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The Paradox Behind the Pattern of Rapid Adaptive Radiation: How Can the Speciation Process Sustain Itself Through an Early Burst?

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Abstract

Rapid adaptive radiation poses two distinct questions apart from speciation and adaptation: What happens after one speciation event and how do some lineages continue speciating through a rapid burst? We review major features of rapid radiations and their mismatch with theoretical models and speciation mechanisms. The paradox is that the hallmark rapid burst pattern of adaptive radiation is contradicted by most speciation models, which predict continuously decelerating diversification and niche subdivision. Furthermore, it is unclear if and how speciation-promoting mechanisms such as magic traits, phenotype matching, and physical linkage of coadapted alleles promote rapid bursts of speciation. We review additional mechanisms beyond ecological opportunity to explain rapid radiations: (a) ancient adaptive alleles and the transporter hypothesis, (b) sexual signal complexity, (c) fitness landscape connectivity, (d) diversity begets diversity, and (e) plasticity first. We propose new questions and predictions connecting microevolutionary processes to macroevolutionary patterns through the study of rapid radiations.



1. INTRODUCTION

The most striking pattern of biodiversity is its uneven distribution across space and time. This disparity transcends all scales: From the Cambrian explosion to microbial microcosms, rapid bursts of diversification are staggeringly uneven across different environments, time periods, and evolutionary lineages (Alfaro et al. 2009b; Blount et al. 2012; Glor 2010; Landis & Schraiber 2017; Rabosky et al. 2012, 2018; Simpson 1944; Uyeda et al. 2011). Phylogenetic comparative analyses of long-standing ecological theories, such as the latitudinal diversity gradient (Hurlbert & Stegen 2014), punctuated equilibrium (Pennell et al. 2014), and the speciation–area relationship (Kisel & Barraclough 2010, Wagner et al. 2014), generally aim to explain these patterns of disparity at global scales. In contrast, mechanistic models of species divergence (Dieckmann & Doebeli 1999, Gavrillets 2004, Kopp et al. 2018, Servedio & Burger 2014), ecological speciation theory (Hendry 2017, Nosil 2012, Schluter 2000), and speciation genomics (Ravinet et al. 2017, Seehausen et al. 2014) attempt to predict and describe phenotypic and genetic divergence within a population at microevolutionary timescales. However, a gap remains between these two scales: We have little understanding of the population-level mechanisms and processes contributing to repeated bouts of speciation within an environment—the initial rapid burst phase of adaptive radiation (Harmon et al. 2010, Losos 2010, Stroud & Losos 2016).

Periodic rapid bursts of diversification contradict many existing speciation models. Many models and mechanisms predict or imply that the rate of speciation should slow down after each speciation event due to increased niche subdivision, weakened disruptive selection, and the limited availability of genetic architectures (e.g., inversions) or sexual traits (e.g., magic traits) that promote speciation (see Section 4). In contrast, at the macroevolutionary scale, bursts of multiple speciation events in rapid succession appear to be common (Estes & Arnold 2007; Gavrillets & Losos 2009; Glor 2010; Landis & Schraiber 2017; Uyeda et al. 2011, 2018). These bursts indicate accelerating speciation rates within some lineages at certain times, rather than continuously decelerating rates as predicted by many speciation models. Indeed, explosive speciation, the temporary acceleration of speciation and trait diversification rates, is often noted as a feature of classic adaptive radiations (Kocher 2004, Rabosky & Lovette 2008). It is this explosive phase of some radiations that we aim to understand here.

The solution to this paradox of rapid radiation has long been the *deus ex machina* of ecological opportunity, generally described as key innovations enabling access to new resources, colonization of new environments with abundant resources and few competitors, or mass extinction events (Futuyma 1998, Hendry 2017, Losos 2010, Schluter 2000, Simpson 1944, Stroud & Losos 2016, Wellborn & Langerhans 2015, Yoder et al. 2010). There is no question that ecological opportunity is associated with adaptive radiation and diversification at global and regional scales; indeed, this remains the dominant explanation within the ecological theory of adaptive radiation. However, on closer inspection of some taxa at microevolutionary scales, key innovations do not always coincide with increased diversification (Alfaro et al. 2009a, Harmon & Harrison 2015, McGee et al. 2015, Rabosky 2017, Seehausen 2006), many taxa colonize new environments and fail to diversify (Arbogast et al. 2006, Lovette et al. 2002, Martin 2016a, Martin & Wainwright 2013a, Meyer et al. 2017, Muschick et al. 2018, Roderick & Gillespie 1998), and diversification of new lineages often precedes or lags long after mass extinction events (reviewed in Erwin 2015). Furthermore, niche axes relevant to ecological opportunity and diversification are rarely tested *a priori* (e.g., Schluter & Grant 1984a; reviewed in Erwin 2015, Stroud & Losos 2016, Wellborn & Langerhans 2015). There are also many examples of rapid radiation within already species-rich communities with no obvious ecological opportunities, such as wild tomatoes (Pease et al. 2016) and Amazonian pike cichlids (Burruss et al. 2018), with no apparent unique key innovations.

Indeed, key innovations can provide access to new resources while not resulting in increased species diversification or decreased extinction rates (Rabosky 2017, Stroud & Losos 2016). Thus, the theory of ecological opportunity is clearly a dominant cause underlying adaptive radiation but sometimes provides limited predictive power without the very difficult step of actually measuring fitness landscapes in natural populations (e.g., Arnegard et al. 2014, Bolnick & Lau 2008, Keagy et al. 2016, Martin 2012, Martin & Wainwright 2013b, Schluter & Grant 1984a; also see Stroud & Losos 2016). These direct measurements of multi-species fitness landscapes provide evidence of the multivariate selection pressures acting on natural populations and could be used to probe the existence of empty fitness peaks in comparable environments without radiations.

Our goal is to review the pattern of rapid, repeated bouts of speciation during early phases of adaptive radiation and emerging theories for understanding how multiple speciation events can occur simultaneously or in quick succession. We define this scale between a single speciation event and global macroevolutionary patterns as mesoevolution (**Table 1**), comprising the study of rapid bursts of diversification within a single clade or a shared environment. This follows Dobzhansky's (1954) first use of the term and departs from the emphasis on parallelism proposed by Abouheif (2008).

Table 1 Hierarchical levels of questions about the evolution of diversity, from case studies of single speciation events (microevolution), to case studies of repeated bouts of speciation (mesoevolution), to global diversity patterns (macroevolution)

Microevolution (speciation)	Mesoevolution (rapid radiations)	Macroevolution (global biodiversity patterns)
<i>Ecological niche</i>		
What niches do sister species occupy?	Did total niche diversity increase due to niche subdivision, new trophic levels, or novel niches?	Which environmental and lineage-specific variables are associated with niche diversification?
What are the reproductive isolating barriers between species?	How do reproductive isolating barriers change after each speciation event?	What are the relative rates of evolution of different types of isolating barriers?
<i>Fitness</i>		
What is the strength of disruptive selection on sister species?	How many fitness peaks exist on the fitness landscape within an environment?	How many fitness optima can be distinguished in multivariate trait space for a given set of taxa?
Do sister species differ in performance within their respective niches (i.e., trait utility)?	How are fitness landscapes shaped by performance constraints versus competitive dynamics?	Do biophysical principles constrain macroevolutionary adaptive landscapes?
<i>Gene flow</i>		
Did gene flow promote or constrain speciation?	Did extinct ephemeral species contribute ancient adaptive alleles to extant radiations?	How do gene trees underlying speciation traits differ from neutral gene trees?
Did speciation occur in parallel across similar environments?	How much parallelism results from sorting of ancient haplotypes?	Are structural rearrangements more likely to be found within rapid radiations?
<i>Mate choice</i>		
How do mate preferences affect speciation?	How does repeated speciation affect mate preference functions?	How stable are mate preference functions over macroevolutionary timescales?
Did magic cues or preferences promote speciation?	Were different magic cues or preferences involved in multiple rounds of speciation?	Are diverse clades associated with more frequent transitions among mating preferences or cues?



