Comparing Adaptive Radiations Across Space, Time, and Taxa

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Running title: Commonalities in Diverse Adaptive Radiations

Abstract

Adaptive radiation plays a fundamental role in understanding the evolutionary process. However, the concept has provoked tremendous controversy, with disagreements linked to the very different systems being examined. Here we seek common ground among disparate adaptive radiations, ranging from plants to insects and vertebrates and remote islands to lakes and continents, to understand processes shared across adaptive radiations. The need for open ecological space into which a group can radiate was identified for all systems. However, radiations differ considerably in the mechanisms of speciation within the radiation, depending on the interplay between selection imposed by the external environment and the evolution of intrinsic incompatibilities arising during speciation. Introgression also may play a role in species differentiation, and hybridization between divergent lineages may generate adaptive novelties via recombination. Moreover, for lineages in which differentiation is tied to the external environment, divergent selection between environments may play a dominant role, with diversity increasing by increasing environmental specialization. In contrast, for lineages that become isolated without any shift in environment or associated divergent selection, secondary sympatry will lead to direct interaction between closely relatives and, given genetic incompatibility, ecological divergence through character displacement. The conclusion is that adaptive radiation is produced by multiple processes, with differences dictated largely by whether the drivers tend to be external to the radiation (mostly the environment) or internal (interactions among members of the radiation). Adaptive radiations will only be useful for understanding evolutionary phenomena if we make these distinctions in comparing processes across lineages.

Background

Adaptive radiation, the evolutionary divergence of members of a single monophyletic lineage into a variety of adaptive forms (Futuyma 1998), has been considered the connector that unites ecology and evolution (Givnish & Sytsma 1997). Since capturing the attention of evolutionary biologists when Darwin discovered his eponymous Galapagos finches, studies of adaptive radiation have been central in developing our understanding of the mechanisms that drive speciation, diversification, and many associated ecological and evolutionary processes (Givnish & Sytsma 1997; Grant & Grant 2014; Schluter 2000; Simpson 1953). However, research on adaptive radiations is often as disparate as the ecologically differentiated species contained within a radiation, presenting the enormous challenge of generalizing across systems. One of the few uniting commonalities is that adaptive radiations generally require some form of ecological opportunity and are thus shaped by some form of divergent ecological selection (Schluter 2000; Stroud & Losos 2016), though many other factors are clearly involved (Poelstra *et al.* 2018). There is limited consensus on what processes shape adaptive radiations across space, time, and taxa. As a result, a diversity of processes has been implicated, but still many questions remain, about the processes that lead to adaptive radiation. The current paper arose from a meeting of the American Genetic Association held in Waimea, Hawaii, in July 2018 with the goals of synthesizing our knowledge of ecologically, geographically, and taxonomically diverse radiations (Fig. 1) to provide a more general understanding of adaptive radiation. We identify common denominators that underlie adaptive radiations in order to inspire a general framework for explaining when - and how - they occur.

We begin by assessing factors important in driving adaptive radiation, with particular focus on factors outlined in Box 1.

Ecological arena (Box 1A): A proper understanding of adaptive radiation requires a joint focus on both ecological and evolutionary processes, and how each influences the other. The primary requirement for adaptive radiation is ecological opportunity, in the form of ecological space that is unoccupied or underutilized by competing taxa and that may be evolutionarily exploited. A powerful form of ecological opportunity appears to be the colonization of novel habitats or areas that are devoid of other ecologically similar species largely due to geographic isolation or similar barriers that limit initial colonization. Examples include the colonization of remote islands and newly formed crater lakes, or - for host-associated organisms - a previously defended host (Ehrlich & Raven 1964) by the evolution a novel adaptation that enabled a taxon to diversify to specialist niches thereby made available (Brown Jr 1958). The importance of opportunity points to the order of colonization of lineages as important in dictating which radiates; priority effects from a diversifying lineage may prevent subsequent lineages from gaining a foothold (De Meester *et al.* 2016; Fukami 2015; Fukami *et al.* 2007) although whether or not immigration history influences the extent of diversification can depend on the founding populations' prior evolutionary history (Knope *et al.* 2012a). Alternatively, priority effects from a non-radiating lineage may preclude establishment by a secondary colonizer from the same lineage within that niche, potentially facilitating ecological exploration in the secondary colonizer. Priority effects may also operate within a radiation, whereby once a given phenotype is occupied by a species then it is rendered unavailable to other species, although ecological character displacement may alter the outcome of such priority effects (Stroud *et al.* 2019).

Evolutionary potential will determine the speed of adaptive divergence, whereas the degree of geographic isolation combined with the dispersal capacity of taxa in the regional species pool will determine the rate at which the habitat can be filled with other species, reducing ecological opportunity for adaptive radiation. Time is thus crucial, in a "race" between adaptation and immigration (Gillespie & Baldwin 2010; Vanoverbeke *et al.* 2016). Thus, in the Hawaiian Islands, the oldest of the current high islands (Kauai, ca. 5 million years old) emerged at a time when previous islands were low and far apart (Price & Clague 2002). With the profound isolation, and hence time, there was greater opportunity for ecological exploration and diversification on Kauai (Gillespie 2016). Subsequent appearance of younger islands has been associated with increased opportunity for island hopping and hence less time for ecological exploration by a single lineage. As a result, a number of lineages are characterized by ecological diversification on the oldest island only, with colonization of the younger islands by island hopping of already diverse ecological forms. Within any given radiation, the tendency for lineages to progress from older to younger islands appears to be indicative of strong priority effects associated with initial establishment on older islands inhibiting back colonization from younger islands – the 'progression rule' (Shaw & Gillespie 2016).

External vs internal factors involved in initial divergence (Box 1B): Here we define external factors as those that arise external to the radiation itself, such as through interactions with the environment and internal factors as those that arise within the radiation itself without the need for interactions with the environment, potentially due to genetic incompatibilities or secondary sexual traits (Mendelson *et al.* 2014).

External barriers coupled with divergent selection – When initial divergence is shaped by ecological adaptation, reproductive isolation may evolve as a consequence of divergent selection (Nosil 2012; Rundle & Nosil 2005; Schluter 2001, 2009). Similarly, host switching in parasites can generate new taxa via divergent ecological selection (Bush 1969; Drès & Mallet 2002; Feder *et al.* 1988; Price 1980). This mechanism has been implicated in many other situations where populations respond to divergent selection in different environments. Thus, the very young lineages of sticklebacks and pupfish show strong evidence of disruptive selection in early divergence (Hendry *et al.* 2009; Martin & Wainwright 2013; Schluter 2000).

Internal barriers coupled with geographic isolation – without divergent selection: The hypothesis involving external barriers described above requires ongoing divergent selection. By contrast, populations experiencing the same selective environments could evolve internal barriers owing to genetic incompatibilities that arise by chance in isolation. When reproductive isolation can be achieved without divergent selection, the taxa formed may be more stable (i.e. less prone to collapse; Seehausen 2006), though they may be formed at a slower rate (Seehausen *et al.* 2014). Included in this type of divergence would be mechanisms such as "mutation-order speciation" (Mani & Clarke 1990), reproductive isolation evolving as a by-product of genetic drift (Schluter 2009) or environment-independent sexual selection, or scenarios where populations have different segregating variants that are incompatible (Agrawal *et al.* 2011). Moreover, population genetic models indicate that reproductive incompatibilities between populations initially experiencing similar natural and sexual selection can be amplified as a result of sexual traits (Mendelson *et al.* 2014). Such effects can lead to the rapid origins of ecologically similar taxa, largely in allopatry and "non adaptive" (Rundell & Price 2009). However, expansion within the environment may occur readily in such situations (Shaw & Gillespie 2016), resulting in secondary sympatry, with interaction and associated ecological character displacement (Cotoras *et al.* 2018).

Role of Gene Flow (Box 1C): Early work on speciation stressed the geographic isolation between populations, with mutation, genetic drift and indirect effects of natural selection causing speciation. It was generally believed that gene flow would counteract differentiation between populations. Thus, much study focused on isolating mechanisms that prevented gene flow (Merrell 1962). The rapidity of adaptive radiation then suggested various ways that differentiation could be achieved, with much attention focused on founder events, and the possibility that premating isolating mechanisms could evolve quickly through sexual selection. Increasingly, it has been recognized that divergence can occur in the face of gene flow (Carson 1997) and more recent work suggests that speciation can occur without complete geographic isolation (Mallet 2008; Servedio & Noor 2003). Various mechanisms have been proposed to promote divergence, including chromosomal rearrangements that can prevent recombination and allow genomic regions to diverge in the face of gene flow (Machado *et al.* 2007).

Recent studies have started to focus on the genomic consequences of admixture of previously divergent populations. When such populations come together, hybridization may lead to introgression or admixture depending on the degree of genetic divergence between the entities involved, in particular because genetic incompatibilities tend to increase with genetic divergence (Matute *et al.* 2010). However, the frequency of phenotypic novelties that can arise spontaneously as a consequence of hybridization also tends to increase with genetic divergence (Stelkens *et al.* 2009). Recent experimental work focusing specifically on the outcome of admixture and hybridization shows how both the genetic difference between hybridizing species and the number of hybridizing species affect the probability of reproductive isolation in the admixed population, with a balance between the amount of genetic variation produced by hybrid speciation and the generation of incompatibilities through novel genetic combinations. There appears to be a "sweet spot" between the minimum divergence necessary for the evolution of novel and advantageous recombinant genotypes and a maximum divergence, beyond which the accumulation of genetic incompatibilities eliminates any further benefit to hybridization (Comeault & Matute 2018). These sweet spots of divergence prior to admixture or hybridization have the potential to play a key role in adaptive radiation.

Co-occurrence of taxa within an adaptive radiation (Box 1D). Taxa within an adaptive radiation are adapted to different ecological niches. However, the geography of co-occurrence varies considerably between adaptive radiations: members of a radiation occur in allopatry, parapatry, mosaic sympatry, or pure sympatry. By definition, allopatry, parapatry, and mosaic allopatry all imply some level of spatial (or temporal) separation of populations, while sympatry requires regular dispersal between populations (Mallet *et al.* 2009) or that individuals are physically capable of regular interaction (Weber *et al.* 2017). Note that sympatry is related to the concept of alpha diversity, with both being spatially scale dependent; i.e., a given local area may contain many species, but very few species in any one portion of that area. Likewise, allopatry is related to beta diversity, or turnover between sites, both again being scale dependent. For the current manuscript we attempt to differentiate between situations where individuals of diverging populations do or do not interact on a regular basis throughout most of their range.

