadic, or spurious, associations. These challenges are not unique to understanding AR, and a better understanding of both will also help disentangle the speciation process more broadly. Additionally, there are a number of complex aspects of ecology (some of which are outlined above) which, despite exhibiting substantial variation across ARs, have yet to be fully integrated into our understanding of how and why some lineages diverge while others do not, and as such are ripe for future investigations into ARs.

Assessing variation through time

To better understand the mechanistic role of organismal or environmental factors in AR, and speciation more broadly, future studies should focus on trying to address questions in Box 1 while accounting, where possible, for the possibility that the factors that drive diversification act at specific timepoints in the AR process. This will involve expanding on correlative investigations based on data from a single timepoint and into time-series based investigations that involve the collection of data spanning organismal traits, environmental characteristics, links between organisms and their environment as well as the establishment of phenotypic and genomic differentiation through time. For example, measuring trait values within and between sister taxa at multiple timepoints will help determine whether changes in reproductive isolation or genetic divergence are positively correlated with trait change across time. While such approaches may not be possible in many old radiations, where contemporary dynamics in traits and reproductive isolation may be heavily influenced by short-term environmental stochasticity, producing and analysing time-series data across systems where evolutionary replicates are known to be of different ages may be particularly valuable. This approach will help characterise the trajectory of phenotypic diversification and will reveal whether species are becoming more or less differentiated over time. Future studies may consider measuring changes in phenotypic differentiation between timepoints i.e., ΔP_{ST} and changes in gene flow or reproductive isolation between timepoints i.e., ΔR_I . These studies would help determine whether the role of different lineage and environmental characteristics in driving diversification is consistent across timepoints, indicating a constant key role of a given organismal or environmental characteristic, or

whether variation in these associations through time reflects a scenario in which different factors play key roles at different parts of the radiation process. Future theoretical work should also aim to complement empirical investigations by explicitly including variable organismal traits, environmental conditions, and interactions to determine the ranges of conditions over which we might expect to see ARs persisting through time, resulting in more realistic and testable neutral expectations. This combination of theoretical and empirical studies would also help identify the role of chance and historical contingency, or a mixture of predictability and chance, in the evolution of ARs (see chapter by Roesti et al., this volume).

Separating correlation from causation

Studying repeated diversification amongst closely related species may be one of the few ways to avoid the pitfalls of trying to compare the causes and outcomes of speciation across taxonomic clades. Experimental approaches where abiotic or biotic factors are modified are also excellent ways to understand their impact in speciation (Rice and Hostert 1993), niche occupation, and coexistence (Pringle et al. 2019). For instance, raising different populations of *Drosophila melanogaster* on similar or different food mediums allows a quantification of the degree of reproductive isolation between pairs of populations (Rice and Hostert 1993). In their review of lab experiments aimed at understanding speciation, Rice and Hostert (1993) concluded that reproductive isolation evolved more readily when populations evolved in different environments, compared to when populations had evolved in similar environments (although a subsequent meta-analysis of research published since has failed to find any empirical support for this claim; B.J. Jarret et al. unpubl.). Findings from experimental evolution approaches can help address key questions, including identifying the role of ecological differentiation in speciation (discussed in more detail above; MacLean 2005; Stelkens and Bendixsen 2022), and can subsequently be used to guide investigations in natural systems such as ARs. Furthermore, ARs with independent instances of repeated diversification are particularly useful systems for undertaking such studies since they provide some degree of evolutionary replication and, depending on the types of ecosystems they span, can even act as natural experiments where biotic and

abiotic conditions and traits vary between independent radiations (Gillespie 2004; Mahler et al. 2013; Cerca et al. 2023).

Are islands the answer?