2. SETTING THE STAGE

2.1. What Is Adaptive Radiation?

The definition of adaptive radiation remains loose but requires a clade to diversify and fill a variety of niches, often within a short timespan (Gavrilets & Losos 2009, Losos 2010, Olson & Arroyo-Santos 2009, Schluter 2000, Simpson 1944, Stroud & Losos 2016). Many researchers consider adaptive radiation to result from repeated bouts of ecological speciation—i.e., speciation driven by ecological divergence (e.g., Glor 2010, Wellborn & Langerhans 2015, Yoder et al. 2010)—in contrast to speciation by sexual selection (Arnegard et al. 2010) or mutation-order speciation (Schluter 2009). However, nearly every reproductive isolating barrier is affected by adaptation in at least one of the two diverging populations (Sobel et al. 2010), including postzygotic intrinsic barriers, which may often be affected by the environment (Fuller 2008, Miller & Matute 2017). Thus, nearly all speciation is ecological speciation. Additionally, rapid is often included in the definition of adaptive radiation but left unquantified following the original framing of Simpson (1944), who described a qualitative distinction between phyletic gradualism and adaptive radiation. More recent definitions require phylogenetic comparative evidence for a rapid pulse or early burst of phenotypic diversification (Glor 2010, Landis et al. 2013) or simply a wide diversity of ecological niches within a clade, regardless of age or diversification rate (Givnish 2015).

Our main goal is to ask whether additional mechanisms outside of ecological speciation are needed to sufficiently understand and predict the occurrence of rapid radiations. Our focus here is on the unique processes that may contribute to exceptionally diverse radiations in sympatry during the rapid burst phase of some adaptive radiations (e.g., Givnish et al. 1997, Kocher 2004, Martin & Wainwright 2011) relative to the continuum of adaptive divergence across taxa.

We define rapid radiation as a young clade (*a*) diversifying rapidly and (*b*) containing at least three or more species occurring in sympatry (often described as species flocks; see Echelle & Kornfield 1984). Our focus on radiations of three or more species ensures that we are discussing processes that apply to repeated bouts of speciation in the same environment, rather than a single speciation event or repeated parallel speciation across similar environments (reviewed in Bolnick et al. 2018). Indeed, processes affecting multiple speciation events in quick succession within a single environment cannot be studied in case studies of a single species pair. More broadly, we view the process of rapid adaptive radiation as encompassing diverse phenomena across a multidimensional radiation space containing the axes of species richness, phenotypic disparity, niche divergence, ecological novelty, levels of sympatry versus microallopatry, frequency of repeated parallel speciation, and habitat, trophic, or sexual diversification (**Figure 1**). This catalog of rapid radiations includes species-rich, but ecologically similar, radiations, such as plethodontid salamanders (Kozak et al. 2005) and Mexican axolotls (Shaffer & McKnight 1996); species-rich sexual radiations, such as *Habronattus* jumping spiders (Masta & Maddison 2002) and mormyrid electric fishes (Arnegard et al. 2010, Carlson et al. 2011); microhabitat-driven radiations existing in microallopatry across heterogeneous landscapes, such as Hawaiian *Metrosideros* trees (Stacy et al. 2014) and Malili Lake shrimp (von Rintelen et al. 2010); and classic examples of adaptive radiation, such as Darwin's finches (Grant & Grant 2011), Hawaiian drosophilids, honeycreepers, and silverswords (Givnish & Sytsma 1997, Landis et al. 2018, Lovette et al. 2002), and East African cichlid radiations (Kocher 2004, Seehausen 2006) (**Figure 1**).

2.2. Why Study Rapid Radiation?

Rapid radiations provide insights into the processes operating above the level of a single speciation event and connect these processes to patterns observed at global macroevolutionary scales (**Table 1**). High levels of sympatry in many rapid radiations provide tractable case studies