The relative importance of external and internal barriers (see above) may dictate the order of ecological divergence: Ecological divergence can arise in allopatry or parapatry (through adaptation to different environments) or sympatry (e.g. through species interactions that bring about ecological character displacement), or in combination. Several models of adaptive radiation have suggested that the initial separation of gene pools during speciation and/or adaptive radiation may follow predictable steps, with ecological divergence occurring along α (within site) and β (between site) axes at different time points during speciation (Ackerly *et al.* 2006; Gavrilets & Losos 2009; Streelman & Danley 2003).

Interactions with the environment and co-occurrence: The “habitat first rule” suggests that initial ecological divergence occurs as a consequence of environmental variability across space (Schluter 2000). A similar scenario has been suggested in a general vertebrate model (Streelman & Danley 2003). Among montane birds of New Guinea, for example, Diamond (1986) concluded that habitat divergence occurred first, and a similar argument might be made for Darwin's finches, given that co-occurrence of species formed early in the radiation tends to be lower than those formed later (Grant & Grant 2011)..

Interactions with close relatives and co-occurrence: Unlike the “habitat first” model discussed above, species attributes that allow local sympatry (e.g. α-niche divergence) appear to occur first in a radiation of western North American *Ceanothus* (Ackerly *et al.* 2006). Indeed, in many groups, divergence of traits that allow co-occurrence (α axis), such as specific leaf area in plants and trophic niche in animals, may be the first axis of divergence. These differences don’t necessarily separate co-occurring species in space, but rather in use of resources within the space. This lies in contrast to the “habitat first” model discussed above where shifts in spatial use of the habitat tend to arise first under conditions of geographic separation. For example, trophic morphology has been suggested to diverge before macrohabitat shifts in cichlids from Lake Tanganyika (Muschick *et al.* 2014). Likewise, in much younger sympatric radiations of pupfishes, divergence in the trophic niche is clearly the initial axis of divergence (Martin & Wainwright 2011).

The arguments above come with many caveats. Thus, in the Darwin's finch case, high co-occurrence of young taxa might also suggest that early habitat divergence is not required for speciation, highlighting the challenge of inferring process from pattern using extant taxa only. Without a temporal sequence of events, it is impossible to test alternative hypotheses, or to infer the role of extinction on these clade-level patterns Likewise, for cichlids, the pattern of initial divergence in trophic morphology appears to be inconsistent with the observation that trophic ecology is typically conserved within genera in Lake Tanganyika (Wagner *et al.* 2009).

Clearly needed are analyses across multiple radiations that can examine how and when ecological divergence occurs during the course of adaptive radiation. In particular, what is the role of (1) geographic isolation in similar environments potentially triggering initial non-ecological divergence, with ecological divergence occurring upon secondary overlap due to interactions between members within a lineage; relative to (2) environmental isolation and disruptive selection triggering habitat shifts in allopatry or parapatry. One of the few studies that has examined the relative timing of ecological and non-ecological factors in the early stages of adaptive radiation across multiple lineages, highlighted the importance of non-ecological processes in potentially serving as the initial axis along which taxa might diverge in many adaptive radiations (Rundell & Price 2009). Thus, initial non-ecological divergence can lead to non-adaptive radiation (see below), and may also be the precursor to adaptive radiation.

Rate and adaptive shifts (Box 1E): Adaptive radiation is frequently associated with an increase in the rate of diversification. However, diversification may be adaptive without any increase in rate, and can increase in rate without adaptation. These differences can arise from entirely different drivers. Hence, understanding of these requires that the different elements be recognized and separated.

Non adaptive radiation - acceleration in rate of diversification only Radiations have been broadly characterized as adaptive and non-adaptive (e.g., Rundell & Price 2009), referencing the extent to which species have ecologically diversified. Non-adaptive radiations, those clades that exhibit little ecological disparity, are classic examples of phylogenetic niche conservatism, in which ecology is conserved among closely related species over evolutionary time scales (Ricklefs and Latham 1992; Peterson 1999; Wiens 2004; but, see Losos 2008). Initially described as 'evolutionary diversification from a single ancestor, not accompanied by relevant niche differentiation' (Gittenberger 1991), such radiations are common in taxa that have low dispersal ability, such as land snails and salamanders. However, in some examples some large species radiations can involve complex mixtures of adaptive and non-adaptive processes (Rundell & Price 2009).

Adaptive shifts without increased rate of diversification Adaptive shifts are not always associated with increased rates of diversification (Wood *et al.* 2012). To this end, it is clear adaptive shifts may arise independently from increased rates of diversification and vice versa (Givnish 2015). Thus, it is important to separate the phenomena.

Adaptive shifts with increased rate of diversification Many of the classic adaptive radiations are associated with both rapid diversification as well as adaptive shifts. Given that adaptive radiations tends to be associated with ecological release (reviewed in Yoder *et al.* 2010), many authors have argued that the associated opportunity may lead to increased rates of lineage or morphological diversification. Indeed, many tests of adaptive radiation have focused on this element, with key innovations often examined in the context of their tendency to lead to increased rates of diversification (Slowinski & Guyer 1993).

Common denominators of adaptive radiation – questions and answers

The lineages under consideration at the American Genetic Association conference included: Hawaiian *Metrosideros* and Hawaiian *Bidens* plants; Galapagos *Naesiotus* land snails; Hawaiian *Tetragnatha*, *Ariamnes*, and *Mecaphesa* spiders; Hawaiian *Laupala* crickets; Hawaiian *Nesophrosyne* leafhoppers; Hawaiian *Drosophila* flies, Hawaiian *Hyposmocoma* moths; South American *Heliconius* butterflies; North American threespine stickleback fish, East African cichlid fish, pre-Alpine European whitefish, Mediterranean labrine wrasses, San Salvador Island pupfishes, and Cameroon crater lake cichlid fish; Eastern plethodontid salamanders (*glutinosus* group); *Anolis* lizards of the Greater Antilles and mainland *Anolis* (subclade Draconura); and Darwin's finches, Tristan finches, and Hawaiian honeycreepers. This collection of study systems is not an exhaustive representation of all adaptive radiations. Here, our aim here is to generate commonalities across this wide array of taxonomic groups and geographic settings. If we can identify a set of commonalities, this will certainly guide future work in other systems.

Contributors addressed the following questions:

1. How did your lineage gain access to the (novel/under-utilized) eco-evolutionary space into which it radiated?

The majority of radiations started with ecological opportunity associated with geographic colonization of a new environment, or key innovations coupled with colonization of a new set of niches. For example, in *Heliconius* butterflies, key innovations arose *in situ* in the neotropics, which led to profound shifts in life history; here, key innovations are thought to have been: shortening of larval development time by specialization on new shoots of *Passiflora*, pollen-feeding, greater adult longevity, coevolution with larval and adult host plants, development of a flexible set of switch loci for Müllerian mimicry, and cognitive improvements (Gilbert & Singer 1975; Merrill *et al.* 2015).

2. How does the ancestral niche compare to what you know of the pattern of establishment of niches in new species?

For the majority of lineages, contributors speculated the ancestor to be a generalist with subsequent diversification leading to multiple specialist species. However, it is often difficult to determine whether the ancestor itself was generalist, or whether the generalist strategy arose during ecological release, or the expansion of ecological amplitude, upon colonization of new ecological space. Subsequently, a generalist ancestor can give rise to multiple descendant species in an adaptive radiation that are not simply partitioning broad niche space, but are also (often greatly) expanding total niche breadth across the descendant species that exceeds that of the generalist common ancestor (e.g., Rubinoff & Schmitz 2010). In cichlids, although the ancestor may be a generalist, its niche is only a small subset of the niche space that members of the radiation acquire (Joyce *et al.* 2005). In Hawaiian insects that feed on plants, some colonizing ancestors are thought to have arisen from generalists that may include polyphagous pests in their ancestral range, facilitating establishment in an ecosystem with restricted and depauperate flora (Bennett & O'Grady 2012). The expansion of total niche breadth in plant-associated insects beyond that of their ancestral range likely arose from (a) release from competition and/or predation that restricted ancestral plant use and (b) the opportunity to diversify by specializing on novel plant lineages from other continents that are not present in the ancestral range of an insect lineage (Bennett & O'Grady 2013; Bennett & O'Grady 2012). In Hawaiian *Metrosideros*, where the recency of the radiation and hybridization among nascent taxa confound phylogenetic approaches (Percy *et al.* 2008; Wright *et al.* 2001), population genetic analyses strongly suggest the evolution of habitat specialists from a widespread relatively generalist taxon (Stacy *et al.* 2014; Stacy & Sakishima in review) and overall increase in niche breadth occupied by the lineage.

However, many of the radiation members are no more specialized than the ancestor, some perhaps even less, with classic examples from cichlid fish (Liem 1980) and Galapagos finches (De Leon *et al.* 2014).

In some lineages it appears that the ancestor was specialized and experienced ecological release at the outset of the radiation; in particular for Hawaiian spiders, moths and crickets (Otte 1994), Galapagos snails, and stickleback fish (cites?). Thus, in Hawaiian *Tetragnatha* spiders, the sister lineage almost certainly builds flimsy webs over water, while the Hawaiian lineage is found in almost every forest habitat and microhabitat (Gillespie 2016). Likewise in snails, the most likely sister group to Galapagos *Naesiotus* snails inhabits dry forest habitats whereas in Galapagos the snails are found to occupy a much wider range of habitats which they have adapted to (ref?).

In the mainland radiation of *Heliconius* butterflies, it appears that colonizing new ecological opportunities in already rather full ecological communities was the main driver. This contrasts with the situation of colonizing islands, where arguably a major trigger for radiation is reduced competition for the organism's normal niche.

3. Which factors best describe initial establishment of new species in your group?

This question addressed whether the radiation started by initial establishment in a preferred niche and exclusion of subsequent colonists, followed by radiation by expansion from this niche into many other niches. Or alternatively, whether the radiation is triggered by exclusion from the ancestral niche (perhaps by earlier colonists) leading to establishment in novel niches and associated radiation. Most contributors considered that initial establishment occurred in the preferred niche with subsequent colonists excluded (cf. priority effects; e.g. in *Laupala* crickets; (Shaw & Gillespie 2016)). However, opinions varied widely even for the same lineage, likely reflecting the difficulties in obtaining data that would support one or the other scenario. Indeed, without a timeline, distinguishing between initial colonization in an ancestral niche with a subsequent shift versus colonization in a new niche without that first step in the ancestral niche is very challenging.