Undoubtedly, some natural systems lend themselves to addressing outstanding questions in ARs more than others, particularly with regard to overcoming the challenges outlined above. ARs that are relatively simple, or even manipulatable, where it is possible to understand organismal and environmental variation and metrics of diversification without resorting to oversimplifying ecosystems are particularly valuable. While many ARs do not fulfil these criteria, with some particularly complex and speciose systems being almost antithetical to a desired simplified system, island radiations represent compelling study systems to address some of the most pressing questions posed in Box 1 while overcoming the challenges outlined above. Island radiations that include islands of different ages may help us establish the trajectory of change in phenotype and reproductive isolation and instances where similar variation has evolved independently across islands may help us better understand causative factors that drive or constrain differentiation (also see chapter by Illera et al., this volume). Semi-isolated island ecosystems including volcanic oceanic islands, mountain tops, and expansive lake systems are known to harbour a substantial number of the world's ARs, and as a result have already formed the basis of a significant amount of research into ARs (Losos and Ricklefs 2009; Gillespie et al. 2020; Schenk 2021; Cerca et al. 2023; Miles et al. 2023). Additionally, since islands have historically been the focus of substantial ecological investigations, we often have a particularly detailed understanding of their biodiversity, climatic variation, and even the mechanisms that led to their formation (MacArthur and Wilson 1967; Simberloff and Wilson 1969; Whittaker et al. 2008; Valente et al. 2020). This glut of information for many island systems lends itself for teasing apart the topics outlined above, and opens the door for more detailed investigations with the power to look across spatial and temporal scales. Perhaps unsurprisingly, given the number of empirical examples of island ARs, theoretical work has confirmed the suitability of island archipelagos for AR (Kagawa and Seehausen 2020), as a result of the metapopulation dynamics that can play out across discrete areas of suitable habitat.

Islands also have a number of unique features which may have promoted ARs, including an abundance of fluctuating geographic barriers which may have provided important opportunities for populations to establish in allopatry, prior to (or in the absence of) ecological differentiation, allowing the subsequent accumulation of differences through genetic drift and founder effects. These dynamics have been well-documented in highly diverse plant radiations on Andean ‘sky-islands’, in which glaciation led to ‘flickering connectivity’ between diverging populations on mountaintops (Nevado et al. 2018; Flantua et al. 2019). Additionally, instances of secondary contact between isolated populations may also lead to character displacement through directional selection (Lack 1983). This scenario has been proposed for explaining diversification across the *Tetragnatha* spiny-leg radiation, where multiple species that represent green morphs are thought to have emerged and subsequently segregated from one another geographically. Eventually, when multiple green morphs come into secondary contact in the presence of open niches, competition is thought to lead to directional selection and the evolution of novel ecomorphs (Cotoras et al. 2018). Similarly, the rearrangement of dispersal barriers and the establishment of hybrid variants upon secondary contact has also been suggested as a way of generating diversity via strictly neutral processes (Sefc et al. 2017). Repeated cycles of disturbance on islands, such as volcanic eruptions, may also drive diversification through the creation and modification of environments, providing the opportunity for geographic isolation (Carson et al. 1990; Vandergast et al. 2004) and ecological variation (e.g., silverswords adapted to different lava substrates; Robichaux et al. 1990).

Finally, other features of islands, such as the degree of unbalanced taxonomic variation on oceanic islands or the total absence of specific taxa (e.g., non-flying mammals), may facilitate rapid diversification. The absence of specific clades may offer lineages the opportunity to occupy new niches, leading to extreme phenotypic and ecological variation. For instance, the plant family Asteraceae comprises mostly herbs and shrubs, but across different archipelagos tree-like forms have evolved repeatedly (Cerca et al. 2022). This in turn may provide opportunities for taxa able to

colonise and establish to occupy niches that were not available across their original ranges, facilitating extreme phenotypic and ecological variation.

Islands may therefore form valuable study systems for advancing our understanding of speciation and the evolution of ARs by allowing us to identify the role of complex aspects of ecology in driving diversification, in turn overcoming some of the most difficult challenges facing the field. Systems with independent radiations with varying degrees of diversity, which have evolved on neighbouring islands (including oceanic islands or lakes) with varying ages and ecology may be particularly fruitful for future research into ARs. Future research should also continue to take advantage of valuable island-like lake systems which preserve evidence of historical diversity in the form of remains and fossils stored in sediment deposits, as these remains provide unique opportunities for disentangling how ARs evolve (as in Muschick et al. 2018 and Ngoepe et al. 2023).

Concluding remarks

ARs provide the opportunity to glean a mechanistic understanding of adaptation and speciation and the aspects of ecology, including various organismal and environmental traits, which underpin these processes. While it is currently unclear which factors drive or facilitate AR across taxa, future studies that aim to address this knowledge gap should purposefully focus on identifying causative factors and determining the role of different factors at various stages of the AR process. Future research should not shy away from complex aspects of ecology (outlined above) and should aim to avoid overly simplistic descriptions of key organismal and environmental features. These detailed future investigations will help advance our understanding of the remarkable phenotypic and species diversity we observe across ARs, the predictability of this diversification, and how applicable these processes are for the speciation process more broadly.

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