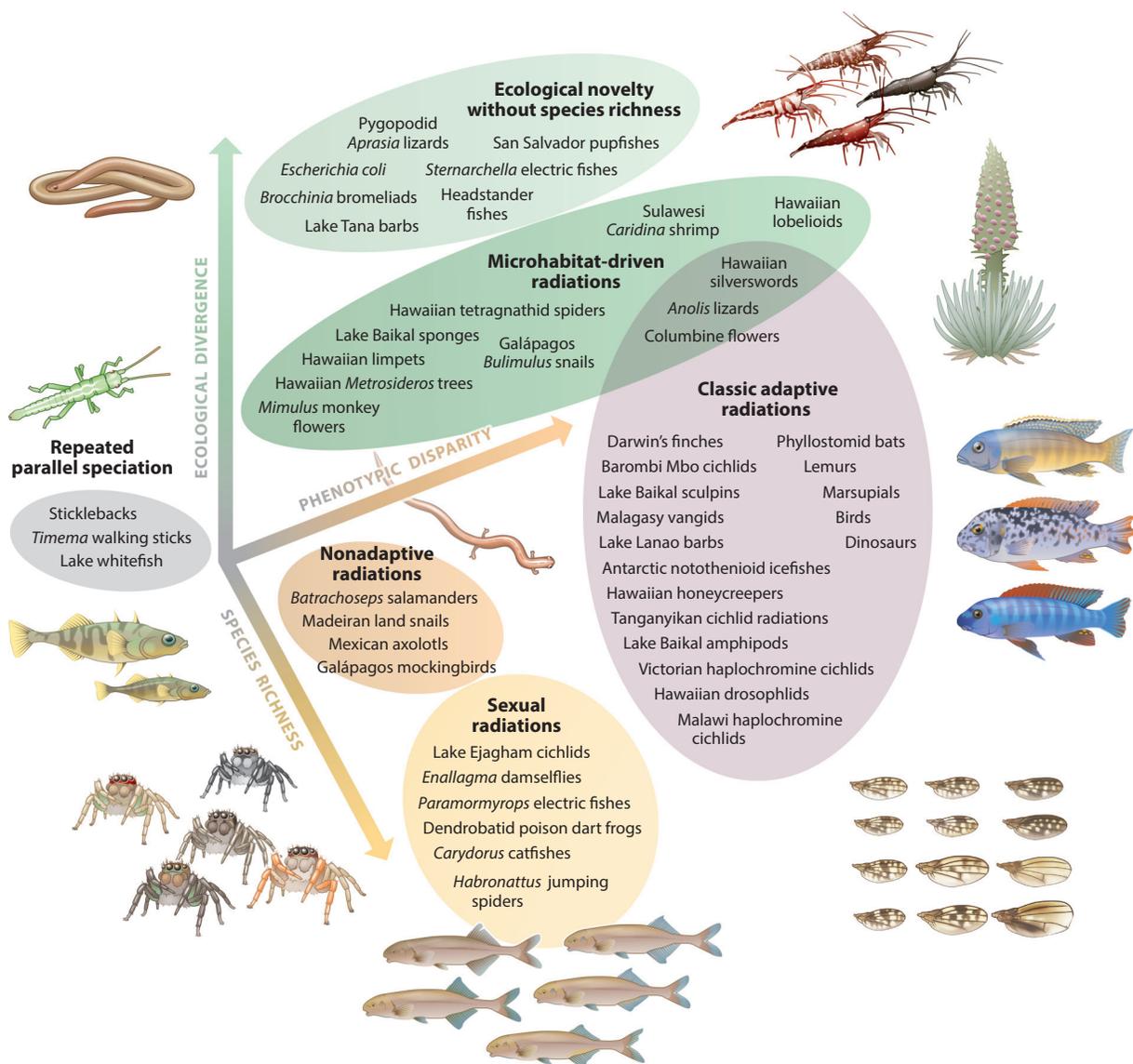


Figure 1

Examples of different types of rapid radiations along the three major axes of adaptive radiation. Representative illustrations of the following groups are shown: ecological novelty without species richness (pygopodid *Aprasia* lizards); microhabitat-driven radiations with extensive microallopatry (Malili lakes *Caridina* shrimp); repeated parallel speciation (*Timema* walking sticks and benthic/limnetic stickleback); nonadaptive radiations (*Batrachoseps* salamanders); sexual radiations (*Habronattus* jumping spiders and *Paramormyrops* electric fishes); and classic adaptive radiations (Malawi cichlids, Hawaiian picture-wing *Drosophila*, and Hawaiian *Argyroxiphium* and *Dubautia* silversword alliance).

of eco-evolutionary dynamics for several reasons: (a) radiations diversify on a shared adaptive landscape, enabling direct measurements of the macroevolutionary contours of this landscape beyond a single diverging population (Arnold et al. 2001, Benkman 2003, Martin & Wainwright 2013b); (b) genetic mapping crosses among closely related species can provide estimates of the

genetic architecture of adaptive traits (Martin et al. 2017a, Miller et al. 2014); and (c) gene flow is pervasive in all rapid radiations examined with genomic data so far (Richards et al. 2019), making rapid radiations excellent for genome-wide association studies connecting genotypes to phenotypes (Matz 2018, McGirr & Martin 2017, Pease et al. 2016).

Finally, it is worth remembering that humans originated within a rapid radiation. Our species most likely evolved within a species flock of at least 3–5 hominin species frequently experiencing gene flow, adaptive introgression, and potentially coexisting in sympatry across most of our range (Crawford et al. 2017, Huerta-Sánchez et al. 2014, Racimo et al. 2015). Understanding the process of rapid radiation will illuminate our own origins.

3. THE PATTERN OF RAPID RADIATION

3.1. Three Fundamental Axes: Species Diversification, Phenotypic Disparity, and Ecological Divergence

Rapid radiations occur along three major axes of diversification: species richness, phenotypic disparity, and ecological niche diversity (**Figure 1**). Although these axes are often correlated in global surveys [e.g., body size and lineage diversification rates in fishes (Rabosky et al. 2013)] and in classic adaptive radiations, they are not always correlated when comparing different types of rapid radiations observed in nature, suggesting a diversity of driving mechanisms. For example, nonadaptive rapid radiations display extensive cryptic species diversity, often with some degree of sympatry, such as plethodontid salamanders and some land snails (Gittenberger 1991, Kozak et al. 2005, Rundell & Price 2009). In other radiations, likewise, many species occupy a small cluster of related niches within a small region of morphospace, such as flannel-mouth characins versus headstanders (Sidlauskas 2008). In the opposite extreme, some radiations display extensive niche diversity and ecological novelty but limited species and trait diversification rates, such as pygopodid lizards. This Australian radiation of burrowing, nearly limbless gekkonid lizards includes specialists on spiders, skinks, insects, and ant larvae (Patchell & Shine 1986). Vampire finch populations are another example of novel niche use without detectable phenotypic or lineage diversity: Sharp-beaked finches drink blood from Nazca and blue-footed boobies on only two of the Galápagos Islands (Schluter & Grant 1984b).

Sexual radiations are another type of nonadaptive radiation that display extensive trait diversification within sexual characters but minimal ecological divergence, leading to common arguments that sexual selection is driving the radiation (Kaneshiro & Boake 1987, Martin 2013). For example, some mormyrid electric fishes exhibit substantial diversity in electrical signals that are used in species recognition and mate choice (Arnegard et al. 2010, Carlson et al. 2011). Numerous other sexual radiations exist across diverse sensory modalities: from mechanical premating isolating barriers in radiations of damselflies (McPeck et al. 2009), to acoustic and visual courtship displays in peacock jumping spiders (Masta & Maddison 2002), to color polymorphisms in poison dart frogs (Reynolds & Fitzpatrick 2007). Sometimes these sexual radiations are also found nested within larger, ecologically diverse radiations, such as some groups of Malawi cichlids, which coexist despite extensive overlap in morphology, diet, depth, and microhabitat but display a diversity of male sexual coloration and bower shapes (Kocher 2004, Martin & Genner 2009a,b).

Degree of sympatry is another variable differentiating radiations—from putative examples of sympatric speciation in a single homogeneous environment (Martin et al. 2015, Richards et al. 2019), to classic adaptive radiations in which species assemblages coexist within heterogeneous habitats and compete for the same resources while reaching alpha diversities in excess of 100 species (Kocher 2004), to habitat-driven radiations in which each species occurs only within a single microclimate or microallopatric niche (Losos 2009, Muñoz et al. 2016, Stacy et al. 2014),

consistent with an automatic magic trait mechanism of speciation if these species mate within their respective microhabitats (Servedio et al. 2011).

Finally, novel ecological niches are a surprisingly common feature of rapid radiations, in the sense of specialization on resources not only unique within the novel environment of the radiation but also unique across closely related outgroups and sometimes across their global range (Martin & Wainwright 2011). For example, radiations of Hawaiian tetragnathid spiders have uncharacteristically evolved to build orb webs, spear their prey, and pursuit hunt (Roderick & Gillespie 1998); radiations of Caribbean *Anolis* lizards have repeatedly evolved chameleon-like ecomorphs (Mahler et al. 2016); and a sympatric radiation of pupfishes on San Salvador Island, Bahamas, contains a scale-eating specialist separated by 168 million years from the most closely related scale-eaters within East African cichlids (Martin & Wainwright 2013a). Although seed-eating is common in Darwin's finches and outgroups, blood-drinking combined with parasite removal in the vampire finch appears analogous to the niche of oxpeckers, separated by 20 million years (Martin & Wainwright 2013a). Simpson's (1944) original concept of adaptive zones also conveys the idea of ecological novelty as distinct from niche diversity: transitioning from a cluster of related niches (e.g., browsing horses) to an entirely different cluster of niches in a new adaptive zone (e.g., grazing).