Variations on these ideas were suggested for cichlids and Mediterranean labrine wrasses with initial establishment in the niche resembling the ancestral niche, but subsequent colonists were not excluded. In other words, secondary colonists were not excluded even though they had substantial niche overlap (both in microhabitat and trophic resources) with the earlier colonists. Ensuing radiation has occurred by rapid but gradual "cladistic expansion" from this niche into many other niches.

4. Which factors best describe initial reproductive isolation (i.e. factors that drive initial divergence between populations, some of which become species) in your group?

There are two clear mechanisms through which initial reproductive isolation can occur. The first is ecological divergence - disruptive selection between different environments; the second is non ecological – divergence in isolation without disruptive selection.

Disruptive selection between different environments - This mechanism was suggested for all plants, fishes, and Galapagos and Tristan finches. Thus, the numerous forms of *Metrosideros*, Hawaii's landscape-dominant tree, apparently formed and persist by disruptive selection with genetic incompatibilities contributing to partial reproductive isolation in hybrid zones of at least two taxa (Stacy *et al.* 2017). Tristan finches (*Nesospiza* spp.) colonized the isolated South Atlantic Tristan da Cunha islands c. 4 million years ago (Ryan *et al.* 2013). The original colonizers were small-billed (Stervander 2015) and the island tree *Phylica arborea*, whose fruits the large-billed finches now specialize on (Ryan *et al.* 2007), only colonized the Tristan da Cunha islands ≤2 million years ago (Richardson *et al.* 2003; Richardson *et al.* 2001). The arrival of this new food source introduced disruptive selection pressure, which resulted in a miniature radiation into replicate taxon pairs of small- and large-billed finches on each of two islands (Ryan *et al.* 2007; Stervander 2015).

The important point here is that selection for different environments appears to be the initial driving force pulling gene pools apart, and this appears to be the driver of speciation in *Heliconius* butterflies as well, where host plant switches or divergent mimicry aids coexistence of new or incipient species (Merrill *et al.* 2015). This mode of initial divergence may mean that few genetic incompatibilities exist; barriers are predominantly ecologically dependent. An exception is the partial reproductive isolation observed between successional varieties of the tree, *Metrosideros polymorpha*, on Hawaii Island, where differential adaptation to new and old lava flows (Morrison & Stacy 2014) is associated with reduced fertility of hybrids, especially backcross trees (Stacy *et al.* 2017). In continuously distributed trees, variation in population size among diverging taxa may explain the simultaneous occurrence of strongly isolated taxa confined to geographically narrow niches and incomplete speciation between two widespread successional taxa, if drift promotes the fixation of incompatibilities only in small populations.

In Lake Victoria cichlids, initial ecological selection between niches is often divergent rather than disruptive; however, disruptive selection emerges from the interaction of sexual selection with the environment (Moser *et al.* 2018; Seehausen *et al.* 2008; van Rijssel *et al.* 2018). In contrast, there is evidence of significant disruptive selection in other cases of Lake Victoria cichlids (genus *Neochromis* (van Rijssel *et al.* 2018)), in Cameroon crater lake cichlids (Martin 2012), Tristan finches (Ryan *et al.* 2007), and Darwin's finches (Hendry *et al.* 2008). In some Cameroon cichlids, disruptive selection gradients were only moderate in strength, suggesting that disruptive ecological selection was not sufficient to drive species divergence (e.g. see Bolnick 2011; Bürger *et al.* 2006; Matessi *et al.* 2002) and that sexual selection instead was the primary driver (Martin 2012, 2013). In the pre-Alpine whitefish radiation (Hudson *et al.* 2010; Vonlanthen *et al.* 2012), divergent selection occurs between different spawning habitats (water depth), possibly coupled with disruptive selection on trophic adaptations in the feeding habitat (which is NOT the same as the spawning habitat in these radiations).

Initial ecological divergence has been demonstrated in Hawaiian insects. For example, trophic interactions initially shape adaptive diversification among native Hawaiian leafhoppers (Hemiptera: *Nesophrosyne*). Much of this ecological diversity among the >200 species in this lineage has resulted from early adaptive diversification as these insects specialized on Hawaii's endemic host-plant lineages (Bennett & O'Grady 2012). Here, there has been subsequent non-adaptive diversification over geological time-frames and landscapes as species numbers were multiplicatively amplified as host plants and their dependent insects colonized, and diversified among, islands in the archipelago (Bennett & O'Grady 2013). A similar mixture of adaptive and non-adaptive processes has been inferred for the large cichlid radiations in East African Lakes Malawi, Victoria, and Tanganyika, where trophic adaptation and sexual selection have repeatedly influenced speciation (Kocher 2004; Seehausen 2015), likely frequently in fine-scale parapatry (e.g., Seehausen & Magalhaes 2011; Seehausen *et al.* 2008), but these processes also play out in a geologically complex landscape that presents, for some lineages, ample opportunity for geographic isolation (e.g., Arnegard *et al.* 1999; Sefc *et al.* 2017; Sturmbauer *et al.* 2001; Wagner & McCune 2009).

Divergence in isolation without disruptive selection - In contrast, the second mechanism through which initial reproductive isolation can occur is through some form of intrinsic reproductive incompatibility. In some situations, this may be a slow process and lead to non-adaptive radiation. Thus, in the plethodontid salamanders of the eastern United States, whose populations became isolated following the formation of the Appalachian mountain range (Kozak *et al.* 2006). Subsequently, isolated populations were unable to maintain connectivity and diversified non-ecologically into a series of morphologically cryptic allospecies; for example, the *Plethodon shenandoah* complex is now isolated on mountaintops, unable to tolerate environmental conditions of intervening lowlands There is minimal coexistence among named species - instead they tend to replace each other geographically (Kozak & Wiens 2010). Among spiders in the Hawaiian Islands, non-adaptive radiation has been well described in *Orsonwelles* (Linyphiidae), with 13 species across the islands: all species have similar ecologies and none co-occurs with any other (Hormiga *et al.* 2003). Similarly, non-adaptive radiation has been well documented in Galapagos mockingbirds (Arbogast *et al.* 2006) and Galapagos tortoises (Beheregaray *et al.* 2004).

Sexual selection can also play a role in initial reproductive isolation without major ecological shifts, and lead to more rapid diversification. The native Hawaiian crickets of the genus *Laupala* show niche conservatism but nonetheless display species coexistence with up to four species in sympatry. Selection likely plays a role in speciation in this group but via divergent sexual selection rather than through ecological differentiation of resource use (Mendelson & Shaw 2005; Otte 1994; Xu & Shaw 2019). However, here again, since divergent sexual selection is often tied to ecology (e.g., Maan & Seehausen 2011) the distinction between adaptive and non-adaptive diversification can become blurred.

Isolation without ecological shifts may also play a major role in adaptive radiations. For example, anoles, Hawaiian insects and spiders, and Galapagos snails all appear to show that initial divergence happens in the same environment, presumably through intrinsic mechanisms, though in allopatry. However, the evidence for the phenomenon is varied and difficult to infer. Thus, most evidence points towards the evolution of reproductive isolation in allopatry in anole radiations (Losos 2009), with character displacement on secondary contact driving phenotypic divergence (Losos 2009, Stroud and Losos 2019). In Galapagos snails, it appears, based on geographical distributions, that initial divergence is the result of geographical isolation (Phillips et al, this volume). When this geographical isolation is accompanied by divergent selection between different environments then ecological speciation might ensue, but the initial stage of divergence is most likely associated with geographical isolation and either premating or postmating intrinsic barriers.

5. Which factors best describe species persistence in your group?

The arguments were whether most entities persist once they have been formed or whether most are ephemeral - eliminated by ecological processes of exclusion or by introgression upon secondary contact, by reversal of speciation in primary contact, or by demographic stochasticity (Rosenblum *et al.* 2012; Seehausen *et al.* 2008). These ideas build on those of ephemeral diversification (Futuyma 1987). Most contributors thought that lineages are ephemeral; in other words, genetic entities often form that do not persist. However, the fate of the ephemeral lineages varies between lineages. In sticklebacks, it is likely that many species are ephemeral and have been extirpated by multiple mechanisms including demographic stochasticity in addition to ecological processes and introgression; ice-ages obliterated perhaps most freshwater species, so that most of today's three-spined stickleback species evolved from the marine species since the most recent glaciation. Likewise in pupfishes, reproductively isolated ecotypes may go extinct due to ecological or geological processes such as loss of hypersaline lake environments. For adaptive radiations involving slow-to-speciate taxa such as trees, the presence of multiple morphologically distinct yet weakly genetically diverged forms may be due to a mismatch between the rate of speciation and the temporal scale of environmental change. For example, in Hawaiian *Metrosideros*, where the most diverged taxa tend to be bounded by sharp ecotones, a large number of sympatric forms appear to be only weakly ecologically diverged and may reflect incomplete isolation on once-sharp ecotones that have since weakened on Hawaii's rapidly changing volcanic islands (Stacy et al., this volume). Such forms are expected to disappear through introgression in this highly interfertile group.

In Lake Victoria cichlids, timelines are a good deal shorter. Thus, most entities persist at least for thousands of years (which is long in a 15,000-years-young radiation), but some get eliminated by speciation reversal. The scale of speciation reversal is mediated by environmental change (natural and anthropogenic), and the impact can be massive in parts of the radiation.

Similarly, local sympatry of sister species in *Heliconius* is widespread, suggesting speciation with gene flow, or if allopatric speciation was involved, rapid range change into sympatry after secondary contact (Rosser *et al.* 2015). Species persistence is due to occupation of different niches and assortative mating, aided possibly by F1 female hybrid sterility (i.e. conforming to Haldane's Rule (Haldane 1922), where the heterogametic sex (here the females) are most likely to suffer developmental disruption).

In several groups, the production of many ephemeral entities might contribute to some form of adaptive admixture. Thus, in *Heliconius*, the coming together of different lineages may, in the long run, lead to more radiation. In Hawaiian *Bidens*, species are generally fully isolated either by geography (on different islands) and/or by habitat (and pollination syndrome for the one bird pollinated *Bidens cosmoides* on Kauai), but when secondary contact occurs the species can meld back together into hybrid swarms since reproductive isolation has not yet occurred amongst any of the endemic Hawaiian species tested (Ganders & Nagata 1984; Knope *et al.* 2013). However, all of the Hawaiian species tested are reproductively isolated from taxa in their Central American sister clade (Knope *et al.* 2013), and this reproductive incompatibility appears to have arisen within the past ~2 Mya (Knope *et al.* 2012b, this volume). In Hawaiian *Metrosideros*, hybridization among taxa appears to be common where ranges overlap along environmental gradients (Stacy *et al.* 2016). Genetic evidence suggests widespread mtDNA leakage in

Hawaiian *Laupala* crickets, indicative of persistent hybridization across the radiation (Shaw 2002; Shaw & Gillespie 2016). Nonetheless, two clades of this group have persistently maintained genetic integrity in sympatry for at least 3.5 MY (Mendelson & Shaw 2005). In San Salvador pupfishes, adaptive introgression from a distant island 10 kya has contributed to the divergent trophic morphology of specialists in the radiation, perhaps arising from a previous ephemeral radiation (Richards & Martin 2017).