3.2. Is an Early Burst Pattern the Hallmark of Adaptive Radiation?

The prevalence of an early burst pattern of species and trait diversification during adaptive radiation versus other evolutionary models, such as a rare pulse or multi-optima Ornstein–Uhlenbeck (OU) model, is increasingly contentious (Givnish 2015, Uyeda et al. 2018). Initial surveys of body size variation found the early burst pattern to be rare (Harmon et al. 2010). However, new comparative analyses suggest that this inference was an artifact of ignoring intraspecific variation and instead found that early bursts of trait diversification are quite common (Landis & Schraiber 2017, Landis et al. 2013, Uyeda et al. 2018). More recent comparative methods employing a Lévy process to model waiting times for rare, stochastic bursts of body size diversification found more support for rare pulses of diversification within many different vertebrate clades than early burst or multi-optima OU models (Landis & Schraiber 2017). Furthermore, detection of an early burst signal within lineage diversification rates is also affected by trait diversification (O'Meara et al. 2006, Uyeda et al. 2018) and variable, unknown rates of extinction (Rabosky 2010). Regardless of prevalence or timing of onset, however, any phase of repeated speciation events in rapid succession presents the question we address in this review: How can the speciation process sustain itself through a rapid burst?

Conversely, the flip side to a rapid burst is the long waiting time before a burst occurs and the subsequent slowdown in diversification rates. For example, body size diversification appears to accelerate only after a waiting period of approximately 1 million years across highly diverse taxa and types of data (Uyeda et al. 2011). One interpretation of this result is the ephemeral nature of species boundaries until postzygotic intrinsic isolating barriers evolve [the waiting time for (Bateson)–Dobzhansky–Muller incompatibilities (DMIs) to evolve (Coyne & Orr 2004, Rosenblum et al. 2012)]. However, similar lags can be observed on microevolutionary timescales. For example, a fine-scale fossil time series for colonization of an ancient lake by stickleback exquisitely depicts the lag in adaptation to a new fitness optimum after colonization, followed by extinction as the lake dries up and the cycle begins anew (Hunt et al. 2008). Similarly, riverine cichlids colonized a small Cameroon lake almost immediately after its formation, but sympatric radiation did not occur until 8,000 years later, coinciding with an influx of olfactory receptor alleles (Poelstra et al. 2018). These lags are expected from theory for a single speciation event; for example, due to waiting



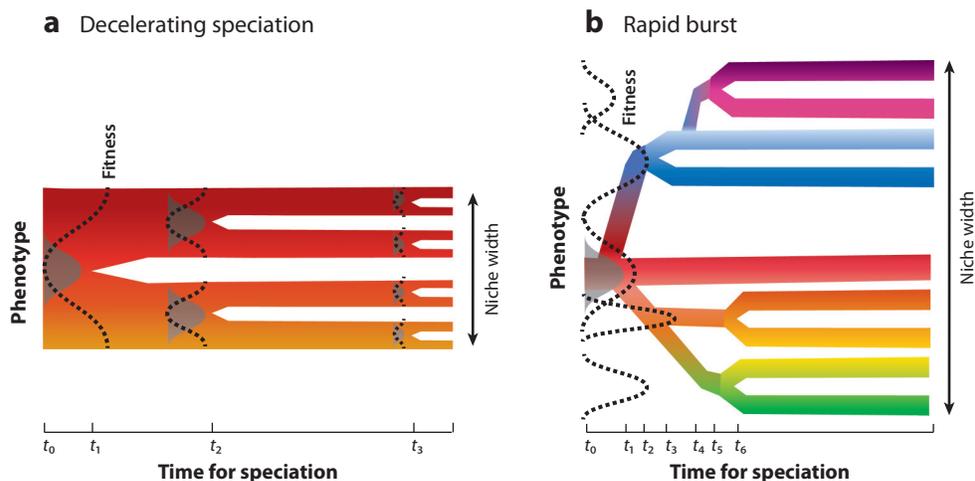


Figure 2

(a) Speciation models predict repeated subdivision of a broad ancestral niche with decreased strength of disruptive selection after each speciation event and decreasing speciation rates. (b) Rapid radiations observed in nature often exhibit an early burst of diversification greatly exceeding niche width and niche diversity in the ancestral population. Fitness functions (dotted lines) are shown for comparison: (a) frequency-dependent dynamics expected under models of speciation with repeated subdivision of the ancestral niche and decreased strength of disruptive selection after each speciation event versus (b) a static and complex adaptive landscape underlying a burst of diversification that greatly exceeds ancestral niche width.

times for the buildup of linkage disequilibrium between ecological loci and mating loci (Gavrilets 2004). However, the paradox is that repeated speciation events within rapid radiations are not each accompanied by long waiting times.

4. THE PARADOX: MODELS AND MECHANISMS OF SPECIATION PREDICT DECELERATING SPECIATION RATES

In contrast to the observed pattern of rapid bursts of diversification, most theoretical models and speciation mechanisms suggest that the interval between repeated speciation events should always increase, not periodically decrease (**Figure 2a**). Furthermore, many models and mechanisms are based on a finite supply of ecological niche diversity, niche width, assortative mating cues, or genetic architectures promoting speciation. In theory, as speciation proceeds rapidly, these promoting factors should be used up, unless their supply is recycled or effectively unlimited (see Section 5).

4.1. Theoretical Models of Adaptive Radiation

There are two main classes of theoretical models of adaptive radiation, often referred to as repeated evolutionary branching processes (Haller et al. 2013). In the first class, spatially continuous models use a single environmental gradient as the resource axis. This scenario underlies most adaptive dynamics models. These models generally rely on negative frequency-dependent competition among similar phenotypes to generate disruptive selection, such as in Dieckmann & Doebeli's (1999) classic model of sympatric speciation and subsequent adaptive dynamics models (Doebeli et al. 2005). After a population mean phenotype reaches a fitness optimum, directional selection on a population changes to negative frequency-dependent disruptive selection for extreme

phenotypes capable of exploiting the tails of the resource distribution. This splits the population if additional factors are favorable, including low costs to strong assortative mating and relatively simple genetic architectures that enable the buildup of linkage disequilibrium between alleles for adaptation and assortative mating by ecotype (Dieckmann & Doebeli 1999; also see the more difficult scenario of speciation by sexual selection, van Doorn & Weissing 2002, Weissing et al. 2011).

Importantly, theorists are drawn to modeling competition on a single continuous resource axis not because of the prevalence of this mechanism in nature but because it is an elegant modeling framework. For example, Polechová & Barton (2005) were enthused that “disruptive selection appears to *emerge* from a continuous unimodal resource distribution, rather than being *imposed arbitrarily*” (p. 1195; emphasis added). Competition for a single continuous resource is exceedingly rare within adaptive radiations, which are generally defined by a diversity of discrete and continuous resource axes in many dimensions (Gavrilets & Losos 2009). Indeed, no one-dimensional resource-based empirical fitness landscapes have been described except for the classic study of seed size distributions and their match with beak sizes in Darwin’s finches (Schluter & Grant 1984a).

Interestingly, the most influential adaptive dynamics model in this class (Dieckmann & Doebeli 1999) actually does result in continued branching after the first speciation event, all the way up to the point at which the phenotype distribution is continuously distributed and matches the resource distribution (Polechová & Barton 2005). In the original study, simulations were not run long enough to observe this behavior and phenotypic variance was constrained so that disruptive selection was always present (Polechová & Barton 2005). This repeated branching process occurs on a single continuous niche axis, resulting in repeated subdivision of the niche axis after each speciation event (**Figure 2a**). Disruptive selection results from available niche width and weakens after each population splitting event due to reduced niche space, until speciation stalls completely when the scale of competition among phenotypes exceeds available niche space (Polechová & Barton 2005). Bolnick (2006) also found that this model can result in the simultaneous emergence of three species. However, simultaneous speciation events in this model still resulted in niche subdivision and weakened disruptive selection after speciation (Bolnick 2006). Adding additional ecological trait axes experiencing directional selection can lead to repeated and recurrent adaptive radiations within multivariate trait space but still results in repeated niche subdivision and weaker disruptive selection after speciation along each axis (Ito & Dieckmann 2007).