6. Which factors best describe how co-occurrence of species is achieved in your group?

Most contributors argued that new incipient species share ecological requirements similar to each other when they come into secondary contact; then character displacement gives rise to ecological divergence in sympatry. This scenario reflects the thoughts of researchers who study Caribbean *Anolis*, Hawaiian spiders, Hawaiian *Drosophila* fruitflies, Hawaiian *Nesophrosyne* leafhoppers, and Darwin's finches. In one case, the Hawaiian *Laupala* crickets, ecological character displacement does not apparently occur (relegating this group into the category of "non-adaptive" radiation). Xu and Shaw (this volume) provide evidence that some conserved features of mating behavior may yield mutual benefit to mate-searching females of co-occurring species, suggesting a novel mechanism stabilizing sympatry without ecological or reproductive character displacement. However, it should be noted that in many cases where similar species come into secondary contact there is extinction/exclusion, but this goes undetected and what we see is what is left, which is the case of successful character displacement. It may thus be difficult to know the frequency of successful character displacement.

In other groups, however, some form of ecological divergence appears to be involved prior to the resumption of sympatry of taxa. In sticklebacks, ecological character displacement is facilitated by initial ecological differences. In cichlids likewise, co-occurrence appears to come about possibly as character displacement, but also perhaps via having distinct ecologies before coming back into contact. The same is true for Darwin's finches (Grant & Grant 2006). The relative importance of these two is not clear in cichlids, and also there is little clear evidence for character displacement in cichlids (van Rijssel et al. 2018).

In the South American mainland radiation of *Heliconius* butterflies, ecological character displacement may begin very early during divergence to become the major driving force of speciation with gene flow (Rosser *et al.* 2015). It is not inconceivable that many island radiations, confronted by multiple available niches, might also diversify in a similar manner.

7. Which factor best describes how ecological disparity is achieved in your group?

The question here was the relative importance of adaptive admixture, developmental plasticity, evolvability, and / or lineage priority. Clearly, all of these may play a role or interact to facilitate radiation. Overall, it appears to be a combination of these factors that allows adaptive diversification, with priority effects involved in the initial establishment and exploration of ecological opportunity presumably setting the stage for subsequent diversification into multiple niches, the latter being achieved through a combination of adaptive admixture, developmental plasticity, and evolvability.

Stickleback evolvability is enhanced by standing genetic variation in the ancestral form (marine), but the source of this variation is likely admixture between marine and older freshwater populations; here, the main role of plasticity is to facilitate colonization and persistence, enabling adaptation. In other fishes, admixture can contribute to genetic variation. Thus, in many cichlid groups, including those from the Rift Lakes and Cameroon (Poelstra *et al.* 2018), and pupfishes (Richards & Martin 2017), admixture may be critically important as a source of adaptive alleles; developmental plasticity can also open immediate access to novel niches in cichlids and evolvability, often facilitated by admixture, permits genetic differentiation and assimilation. Similarly, admixture likely contributed to evolvability in Galapagos finches (Chaves *et al.* 2016; Lamichhaney *et al.* 2015) and *Heliconius* butterflies (Merrill *et al.* 2015).

A second element here is whether, if a lineage occurs in discrete areas (eg islands within an archipelago; network of habitats), then does ecological disparity arise (i) at the base of the radiation (species related across "islands"); (ii) within "islands" in a replicated fashion (same ecological sets of taxa on each "island"); or (iii) within "islands" in an unpredictable fashion. In lineages where ecological disparity arises within a given island or lake, some degree of repeatability and the evolution of similar sets of habitat specialists, sometimes called ‘ecomorphs’ within each island/lake of an archipelago is a common pattern that is well known in Caribbean *Anolis* (Losos 2009), cichlids of the Rift Lakes (Brawand *et al.* 2014; Muschick *et al.* 2012)(Brawand *et al.* 2014; Muschick *et al.* 2012), sticklebacks (Rundle *et al.* 2000), alpine whitefish (Vonlanthen *et al.* 2012), Tristan finches (Ryan *et al.* 2007), Hawaiian *Tetragnatha* spiders (Gillespie 2004), and Hawaiian *Ariamnes* spiders (Gillespie *et al.* 2018). However, in other groups, the ecological disparity arises at the base of the archipelago-wide radiation, notably in Hawaiian *Hyposmocoma* moths (Haines *et al.* 2014), Hawaiian crab spiders (Garb & Gillespie 2009), Hawaiian *Nesoprhosyne* leafhoppers (Bennett & O'Grady 2013), Hawaiian *Drosophila*, and Hawaiian *Bidens* (Knope et al., this volume). In other lineages, the pattern of diversification between islands is unpredictable, notably in Cameroon crater lake cichlids, Caribbean pupfish, Galapagos land snails, and Hawaiian *Metrosideros*.

Based on the responses above, we discuss generalities that may exist *within* a lineage that is undergoing adaptive radiation, in the context of **(1) Initial divergence, (2) Persistence of reproductive isolation, (3) Admixture leading to exchange of adaptive traits among diversifying lineages, (4) Ecological shifts and sympatry.**

Common denominators – initial divergence within the radiation

To initiate species formation in the course of adaptive radiation, a population generally must establish in a new environment or a new geographic location in the same environment (Mayr 1947)(Coyne & Orr 2004), although there are exceptions (Feder *et al.* 2012; Hendry *et al.* 2009; Mallet *et al.* 2009). However, the nature by which initial separation of colonists may be achieved is multifaceted, and comparisons across radiations often fail to find commonalities. While the first step clearly requires the founding of a new intraspecific population, in some situations this requires a shift in ecological tolerance where there are different selection pressures (Mayr 1947); in other situations the new population experiences no ecological shifts; here, ecological divergence is associated with subsequent interaction with close relatives (Brown & Wilson 1956).

It is important to separate the roles of external selection versus internal incompatibilities fostering initial divergence (Fig. 2). Both can give rise to reproductively isolated species in allopatry, although stable local co-occurrence requires a mechanism to overcome gene flow (Seehausen *et al.* 2014). Thus, we divide this part of the process into the relative roles of its two key elements – (i) isolation as a result of external effects coupled with divergent selection, (ii) isolation due to internal barriers *without* external divergent selection. The importance of these two factors is also related to the degree of isolation; and the length of time of isolation, which we will discuss later. Divergent sexual selection, depending on the specific mechanism and the role of the environment, may fit comfortably within either element.

Which taxa are likely to diverge in which way? One of the major difficulties in dissecting out the relative importance of *external factors and initial divergent selection* versus *internal factors without divergent selection* (ecological differences may evolve later through interaction) in initiating early divergence within an adaptive radiation, is that we lack an adequate timespan over which to observe the early stages of radiation together with later stages. Thus, in many of the classic cases highlighting the role of disruptive selection in fostering early divergence, the lineages are very young (<50 ky) and tend not to co-occur, making it debatable as to whether the divergence translates into a full blown adaptive radiation. Where radiations are evident, it can be difficult to infer whether selection or geographic isolation alone created conditions for early divergence, and both factors are likely involved in cichlids. Similarly, in mainland anoles it seems likely that both mutation-order and ecological speciation may have taken place, as there has been abundant opportunity for both divergence in allopatry and sympatry respectively (Poe *et al.* 2017). Specifically, following initial colonization of upper Central America and the Nearctic ~30MY (at the time disconnected from South America and the incumbent mainland anoles), preliminary data suggests that Draconuran anoles rapidly dispersed across the hitherto uncolonized landmass, potentially initiating mutation-order speciation (Patton et al., unpubl.). As diversity in this group accumulated, so did the number of sympatrically distributed species, consequently increasing the opportunity for ecological speciation. However, due to limited (as compared to their Caribbean counterparts) understanding of the ecology and evolutionary history of this group, these observations are at least in part speculative.

Plant radiations highlight the role of external factors and divergent selection: Bidens more likely are at the early stages of divergence driven by external factors, in that all endemic Hawaiian species that have been tested are cross-compatible with one another, but 70% of the 19 Hawaiian endemic species are single island endemics and 85% are allopatric when additionally considering habitat isolation within islands, and at least one species is reproductively isolated due to differences in pollination syndrome (Ganders & Nagata 1984). The numerous, predominantly infraspecific, morphotypes of *Metrosideros* differ in vegetative traits and are highly interfertile (Stacy *et al.* 2016) despite evidence of differential local adaptation across contrasting environments (e.g., (Ekar *et al.* in review; Morrison & Stacy 2014), Sakishima et al., in prep.,). Common garden experiments with both *Bidens* (Gillett & Lim 1970; Knope *et al.* 2013) and *Metrosideros* (Cordell *et al.* 2000; Cordell *et al.* 1998; Corn & Hiesey 1973; Kitayama *et al.* 1997; Stemmermann 1983) show that the striking morphological differences amongst taxa are indeed due to genetic differences and not phenotypic plasticity.

Some animal radiations highlight the role of external factors and divergent selection The simultaneous use of specialized ecological niches for food and reproduction is likely important in shaping invertebrate radiations (e.g., singing, specializing on host plants for oviposition such as the Hawaiian *Drosophila* and Hemiptera, egg laying in open environments, etc.). Under such conditions, where strong connections with the external environment can clearly play a selective role, the initial stages of speciation may be external, due to the environment.

Some animal radiations highlight the role of internal factors and drift: For many animal radiations, whether or not the end result is co-occurrence, the initial stages of divergence are associated with geographic isolation and fostered by genetic drift rather than disruptive selection drift (Schluter 2009). The role of geographic isolation without apparent disruptive selection has been well demonstrated in Hawaiian spiders (Cotoras *et al.* 2018){Gillespie, 2005 #200}, crickets, and flies (Hiller *et al.* In press). It has also been suggested for the early stages of divergence in *Anolis* lizards (Glor *et al.* 2004; Glor *et al.* 2003; Knouft *et al.* 2006; Losos 2009) and Galapagos snails (C. Parent, unpubl. data).

To conclude, the mechanism through which initial divergence is achieved during the course of an adaptive radiation varies considerably across radiations depending on the interplay between external selection versus internal incompatibility fostering initial divergence (Schluter 2009) (Box 1B, Fig. 2). Organisms that exploit – and have strong associations with - different environments, including many plants and plant-associated insects, will experience external divergent selection (Schluter 2001). In contrast, organisms that become isolated while remaining in the same kind of environment (Rundell & Price 2009), may diverge through internal mechanisms unrelated to divergent selection, potentially associated with sexual recognition (Carson 1997; Mendelson *et al.* 2014); here, ecological divergence can occur via secondary sympatry (Cotoras *et al.* 2018; Hiller *et al.* In press; Rundell & Price 2009) (see below).

Common denominators – the role of admixture

Many of the differences between populations are likely contingent on the genetic variability within each lineage, and on the availability of accessible new niches to that lineage. Contingency will thus determine the outcomes of divergent natural selection, and whether it can lead to speciation or adaptive radiation. One source of such contingency is whether colonizing lineages had an opportunity to hybridize and generate admixture variation.

Reproductive isolation often does not reach completion in speciation; occasional gene exchange may continue long after population separation, and sometimes for species that are millions of years divergent (Arnold 1997; Mallet 2005, 2008). Although gene flow between diverging populations tends to be thought of in general inhibitory to divergence, gene flow between more distantly related populations and species can bring together hitherto un-combined adaptive loci from different species that may prove advantageous for survival and further niche colonization and diversification (Abbott *et al.* 2013).

Admixture may act to facilitate adaptive radiation in two distinct scenarios (Seehausen 2004): 1) admixture between divergent taxa prior to adaptive radiation may facilitate the onset of adaptive radiation, a concept referred to as *hybrid swarm origins*; 2) admixture may occur during adaptive radiation, facilitating ongoing speciation within the adaptive radiation, a concept known as the *syngameon hypothesis*. Especially in the case of hybrid swarm origins to adaptive radiation, admixture may introduce new combinations of genes that prove adaptive in their new genomic context. Thus, admixture between divergent taxa has been implicated in establishing the radiation of Hawaiian silverswords (Barrier *et al.* 1999) and cichlids (Irisarri *et al.* 2018; Meier *et al.* 2017). It is possible that propensity for hybridization may help explain why only some lineages that colonize remote volcanic islands such as Hawaii radiate adaptively, whereas others persist and form minor allopatric variants of their progenitor species. As our ability to test for these patterns with genomic data mounts, tests of this hypothesis become more and more feasible.

Likewise for ongoing speciation, the role of admixture in the course of adaptive radiation has been well documented in a number of classic adaptive radiations such as Ko‘oko‘olau (*Bidens*) and silverswords in Hawaii (Carlquist *et al.* 2003; Carr 1987), Darwin's finches in the Galapágos (Lamichhaney *et al.* 2015), *Heliconius* butterflies (Heliconius Genome Consortium 2012), and African cichlid fish (Seehausen 2015). This sets up a scenario where gene flow and selection towards local adaptive peaks may interact. This will often happen between diverging sister taxa but it may also happen between more distantly related taxa within a radiation. Especially in that latter case, gene flow may introduce new combinations of genes that prove adaptive in the recipient population. Thus, speciation with occasional introgressive gene exchange may be important for construction of new adaptive combinations in rapidly radiating taxa (Meier *et al.* 2017; Meier *et al.* 2018), in some cases leading to hybrid speciation (Marques *et al.* In press; Schumer *et al.* 2014) as well as adaptive introgression (Lamichhaney *et al.* 2018).

Whether admixture among members of a radiation actually enhances further speciation within adaptive radiation (Carr 1987) can be difficult to test as many well-studied adaptive radiations consist of young species that would be expected to be more compatible and therefore to undergo more introgression than older species in non-radiating lineages; yet this introgression does not necessarily increase speciation rate. Testing the syngameon hypothesis of adaptive radiation therefore requires combining population genomic, demographic and phenotypic analyses (Meier et al. 2018). Additionally, cases of hybrid speciation in adaptive radiation are a specific case of how admixture can directly lead to increased speciation (Lamichhaney *et al.* 2018). The hybrid swarm origin hypothesis for adaptive radiation on the other hand, makes predictions that cannot be confounded by the fact that young radiation species tend to hybridize. Its unique predictions are, first, that the most recent common ancestor of all members of a radiation is a population of hybrid origin between distinct species, and second, that new combinations of old genes that arose from the hybridization (i.e. that did not exist in either of the parental lineages alone) are important in speciation and adaptation during the radiation (Seehausen 2004). This combination of hypotheses receives its strongest support to date from work on the Lake Victoria Region superflock of cichlid fish radiations that all originated from hybridization between ecologically not very divergent *Astatotilapia/ Thoracochromis* species from the Upper Nile region and the upper Congo river, lineages which are not strongly ecologically divergent (Meier *et al.* 2017). Finally, there is abundant evidence for gene flow among different species during adaptive radiation which may facilitate adaptive divergence and speciation (e.g., Irisarri *et al.* 2018). There is also evidence that adaptive introgression from multiple outgroups may trigger adaptive radiation (Poelstra *et al.* 2018; Richards & Martin 2017; Richards *et al.* 2018).

To conclude, mechanisms for the separation of gene pools are clearly required for adaptive radiation (Box 1C). However, it appears that admixture may sometimes facilitate radiation, likely in conjunction with spatially heterogeneous or ecologically multifarious selection. There is now clear genomically-based evidence for both the hybrid swarm origin hypothesis and also for the mechanisms associated with the syngameon hypothesis of adaptive radiation. However, as genomic evidence for admixture in the history of adaptive radiations increases, there is a need to clearly distinguish between the processes associated with the models. Furthermore, these processes are distinct from the commonly discussed evidence for speciation-with-gene flow. Because there is a tendency of gene flow to homogenize variation if lineages are not strongly divergent and also a tendency for genetic incompatibilities to prevent any admixture of lineages when they are too divergent, there may be an optimal degree of divergence between populations or species at which admixture

might facilitate adaptive radiation (Comeault & Matute 2018; Stelkens *et al.* 2010). The timing of admixture is critical (Marques *et al.* In press) and likely depends on attributes of the lineage in question, highlighting the need for comparative studies.

Common denominators – persistence, ecological shifts & sympatry within the radiation

Genetic entities – which may be distinct populations or incipient species - are formed continuously during adaptive radiation, but they tend to be ephemeral. Estimates of speciation rates from the fossil record are much slower than both those predicted from mathematical models and empirical data from recent diversification (Seehausen *et al.* 2014). Thus, while speciation - or at least the formation of phenotypically distinct ecotypes - can be common and rapid in the context of adaptive radiation, the persistence of most new entities may be short lived. Evolutionary studies should therefore focus on not only the formation but also the *persistence* of new species. Many, perhaps most, adaptive radiations have occurred so rapidly that it is difficult to infer phylogenetic relationships among species (Rosenblum *et al.* 2012). Thus, in the case of very young lineages that are not fully resolved radiations, many reproductively isolated ecotypes form, but they tend to be eliminated by geological or climatological processes such as loss of lake environments (e.g., paleo-lake Makgadikgadi: (Joyce *et al.* 2005)), or by glaciation (e.g., stickleback and whitefish), or by ecological processes of predation and exclusion (e.g., stickleback (Gow *et al.* 2006; Taylor *et al.* 2006) and Laguna Chichancanab pupfishes (Strecker 2006)). Another cause of non-persistence of many species in adaptive radiations is that as long as reproductive isolation (and hence speciation) is merely a consequence of divergent adaptation to alternative fitness optima or ecological niches, species will persist only as long as the fitness optima exist. Fitness landscapes can change with changes in the physical and biotic environment, and when such changes lead to the convergence of formerly distinct fitness peaks, the causes of reproductive isolation will no longer persist and species will coalesce back into a single gene pool. Such speciation reversal has been described in adaptive radiations of cichlids (Seehausen *et al.* 1997), stickleback (Taylor *et al.* 2006); whitefish (Vonlanthen *et al.* 2012) and Darwin's finches (Kleindorfer *et al.* 2014), and it may be widespread in some highly sympatric radiations in general.

A major question centers on the circumstances that lead to persistence of entities as adaptive radiation proceeds and as the environmental theater changes. To get at this, we must first assess the hallmarks of adaptive radiation, notably the context of co-occurrence that allows species to accumulate. Co-occurrence, or sympatry, can occur at multiple scales (Webb *et al.* 2002). For the purposes of understanding adaptive radiation, the critical component is the extent to which the co-occurrence involves interaction between closely related species.

Regional co-occurrence. Taxa may diverge in different habitats or microhabitats within a given region. Thus, although they may appear that they co-occur on a broad scale, interactions will tend to be limited to narrow zones of overlap. For example, the tendency in some fish to specialize either on a littoral/benthic or a pelagic/limnetic life style can lead to divergent selective pressures between juxtaposed habitat types. If these fish also breed in the habitat where they feed, the inhabitants are sympatric at the scale of the lake, yet interact ecologically and sexually across only a very narrow zone. Likewise, elevation zones may pose physiological barriers to many organisms (De Busschere *et al.* 2010): On islands, this may lead to sympatry at the island level but provides little opportunity for interaction. When perceived gradients are more interdigitated, the distinction between sympatry and allopatry can become less apparent, though equally important in imposing external selection. For example, plants may be affected by fine-scale environmental heterogeneity, with interaction between close relatives playing a more minor role in shaping patterns of co-occurrence (Anacker & Strauss 2014). In some fish, feeding grounds are distinct from breeding grounds, and when pelagic and littoral species converge on shared spawning habitats during breeding, ecological interactions may be limited but sexual interactions (and potential for gene flow) can be very strong. This is the case in some stickleback species pairs (Marques *et al.* 2016). The opposite can also be true, e.g. shared feeding habitat but separate spawning habitat, as in some salmonid radiations (Doenz *et al.* 2018).

In all of these situations, the external environment plays the major role in shaping the ecological and the mating traits of the organism.

Local co-occurrence. Here, species interact with each other through the large proportion of their range, as a result of which, ecological and mating traits might both be expected to be shaped by interactions between closely related species (Webb *et al.* 2002). Prior to such local co-occurrence, incipient species must be reproductively isolated to some extent, in order that interactions do not lead to homogenization.

We can now consider the probability that populations that have started to diverge either through external effects and disruptive ecological selection, or internal factors during geographic isolation without disruptive selection, will tend to persist.