Thus, the strong preference of many theorists, particularly within the adaptive dynamics school, for the elegance of disruptive selection emerging naturally from competitive interactions along a single, unimodal resource axis has resulted in model predictions that do not explain observations of increased speciation rates and expansion of niche breadth during rapid radiation, rather than the subdivision predicted. In the second class of models, populations evolve on fixed fitness landscapes, such as patchy heterogeneous habitats of varying fitness (e.g., Gavrilets 2004, Kondrashov & Kondrashov 1999, Wilson & Turelli 1986). These models often result in the spontaneous evolution of habitat specialists under a variety of conditions (Gavrilets & Vose 2005) and can explain the evolution of trophic specialization (Futuyma & Moreno 1988, Holt & Gaines 1992). Although criticized for failing to model fitness landscape dynamics (Doebeli & Dieckmann 2005), static fitness landscapes with multiple optima may be most appropriate for modeling bursts of adaptive radiation (**Figure 2b**) in which divergent resource specialists may be constrained to different fitness optima by absolute performance tradeoffs and biophysical constraints instead of competing directly on the same resource axis (Benkman 2003, Hendry 2017, Higham et al. 2016, Martin 2016b).

Recent models have begun to investigate the origins of transitions between adaptive zones (Kagawa & Takimoto 2017) or chasing a moving fitness optimum (Hansen et al. 2008, Kopp &



Hermisson 2007). For example, increased phenotypic variance facilitates transitions between peaks and may be caused by transgressive segregation (Kagawa & Takimoto 2017), gene flow (Gavrilets 2004, Gavrilets & Vose 2005), or ubiquitous negative frequency-dependent disruptive selection (Haller & Hendry 2014). Challenging work remains in combining complex empirical fitness or performance landscapes with complex genetic architectures for ecological and mating loci originating within diverse spatial and temporal contexts. This complexity may be needed to actually make predictions about the extent of diversification in natural case studies of rapid radiation (e.g., Bolnick 2011, Gavrilets 2014, Gavrilets et al. 2007, Martin 2013, Recknagel et al. 2014, Stayton 2019, Wagner et al. 2012). Furthermore, most speciation models have yet to confront the real-world problems of a distribution of allelic effect sizes for each complex trait (Kopp & Matuszewski 2014, Matuszewski et al. 2015, Rockman 2012), each with its own distinct spatiotemporal origins (e.g., Marques et al. 2019, Richards & Martin 2017). This is compounded by a complex genetic basis and fitness epistasis among multiple, interacting reproductive isolating barriers. It not yet clear in any empirical system how to make predictions from existing speciation models when the diversity of mechanisms, effect sizes, and evolutionary origins of ecological and mating loci within a single speciation event often exceeds the diversity of mechanisms explored separately in all models to date.

4.2. Speciation Mechanisms and Their Implications for Rapid Radiation

Various types of traits and genetic architectures are known to promote speciation (Coyne & Orr 2004, Gavrilets 2004, Kirkpatrick & Barton 2006, Kopp et al. 2018, Servedio et al. 2011, Yeaman & Whitlock 2011). For example, assortative mating cues or preferences also experiencing divergent ecological selection are known as magic traits and promote speciation (Gavrilets 2004, Kopp et al. 2018, Servedio et al. 2011). Despite their name, magic traits are common and include many different classes of traits, including sensory drive, communication signals affected by the environment, and condition-dependent traits affected by local adaptation (Servedio et al. 2011). Assortative mating mechanisms may involve either a preference for some cue (independent preference/trait loci) or phenotype matching [e.g., imprinting (Kopp et al. 2018, Verzijden et al. 2005, Yeh et al. 2018)], which promotes speciation (Felsenstein 1981). Similarly, the evolution of strong assortative mating by ecotype with low costs to choosiness is needed for speciation with gene flow (Doebeli et al. 2005), although many taxa may pay minimal costs for choosiness (Martin 2010, Puebla et al. 2012).

A second broad class of speciation-promoting mechanisms occurs at the level of genetic architecture, including physical linkages between mating loci and ecological loci, between different types of ecological loci involved in adaptation to the same niche (Yeaman & Whitlock 2011), or between ecological loci and intrinsic reproductive incompatibilities (Seehausen 2013). Inversions can capture physically linked adaptive alleles and suppress recombination (Fuller et al. 2017, Kirkpatrick & Barton 2006). Physical linkage of ecological or mating loci to DMIs may also promote speciation by effectively reducing the breakdown of beneficial haplotypes due to recombination between divergent species' backgrounds after secondary contact (e.g., Wright et al. 2013), or ecological divergence may directly result in DMIs through hybrid gene misregulation (Mack & Nachman 2017, McGirr & Martin 2019).

Although all these mechanisms are widely appreciated for their role in speciation, if and how they promote more than a single speciation event during rapid radiation is often unclear. In many cases, traits and architectures promoting speciation are discussed as if they are in limited supply and may thus be depleted after one speciation event. For example, magic traits may become species recognition cues distinguishing sister species, or genetic architectures, such as inversions containing coadapted loci, may become fixed between diverging populations. Even when multiple such

MODELS AND MECHANISMS OF SPECIATION IMPLY DECELERATING TRAITS

Summary of Pattern

- Rapid radiations result from periodic bursts of diversification on three major diversification axes and lead to a diversity of outcomes within radiation space, including classic, sexual, nonadaptive, habitat-driven, and ecological novelty radiations (**Figure 1**).
- The early burst pattern was once considered the hallmark of adaptive radiation but now shows limited empirical support across clades relative to other evolutionary models.

Summary of Model and Mechanism Predictions

- Frequency-dependent speciation models based on a single continuous resource axis predict decelerating speciation rates and increasingly subdivided niche widths (**Figure 2**).
- If speciation-promoting traits and genetic architectures are in limited supply, they may be used up after each speciation event, resulting in decelerating speciation rates.

traits are segregating within a population, those with the largest effect sizes for adapting to a new fitness peak are most likely to be used first, resulting in a decelerating rate of adaptation, a general prediction of Orr's extension of Fisher's geometric model (Orr 2005) for any adaptive walk. This behavior is often observed when populations adapt to similar environments using the same large-effect standing genetic variation [e.g., armor loss in sticklebacks (Brown et al. 2015, Colosimo et al. 2005)]. Thus, many speciation-promoting mechanisms would appear to imply a decelerating rate of speciation, not a rapid burst pattern (see the sidebar titled Models and Mechanisms of Speciation Imply Decelerating Traits).

5. SOLUTIONS TO THE PARADOX OF RAPID RADIATION

Explanations for rapid radiation must explain not only the speciation process itself but also how this process is able to briefly sustain itself at rates far exceeding typical background levels of population divergence. In this section, we discuss general mechanisms in order of strongest to weakest evidence. None of these mechanisms are mutually exclusive and exclude many additional system-specific mechanisms, such as repeated genomic conflict (Fishman et al. 2013, Lande et al. 2001), species pumps driven by cycles of geographic connectivity and fragmentation (Papadopoulou & Knowles 2015), and transposable element mobilization (Zeh et al. 2009).