1. *Entities formed by external factors and divergent selection*. The external environment and divergent selection can lead to reproductive isolation between descendant lineages, owing to genotype by environment interactions that disfavor intermediate phenotypes (Fig 3). Local adaptation can proceed most rapidly when it operates on standing genetic variation controlled by many genes (Schluter & Conte 2009) with F1 hybrids between nascent species having reduced fitness in either parental environment (Rundle & Nosil 2005). After such isolation, taxa may or may not come back together in local sympatry:

Returning to local sympatry (α scale): Nascent species are partially reproductively isolated, so maintenance of nascent species as genetically distinct requires ongoing divergent selection until genetically "intrinsic" reproductive barriers accumulate. These nascent species will be vulnerable to ecological perturbations that disrupt the regimes of divergent selection and dispersal (Nosil *et al.* 2009). Thus, lineages formed through ecological speciation may be particularly likely to be lost due to changes in selective regimes (Cutter & Gray 2016). The interplay between the temporal scales over which environments change and intrinsic barriers become fixed within diverging populations is therefore important, but an unanswered question is also whether intrinsic barriers will evolve and spread at all in nascent species that have some ongoing gene flow between them and are maintained by disruptive ecological selection.

Remaining in allopatry (β scale): Based on the arguments above, it is likely that entities formed in the context of divergent selection will tend to persist provided the pressure imposed by disruptive selection is maintained (Seehausen *et al.* 2014). Thus, β diversity (difference between sites) may increase by shrinking the scale of turnover, though diversity at the α scale (involving direct interaction among close relatives in sympatry) will not change. Besides the different selective pressures preventing secondary sympatry, there may exist barriers to return to sympatry, again leading to continued increase in β diversity but not α diversity. Barriers related to return to sympatry may involve ecological interactions (Pigot & Tobias 2013) or behavioral ones (Freeman *et al.* 2019). The opportunity for build-up of α diversity may also be limited as the sibling species will each tend to perform better within their respective habitats or microhabitats.

2. Entities formed by internal factors with ecological divergence through secondary sympatry. The alternative to separation along the environmental/ habitat boundary is separation in geographical space without any obvious disruptive selection (Fig. 4). In this case, populations in similar and/or distinct environments become isolated for a period of time, potentially sufficient to lead to the fixation of genetic incompatibilities. Here again, after such isolation, taxa may or may not come back together in local sympatry:

Returning to local sympatry (α scale): First, returning to local sympatry may be quite straightforward for entities thus formed because the environments are effectively the same. Thus, ecologically similar entities will have the opportunity to interact (Cotoras *et al.* 2018). The expectation is that, assuming competition for resources, ecological character displacement may occur and stabilize coexistence among competing species (Germain *et al.* 2018), or competitive exclusion may occur and return α-diversity to its original value. Which of these occurs when, and why some lineages are more prone to one or the other outcome of competition, is an open question in adaptive radiation research.

Remaining in allopatry (β scale): Second, sibling taxa may not return to local sympatry. Rather, they may remain in allopatry as in the classic non adaptive radiations (Rundell & Price 2009). Or alternatively, they may occur in various forms of microallopatry or mosaic allopatry, but again without local interaction.

To conclude, during adaptive radiation, when differentiation is tied to the environment, divergent selection between environments will play the dominant role in shaping patterns of diversity. Persistence of nascent species thus requires ongoing selection for different environments. However, diversity can increase by reducing the scale of β diversity (ie, higher rate of turnover between sites). In a number of lineages, however, the environment plays a more minor role, and ecological divergence is achieved only through direct interaction between closely related species (secondary sympatry), leading to accumulation of *α* diversity through character displacement.

Conclusions

The most important outcome from the current assessment is that adaptive radiation proceeds along multiple distinct evolutionary trajectories, with different associated processes, and the concept of adaptive radiation has been used to cover these multiple processes. Open ecological space is one factor that seems to be common to all radiations, but even here, the nature of the space and the extent to which it can be shared with and exploited by other lineages varies substantially across radiations. The common view that adaptive radiations are identifiable by an acceleration in rate of speciation and adaptive diversification, while fundamental to many concepts, is not necessary in others. But perhaps most importantly, the processes involved in species diversification within a radiation differ radically, and result in differences in spatial and ecological patterns of species accumulation. In order to make progress in evolutionary theory, we need to understand both commonalities and differences across many radiations. Thus, certain lineages of lizards and spiders are known for the repeated evolution of co-occurring and interacting ecomorphs (Gillespie *et al.* 2018; Losos 2009); this pattern may be associated with the tendency for initial divergence to occur in similar environments in geographical isolation, while ecological character displacement occurs in secondary sympatry (Fig 4). In contrast, other lineages are known for repeated divergence in adaptation to the same two environments, such as high- and low-elevation wolf spiders in the Galapagos (De Busschere *et al.* 2010) and adaptation to wet and dry habitats in Hawaiian silverswords (Blonder *et al.* 2016). Once we recognize similarities and differences in processes underlying diversification across lineages, we can look at other aspects of the evolutionary process upon which adaptive radiations can shed light, most notably concepts of specialization, abundance, and equilibrium diversity, to name a few.

Glossary

- **Adaptive radiation** - evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms (Futuyma 1998)
- **Admixture** - when individuals from two or more previously separated populations begin interbreeding resulting in the introduction of new genetic lineages into a population.
- Developmental plasticity - a developmental change in form or behavior caused by environmental conditions (West-Eberhard 2003).
- Divergence - can occur along different axes:
    - **Alpha (α) niche axes** are those that allow local sympatry such as microhabitat, temporal, or other resource partitioning
    - **Beta (β) niche axes** are those that reflect larger scale habitat and climatic variables.
- **Divergent selection -** selection in which a trait at either end of a spectrum has an advantage over the average
- **Diversification** - evolution of phenotypically and reproductively distinct species in a clade
- **Disruptive selection** - natural or sexual selection that favors extreme over intermediate phenotypes within a single population (Seehausen 2004)
- **Ecological character displacement** - the divergence of sympatric species to minimize ecological overlap
- **Ecological opportunity** - the availability of ecologically accessible resources that may be evolutionarily exploited (Stroud & Losos 2016)
- **Ecological speciation** - the process by which barriers to gene flow evolve between populations as a result of ecologically based divergent selection (Schluter 2009)
- **Evolvability -** the capacity to generate heritable phenotypic variation (Stroud & Losos 2016)
- **Key innovation** - the evolution of a trait that allows a species to interact with the environment in a novel way
- Geographic separation terms:
    - **Allopatry**: Separated in space in such a way as to prevent the organisms from interacting during normal activity
    - **Sympatry**: No spatial separation, allowing organisms to interact regularly during normal activity
    - **Mosaic allopatry**: Separated in space in a mosaic manner, ie with no single clear boundary, but the separation still preventing the organisms from interacting during normal activity
    - **Microallopatry**: Despite overlapping range, microallopatric taxa are still separated in space with interaction between taxa prevented because they occupy different ecological niches**.**

- **Mutation-order speciation** - different and incompatible mutations fix in different populations adapting to the same selective pressure (i.e. uniform selection (Mani & Clarke 1990)). Mutations can arise stochastically in different order, allowing 'mutation-order' to serve as a stochastic driver of divergence (Nosil & Flaxman 2010).
- **Nonadaptive radiation** - lineage diversification with minimal ecological diversification, resulting in allopatric or parapatric (Rundell & Price 2009) and sometimes even sympatric taxa (Xu and Shaw this volume)
- **Prezygotic barriers** - anything that prevents mating and fertilization; **postzygotic barriers** - act after fertilization (zygote mortality, hybrid sterility)
- **Priority Effects** (De Meester *et al.* 2016; Fukami *et al.* 2007):
    - Ecological priority effect: the arrival order of species influences community dynamics and structure.
    - Genetic priority effect: an evolutionary priority effect whereby the arrival order of genotypes influences population genetic structure.
    - Evolution-mediated priority effect: the arrival order of genetic lineages or species and their evolution influences population genetic or community dynamics.
- **Reinforcement** - the evolution of traits that minimize hybridization between incipient species
- Reproductive isolation - factors involved in initial stages
    - **Extrinsic reproductive isolation**: Fitness reduction in hybrids that is dependent on the environment and that is mediated by genotype–environment interactions.
    - **Intrinsic barriers**: often due to genetic incompatibilities; these occur independent of the environment (for example, Bateson–Dobzhansky–Muller incompatibilities).

Boxes

Box 1. The poles of adaptive radiation. A. Ecological opportunity is a general requirement for adaptive radiation. The existence of opportunity often necessitates a barrier, the extent of which depends on the distance – which may be physiological or geographic – from the source and the degree to which organisms can survive in the surrounding matrix. **B. Within a given adaptive radiation**, initial divergence of species may be due to two factors, (i) external factors associated with divergent selection for a given environment, or (ii) internal factors due to reproductive barriers developing, often due to a period of isolation between sites, in the same kind of environment (Seehausen *et al.* 2014). In the former case, ecological divergence is associated with the environment. In the latter case, it may be associated with interaction between close relatives as a result of secondary sympatry (Cotoras *et al.* 2018). **C. The degree of co-occurrence among members of an adaptive radiation** varies widely, with many radiations requiring little interaction between close relatives. For example, sympatric speciation in Nicaragua cichlids appears to be the result of divergent selection between different environments (Barluenga *et al.* 2006); likewise for sticklebacks (Bolnick 2011), and wolf spiders in the Galapagos (De Busschere *et al.* 2010). In other situations, local sympatry and interaction between close relatives appears to be a critical part of the process of adaptive radiation, for example in Caribbean *Anolis* (Losos 2009) and Hawaiian spiders (Cotoras *et al.* 2018; Gillespie *et al.* 2018). **D.**

Gene flow, traditionally considered to hinder divergence between incipient species, can serve to infuse variability that may foster adaptive radiation. The phenomenon has now been well documented in cichlid fish (Meier *et al.* 2017) and Heliconius butterflies (Mallet 2005), as well as many plants (Barrier *et al.* 1999; Friar *et al.* 2008), although it is also found in many other lineages (Lamichhaney *et al.* 2018). Indeed, the process may be common to many adaptive radiations. However, it is important to distinguish between how admixture is achieved in order to assess its effects on the process of adaptive radiation (Brock & Wagner 2018). **E. Rate of diversification** in adaptive radiation. Adaptive radiation is frequently thought to be associated with an increase in the rate of diversification (Gavrilets & Losos 2009; Schluter 2000); however, it may be that adaptive radiations do not require increased diversification rates (Givnish 2015).