5.1. The Transporter Process: The Ancient Origins of Adaptive Alleles

One emerging pattern is that the adaptive alleles and genetic architectures differentiating each species within a rapid radiation are older than the radiation itself. These ancient polymorphisms may be maintained by balancing selection in divergent environments as the speciation process repeatedly unfolds (reviewed in Guerrero & Hahn 2017, Marques et al. 2019). Here, we extend this mechanism to an entire radiation, rather than to a single speciation event, by invoking multiple axes of ecological divergence and multiple balancing polymorphisms.

The role of ancient balancing polymorphism is rapidly gaining empirical support in genomic studies of single speciation events. For example, most stickleback colonized glacial lakes formed 10–20 kya using an ancient adaptive allele for armor loss dated to 2 Mya and maintained as standing variation in marine populations, as initially reported in Colosimo et al. (2005), and later termed the transporter process (Schluter & Conte 2009). This pattern is now reported for most adaptive



alleles underlying adaptation to glacial lakes (Nelson & Cresko 2018). The large-effect causative regulatory SNP (single nucleotide polymorphism) underlying armor loss is also tightly physically linked to alleles involved in immune system function, suggesting that this haplotype may consist of multiple beneficial mutations for adaptation to glacial lakes (Brown et al. 2015). Importantly, this physical linkage is highly unlikely to have occurred within the past 10–20 kya during the most recent colonization of glacial lakes, instead it likely reflects longer timescales for selection on chromosomal structural rearrangements containing physical linkages of adaptive loci. In taxa with labile structural evolution (e.g., fish, mammals), simulations indicate that chromosomal rearrangements are likely to produce physically linked clusters of coadapted alleles (Yeaman 2013). Alternatively, inversions may be segregating within ancient populations, and adaptive alleles may be more likely to fix within them later, as recently found in the *Drosophila persimilis* and *D. pseudoobscura* species pair (Fuller et al. 2017).

More broadly, there are numerous other examples of introgression or sorting of ancient adaptive alleles during adaptive radiation, such as *Heliconius* butterflies (Heliconius Genome Consortium 2012), *Rbagoletis* flies (Feder et al. 2003), Caribbean pupfishes (Richards & Martin 2017), Cameroon crater lake cichlids (Richards et al. 2018), and tomatoes (Pease et al. 2016). Even within hominins, ancient alleles for pigmentation and adaptation to high altitude persisted within different species and later arrived in our own species via introgression (Crawford et al. 2017, Huerta-Sánchez et al. 2014, Racimo et al. 2015). Interest is also growing in the hybrid swarm hypothesis as a trigger of rapid radiation (Martin 2016a, Meier et al. 2017, Poelstra et al. 2018, Richards et al. 2018; reviewed in Marques et al. 2019, Seehausen 2004). However, hybridization is so pervasive during the speciation process that it is difficult to argue it might play some special role in the process of rapid radiation (reviewed in Richards et al. 2019).

This view of speciation as the recent sorting of ancient ancestral adaptive alleles can be extended to help explain the paradox of rapid radiation. This requires the periodic colonization of more complex environments supporting a diversity of niches, rather than two-niche environments such as glacial lakes (from a stickleback's perspective). For example, rare isolated environments in which rapid radiations can occur may have formed repeatedly over time, followed by radiation collapse and resorption of adaptive alleles back into a larger continental-scale population as environments change (also see the species pump hypothesis, Papadopoulou & Knowles 2015). This repeating process would create the opportunity for selection on physical linkage among adaptive alleles, not just along a single speciation axis but for each species within the radiation, which could maintain these adaptive alleles in linkage disequilibrium even as environments change (**Figure 3a**). Thus, rapid radiations may proceed more rapidly after repeated cycles of origination and extinction through hybrid collapse as their underlying beneficial haplotypes experience selection to resist the decay of linkage disequilibrium due to gene flow. Theory predicts that these haplotypes should show increased fitness effect sizes over time by gaining many small-effect mutations (Yeaman 2013, Yeaman & Whitlock 2011). Over time, new beneficial haplotypes may originate within this metapopulation, potentially contributing to more rapid species diversification in the next cycle.

Future work should evaluate the prevalence of structural rearrangements, such as inversions, and estimate the age of these events and the adaptive alleles within relative to the age of the radiation (e.g., as recently done for a single species pair, Fuller et al. 2017). Absolute divergence time estimates are highly dependent on unknown and highly variable spontaneous mutation rates across taxa at the recent timescales of rapid radiation (Ho et al. 2011, Lynch 2010, Martin & Höhna 2017, Martin et al. 2017b); however, relative time estimates are feasible, particularly when adaptive alleles are often orders of magnitude older than the species in which they occur (Colosimo et al. 2005, Nelson & Cresko 2018).