Figures

Figure 1. Model systems studied by contributors of the AGA 2018 President's Symposium: Origins of Adaptive Radiation. Yellow dots represent areas where field studies have been conducted and do not accurately represent the full range of each group. Anti-clockwise from top-right; Cameroon crater lake cichlids, Caribbean *Anolis* lizards, San Salvador pupfish (*Cyprinodon* sp.), Mexican (Lake Chichancanab) cichlids, spadefoot toads (*Spea* sp.), stickleback fish (*Gasterosteus aculeatus*), Hawaiian spiders, *Laupala* crickets, *Nesophrosyne* leafhoppers, Hawaiian *Metrosideros* plants*, Hyposmocoma* moths, Hawaiian honeycreepers, Hawaiian *Bidens*, Galapagos land snails (*Bulimulus* sp.), Darwin's finches *(Geospiza* sp.*),* mainland *Anolis* lizards, *Heliconius* butterflies, Cameroon crater lake cichlids, *Neospiza* finches of the Tristan da Cunha archipegalo, and African Rift Lake cichlids. Photography credits anti-clockwise from top right: C. Martin, J.Stroud, C.Martin, C. Martin, D. Pfennig, A. Hendry, R. Gillespie, K. Shaw, G. Bennett, E. Stacy, D. Rubinoff, J. Jeffreys, M. Knope, C. Parent, A. Hendry, J. Stroud, J. Mallet, P. Ryan, C. Wagner.

Figure 2. Contrasting roles of external factors and divergent selection associated with the environment versus internal factors and incompatibility fostering initial divergence

Figure 3. Entities formed by external factors and divergent selection. The external environment and divergent selection can lead to reproductive isolation between descendant lineages, owing to genotype by environment interactions.

Figure 4. Entities formed by internal factors - separation in geographical space without any obvious disruptive selection.

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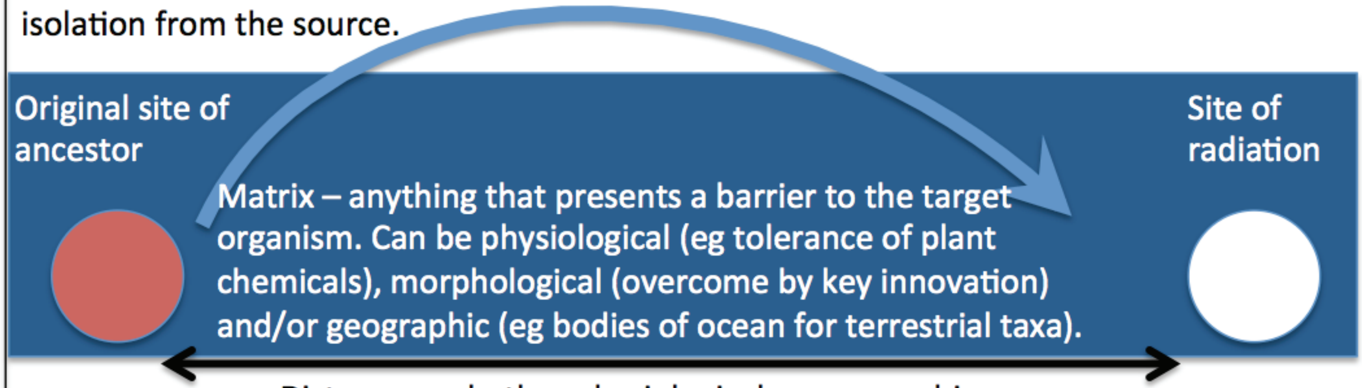
Box 1. The poles of adaptive radiation

A. Ecological opportunity: A feature of adaptive radiations is that they require novel niche space with associated "ecological opportunity". This opportunity requires isolation from the source.



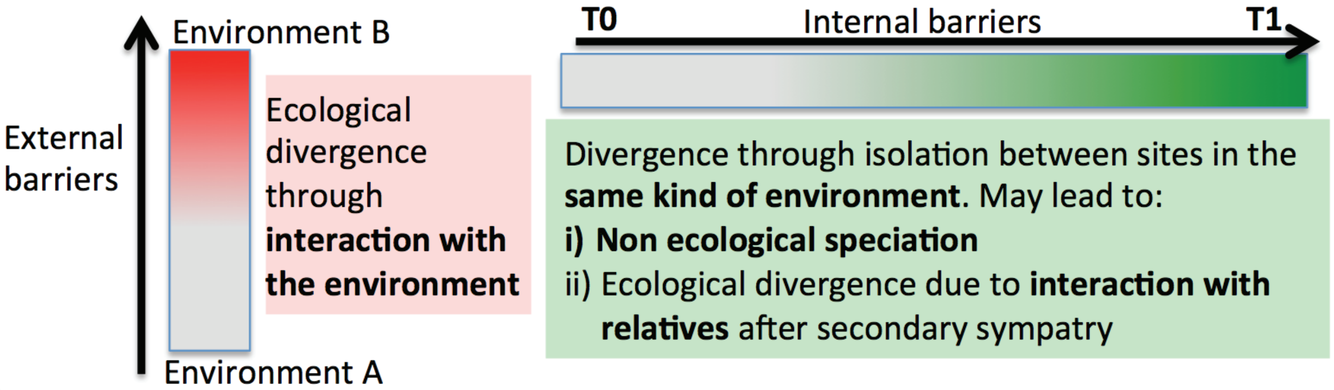
Original site of ancestor

Site of radiation

Matrix – anything that presents a barrier to the target organism. Can be physiological (eg tolerance of plant chemicals), morphological (overcome by key innovation) and/or geographic (eg bodies of ocean for terrestrial taxa).

Distance – whether physiological or geographic – between source and target

B. Divergence due to external vs internal factors. Initial reproductive isolation may be caused by **divergent selection due to different environments**, or alternatively formation of **intrinsic barriers due to isolation between sites in the same kind of environment**



Environment B

External barriers

Ecological divergence through **interaction with the environment**

Environment A

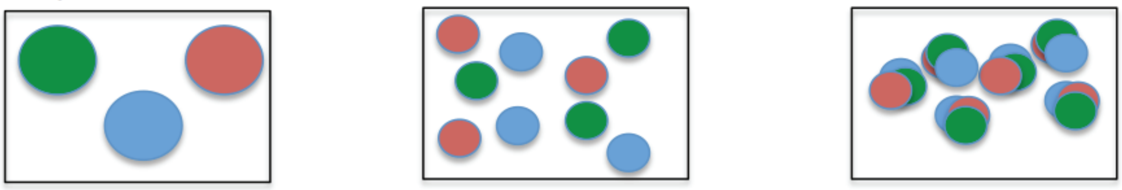
T0 Internal barriers **T1**

Divergence through isolation between sites in the **same kind of environment**. May lead to:

i) Non ecological speciation

ii) Ecological divergence due to **interaction with relatives** after secondary sympatry

C. Co-occurrence of taxa within an adaptive radiation. Adaptive radiations differ widely in terms of local sympatry of component species. These differences can arise from radically different processes, and teasing apart these different perceptions is critical to inference of common process

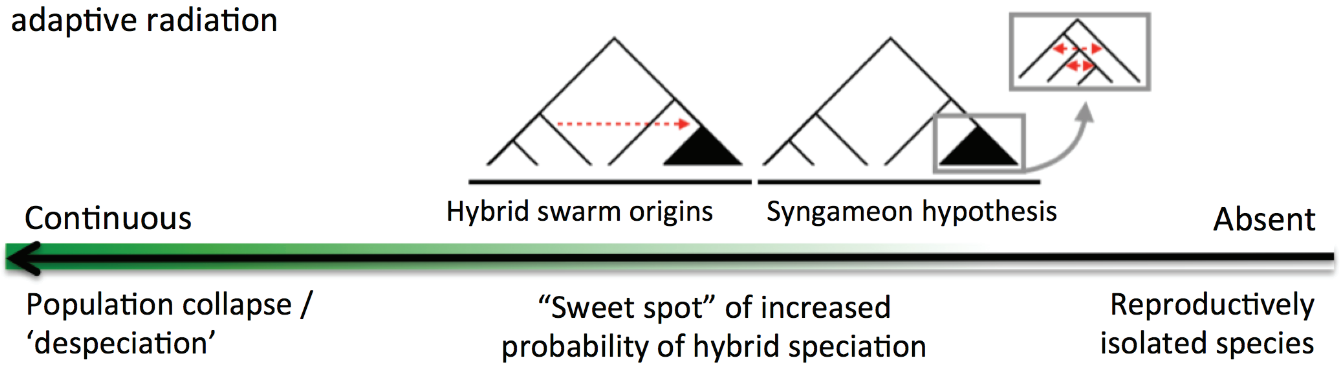


Non interactive; locally allopatric

Non interactive; locally mosaic or micro-allopatric

Interactive; locally sympatric

D. Gene flow. Gene flow can hinder divergence, but can also infuse variability to allow adaptive radiation. This can take place through hybrid origins of entire radiating clades ("hybrid swarm origins") wherein admixture between one or more divergent lineages happens prior to the onset of radiation, or via hybridization within adaptive radiations that facilitates further speciation ("syngameon hypothesis"). There may be a "sweet spot" in which divergent lineages can admix or hybridize and give rise to variability that is key to adaptive radiation



Hybrid swarm origins

Syngameon hypothesis

Continuous

Absent

Population collapse / 'despeciation'

"Sweet spot" of increased probability of hybrid speciation

Reproductively isolated species

E. Time and rate of diversification.

Acceleration in **rate of diversification only.** Non adaptive radiation	**Adaptive shifts only.** Slow accumulation of adaptive shifts over time	**Acceleration in rate of diversificaiton coupled with adaptive shifts**