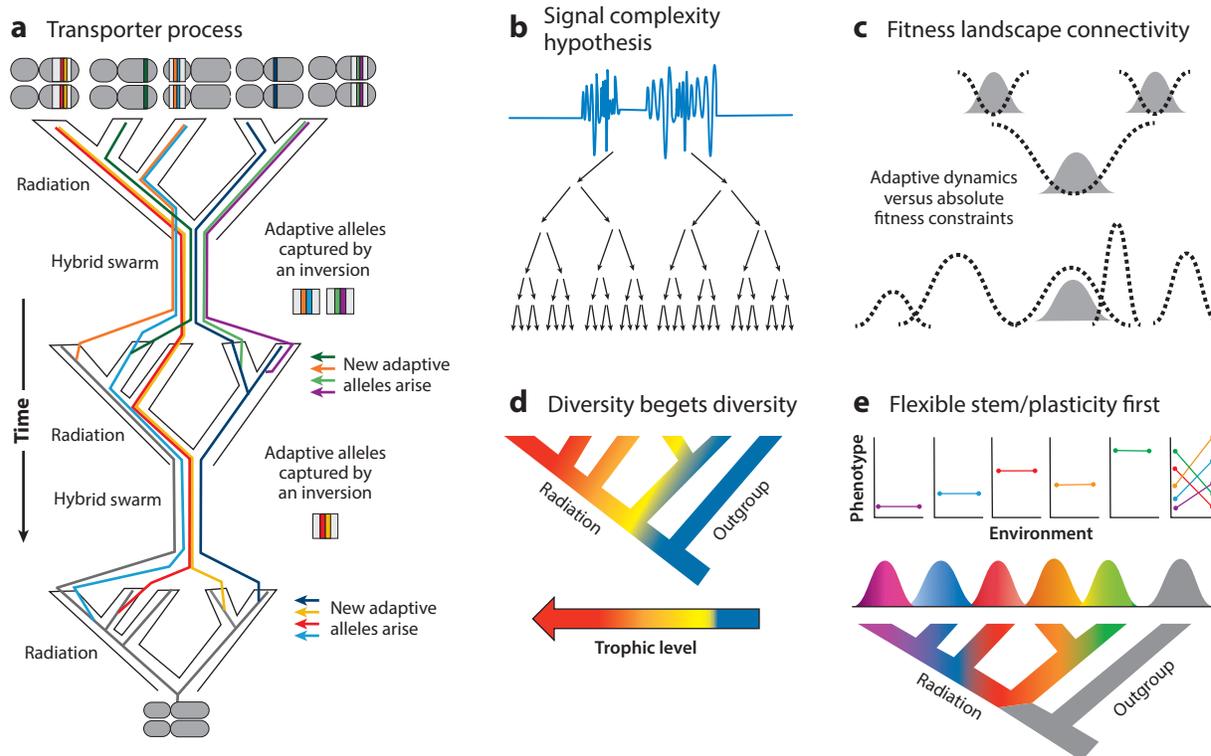


Figure 3

Five mechanistic hypotheses to explain how speciation may sustain itself through a rapid burst. (a) The transporter hypothesis: Ancient adaptive alleles are repeatedly recycled through periods of diversification then species collapse and gain physical linkages over time, resulting in faster sorting of coadapted complexes of alleles following periods of hybrid swarm. (b) Signal complexity hypothesis: Sexual signals that promote speciation, such as magic traits, can be nearly infinitely subdivided due to the receiver's extensive and multidimensional perceptual abilities for some signaling modalities, such as sound and olfaction. (c) Fitness landscape connectivity hypothesis: A group of highly connected fitness optima that are stable due to absolute fitness or performance constraints is more likely to promote rapid radiation than competitive speciation resulting from negative frequency-dependent disruptive selection (adaptive dynamics). (d) Diversity begets diversity hypothesis: Adaptation to higher trophic levels and new trophic interactions during radiation can lead to additional opportunities for speciation. (e) Flexible stem/plasticity first hypothesis: Rapid radiations result from the sorting, loss, and refinement of ancestral phenotypic plasticity (i.e., diverse reaction norms shown in phenotype by environment plots) through the process of genetic assimilation.

5.2. The Signal Complexity Hypothesis

An open question arising from the literature on sexual traits promoting speciation is whether rapid radiations eventually run out of speciation-promoting mating cues (Table 1). One potential solution is the nearly infinite complexity of signaling space within some signaling modalities (Figure 3b). For example, despite our weak sense of smell, humans can discriminate among 1 trillion different olfactory signals (Bushdid et al. 2016). This is due to hundreds of different olfactory receptors that outperform our other senses in differentiating among signals (Bushdid et al. 2016). Similarly, complex courtship calls in most organisms can diverge in nearly infinite variations of pitch and rhythm.

As opposed to ecological niche space, which cannot be infinitely subdivided because it must sustain a viable population size, signaling space is only constrained by the perceptual abilities

of the receiver (Hebets & Papaj 2004). For example, after a clade of mormyrid electric fishes gained an increased ability to distinguish electrical signals used for communication, navigation, and sexual selection (i.e., a magic trait), this clade rapidly diversified into a sympatric radiation of ecologically similar species with diverse species-specific electric signals (Arnegard et al. 2010, Carlson et al. 2011). In contrast, female zebra finches perceive the continuous beak color of male finches as only two distinct color categories (Caves et al. 2018). Similarly, mechanical mechanisms of premating isolation and species recognition may provide a clear example of limited shape diversity for premating mechanical isolation [the observed diversity may be due to sexual selection (Eberhard et al. 1998)], which may constrain the diversity of some species assemblages, such as damselflies (McPeck et al. 2009). Finally, *Corydoras* catfishes are one of the most species-rich radiations (Rabosky et al. 2013), despite minimal diversity in patterning, morphology, ecology, and color, but these species also use olfactory and auditory signals (Alexandrou et al. 2011).

Complex signaling is not sufficient for rapid radiation to occur: For example, populations must also maintain polymorphic mating signals despite the tendency of Fisherian runaway selection to drive one signal to fixation (Norvaišas & Kisdi 2012) followed by strong stabilizing selection on the dominant signal [e.g., on moth pheromones (Groot et al. 2006)]. However, consideration of the nearly infinite diversity of some sexual signaling modalities and of their fine-scale perception indicates that many speciation-promoting sexual signals will not be used up during a rapid burst of radiation. For example, if any magic traits exhibit such diversity, sexual radiations may be able to proceed rapidly—particularly if mechanisms such as reproductive character displacement can rapidly drive the evolution of reproductive isolation among different ecotypes in sympatry (e.g., Arnegard et al. 2010, Groot et al. 2006, Martin & Genner 2009b). Future work identifying the sensory modalities used for sexual selection and mate discrimination in rapid radiations is needed to test if the availability of signaling bandwidth constrains diversification. Most likely it does not, given the complex multivariate signaling systems of most taxa. However, in the rare taxa reliant on a single sensory modality for species recognition (e.g., electric fishes), increased signaling bandwidth may directly correspond to rapid radiation (Arnegard et al. 2010, Carlson et al. 2011).

5.3. The Connectivity of Fitness Landscapes

The connectivity and shape of fitness landscapes are key to understanding how populations can rapidly navigate multiple fitness peaks during a rapid burst of radiation, yet we currently have almost no understanding of the connectivity and dynamism or stability of complex empirical fitness landscapes because most empirical work on phenotypes and genotypes has focused on quadratic fitness curves within a single population (Svensson & Calsbeek 2012). The broader topography of the adaptive landscape can solve the niche subdivision problem, depending on whether different adaptive zones (i.e., clusters of related niches) are connected by stable fitness ridges or by frequency-dependent adaptive dynamics as often assumed in speciation models.

The fitness landscape is fundamentally a property of the organism interacting with the environment and the relative abundance of competitors (Simpson 1944, Svensson & Calsbeek 2012). It is unknown what forces shape the broader structure of fitness landscapes or if a stable relationship among multiple fitness optima even exists. Numerous studies document negative frequency-dependent disruptive selection due to intraspecific competition within a population (Bolnick & Lau 2008, Bolnick & Stutz 2017, Hendry & Kinnison 1999, Pfennig & Pfennig 2012, Schluter 2000). However, it remains an open question how competition among phenotypes scales with phenotypic distance on fitness landscapes, particularly between distinct ecological niches. Some studies find no evidence for negative frequency-dependent competition in experiments spanning hybrid phenotypes and multiple species (Keagy et al. 2016, Martin 2016b). Instead, performance

of an individual phenotype appears to matter far more than competitor frequency at these broader phenotypic scales (Higham et al. 2016, Holzman et al. 2012, Stayton 2019). Similarly, stable fitness peaks may also arise from heterogeneous resource distributions within an environment, most notably the complex adaptive landscape inferred from the abundance of seed sizes for Galápagos finches (Schluter & Grant 1984a) or the diversity of cone types used by crossbills (Benkman 2003).

In conclusion, the stability of multiple fitness peaks on the adaptive landscape could promote a rapid burst of radiation if a population were able to colonize a cluster of stable fitness optima reflecting performance or resource constraints instead of the weakened disruptive selection after every speciation event predicted by negative frequency-dependent disruptive selection (**Figures 2 and 3c**). Thus, rapid radiations may be better understood by modeling their performance dynamics and allowing the possibility of empty niches rather than by focusing on intraspecific competition, which may only operate over small phenotypic and ecological scales.

5.4. Does Diversity Beget Diversity?

Additional niche space may be created with the evolution of each new species through new biotic interactions potentially creating an expanding source of divergent ecological selection and rapid radiation [Stroud & Losos 2016; described as upward adaptive radiation in a recent review by Brodersen et al. (2018)]. This can be visualized as the evolution of the fitness landscape itself as populations colonize new peaks (Erwin 2017), providing a continuous source of new and potentially stable fitness peaks to fuel rapid radiation (**Figure 3d**). An excellent example comes from parasitoid wasps that coevolved with the rapid radiation of their prey, *Rhagoletis* flies, which specialized on at least five different host fruits, some recently introduced to the New World (Forbes et al. 2009). For every new plant specialist herbivore, a new parasitoid specialist may also evolve in a coevolutionary radiation, suggesting that diversity in many rapid radiations may have cascading trophic effects on their predators, prey, or parasites.