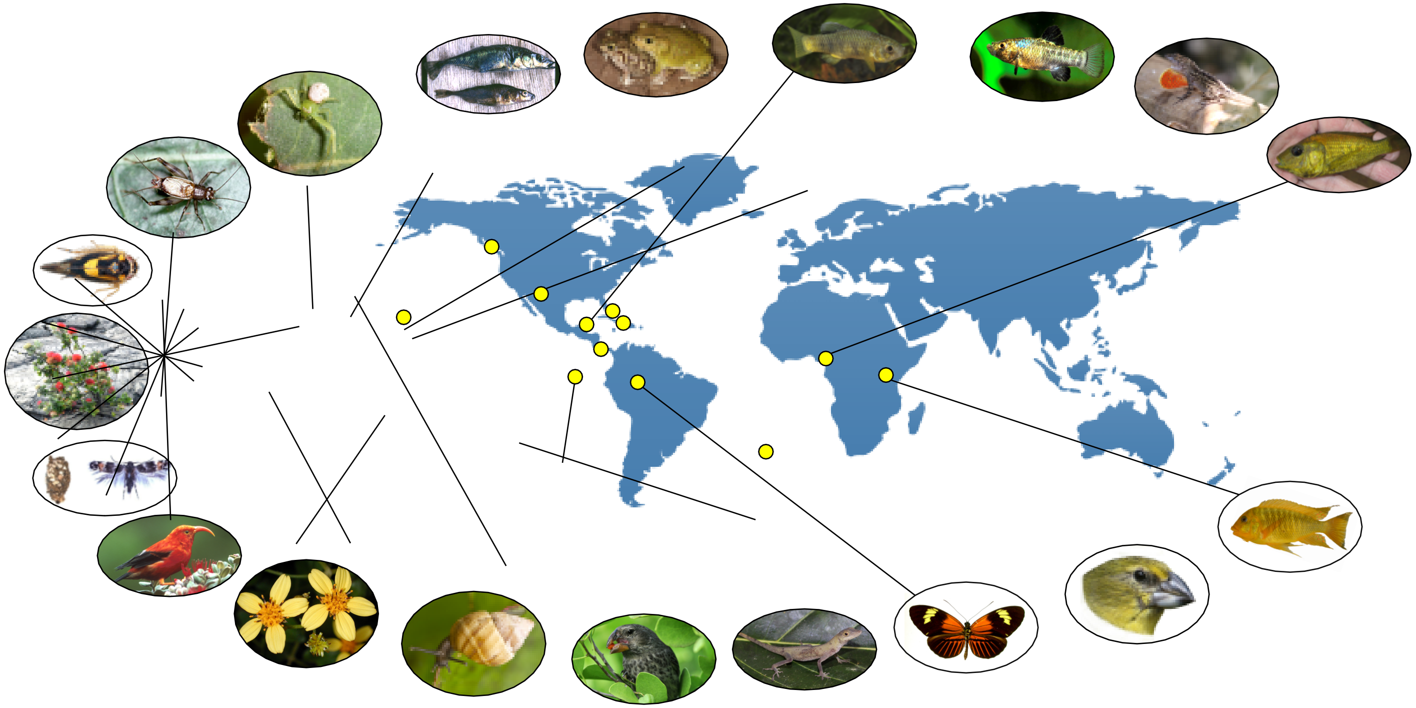


Figure 1. Model systems studied by contributors of the AGA 2018 President's Symposium: Origins of Adaptive Radiation. Yellow dots represent areas where field studies have been conducted and do not accurately represent the full range of each group

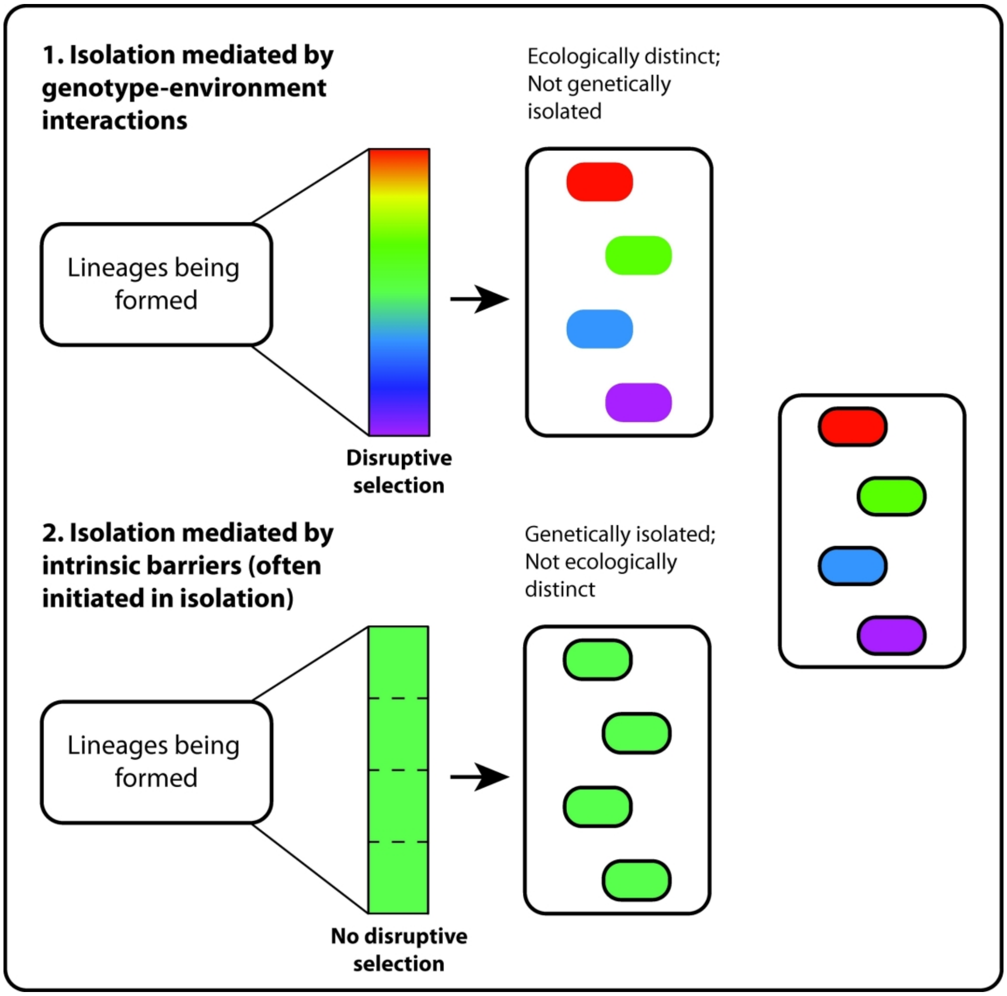


Figure 2. Contrasting roles of extrinsic selection associated with the environment versus intrinsic incompatibility fostering initial divergence

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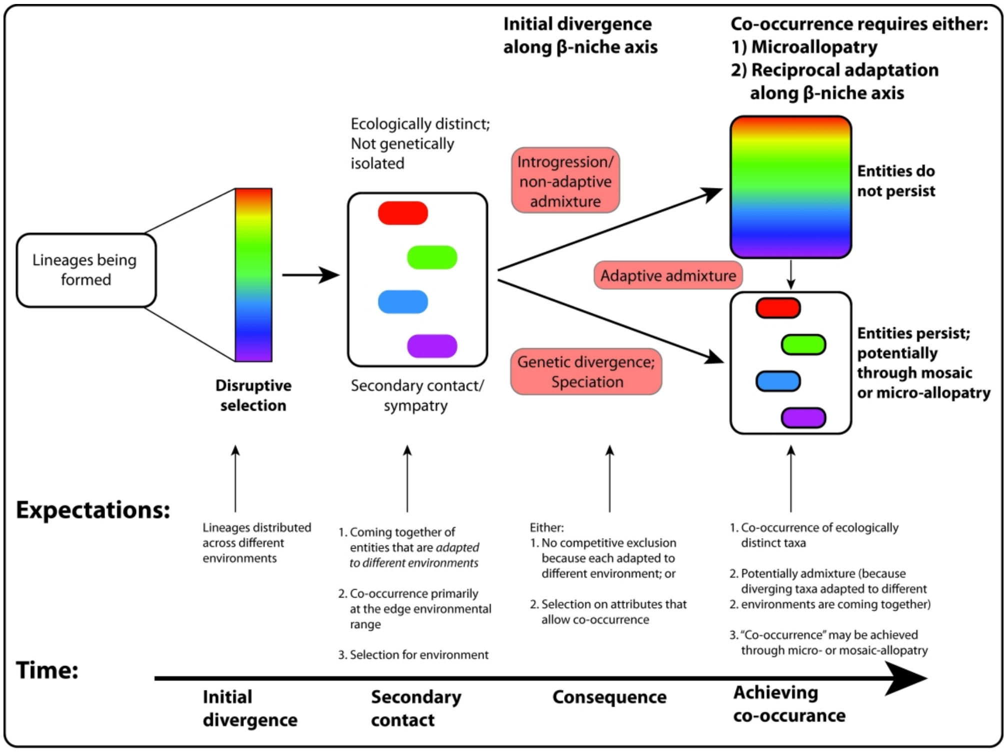

Figure 3. Entities formed by extrinsic factors and divergent selection. The extrinsic environment and divergent selection can lead to reproductive isolation between descendant lineages, owing to genotype by environment interactions

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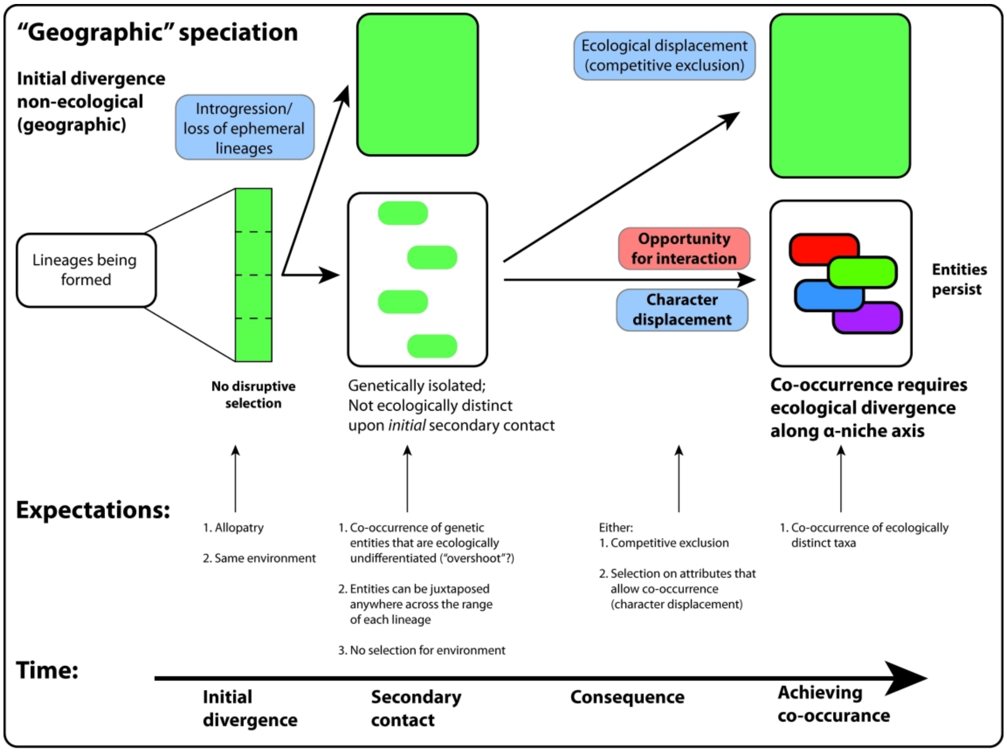

Figure 4. Entities formed by intrinsic factors - separation in geographical space without any obvious disruptive selection.

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