New trophic levels may also evolve within a radiation. There are many examples of this in most rapid radiations, including scale-eating, carnivory within plants, and even parasitism within Lake Baikal amphipods (Givnish et al. 1997, Koblmüller et al. 2007, Macdonald et al. 2005, Martin & Wainwright 2011, St. John et al. 2019). The most spectacular examples are the diverse assemblage of 15 predatory cyprinids within the Lake Tana radiation (Sibbing & Nagelkerke 2000) and the diverse range of specialist predators within East African cichlid radiations, including not only typical ram-feeding and ambush piscivores but also a death feigner (*Nimbochromis livingstonii*), a parasite cleaner (*Pseudotropheus crabro*), a diversity of scale-eaters, and three sympatric paedophage species purportedly specialized for different attack angles on mouthbrooding females (Fryer & Iles 1972, McKaye & Marsh 1983). Nonetheless, the proportion of species and niche diversity within nearly all rapid radiations (except Lake Tana cyprinids) due to colonization of higher trophic levels remains in the minority. This makes sense given energetic constraints on higher trophic levels and is consistent with the current view that the majority of species within a radiation evolve due to competitive selective pressures, rather than transitions to higher trophic levels for predation or parasitism (Pfennig & Pfennig 2012, Schluter 2000).

The evolution of one species during rapid radiation may also promote the evolution of another at the genetic level through shared adaptive changes. For example, seemingly divergent specialist trophic niches for scale-eating and molluscivory in pupfishes are still connected through shared metabolic adaptations to a higher trophic level and exhibit substantial parallel gene expression (McGirr & Martin 2018). Thus, the evolution of one specialist species may increase adaptive allele frequencies within a population, promoting the evolution of another ecotype if it also benefits from some of these same alleles. Similarly, an outstanding example of connectivity within genotype



space comes from Lenski's long-term evolution experiment in which neutral or nearly neutral potentiating mutations enabled one *Escherichia coli* strain to colonize a new adaptive peak for citrate metabolism, resulting in the coexistence of multiple strains in this simple environment (Blount et al. 2012). In conclusion, more connectivity within complex fitness landscapes—either at the level of the ecological niche or through shared adaptive or potentiating neutral mutations—may promote rapid radiation.

5.5. Flexible Stem: Plasticity-First Evolution

Adaptive phenotypic plasticity in an ancestral population could precede adaptation to a new environment through the process of genetic assimilation (Levis & Pfennig 2016, Pfennig et al. 2010). This is the flexible stem hypothesis: A phenotypically plastic ancestral population can rapidly adapt to a new environment and diverge into multiple ecomorphs, potentially followed by selection against plasticity in each of these specialists (Figure 3e). This mechanism could rapidly generate new niche diversity in a rapid burst of radiation; however, nearly all existing examples of flexible stem occur between only two sister species (i.e., a single phenotypic axis), such as omnivore/carnivore spadefoot tadpoles (Levis & Pfennig 2016), pelvic fin loss in desert pupfishes (Martin et al. 2016), or benthic/limnetic stickleback (Wund et al. 2008). One outstanding exception are microcommunities of *Pristionchus* nematodes found within tropical figs (Susoy et al. 2016). Genetic switches identified for polyphenisms within this group result in predator-prey communities of up to five discrete adult trophic morphs coexisting within a single fruit (Bento et al. 2010, Susoy et al. 2016). Another example is the reuse of an allele for oral jaw plasticity in radiations of Lake Malawi rock-dwelling cichlids (Parsons et al. 2016). Some classic adaptive radiations do exhibit some degree of plasticity (Losos et al. 2000), but this is rarely measured in multiple outgroups to obtain estimates of ancestral plasticity (Levis et al. 2018). Nonetheless, the role of phenotypic plasticity and genetic accommodation in rapid radiation rarely appears dominant over genetic adaptation (Wray et al. 2014). Future studies should focus on phylogenetic inference of ancestral phenotypic plasticity from measurements of reaction norms in a sufficient number of closely related outgroups (or resurrection studies of the ancestral population), rather than species within the radiation, in which reduced plasticity is consistent with theory (Lande 2009, Levis & Pfennig 2016) (see the sidebar titled Predictions Arising from the Paradox of Rapid Radiation).

PREDICTIONS ARISING FROM THE PARADOX OF RAPID RADIATION

1. Rapid radiations result from the repeated sorting and refinement of ancient adaptive haplotypes contributing to reproductive isolation among multiple species.
2. Sexual radiations diversify on complex signaling axes or following the evolution of new signaling modalities or signal perception abilities.
3. Stable fitness optima corresponding to performance tradeoffs, biophysical constraints, or resource abundances enable rapid radiation as opposed to frequency-dependent dynamics in which the strength of disruptive selection weakens after each speciation event.
4. Rapid radiations result from new food webs and trophic interactions among new species or increased frequencies of shared adaptive alleles.
5. Rapid radiations result from genetic accommodation of adaptive plasticity in the ancestral population.

6. CONCLUSIONS

Here we hope to call attention to the neglected scale of mesoevolution connecting microevolutionary divergence between populations (speciation) with global macroevolutionary patterns along the three major radiation axes of species richness, phenotypic disparity, and ecological diversity (**Figure 1**; **Table 1**). The paradox is that speciation models based on negative frequency-dependent disruptive selection and speciation-promoting mechanisms such as magic traits predict decelerating speciation rates and do not explain how the speciation process sustains itself through a rapid burst of diversification (**Figure 2**; see the sidebar titled Models and Mechanisms of Speciation Imply Decelerating Traits). These models should be extended to include complex fitness landscapes influenced by performance constraints or by expanded access to new resources that may promote accelerating speciation rates, rather than only intraspecific competitive dynamics (**Figure 3**). Verbal models of the transporter process should consider how genetic architectures promoting a rapid burst of repeated speciation can build up over time as balanced polymorphisms in ancestral populations or ancestral plasticity. We should also explain how speciation-promoting mechanisms, such as magic traits, are not exhausted. One solution is that some signaling modalities can be almost infinitely subdivided given the fine-scale sensory discrimination of receivers. This hypothesis shifts discussion of these traits from being in short supply to being an intrinsic feature of many global clades of organisms and shifts the focus to ecological limits on diversification. Alternatively, the sexual traits, adaptive alleles, and genetic architectures promoting speciation may be repeatedly reused during rapid radiation, even within different species adapting to divergent ecological niches.

Challenges remain for theorists to construct predictive models that can incorporate the complexity of the radiation process in any given system, including a distribution of effect sizes for a diverse set of polygenic traits contributing to reproductive isolation, diverse assortative mating mechanisms, complex fitness landscapes, and long-term structural evolution of the genome. In turn, many of the parameters most relevant to rapid radiation are still unknown in most case studies, including the ubiquity of phenotype matching (Kopp et al. 2018), the proximity of neighboring fitness peaks in phenotype and genotype space (Blount et al. 2012, Erwin 2017, Martin & Wainwright 2013b), and the frequency and timescale of physical linkages among adaptive alleles and DMIs (Fuller et al. 2017, Wright et al. 2013). Only with these models and data in hand will we be able to predict the full spectrum of the process of adaptive radiation.

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