Ecological Opportunity and Adaptive Radiation

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Abstract

The process of adaptive radiation—the proliferation of species from a single ancestor and diversification into many ecologically different forms—has been of great interest to evolutionary biologists since Darwin. Since the middle of the last century, ecological opportunity has been invoked as a potential key to understanding when and how adaptive radiation occurs. Interest in the topic of ecological opportunity has accelerated as research on adaptive radiation has experienced a resurgence, fueled in part by advances in phylogenetic approaches to studying evolutionary diversification. Nonetheless, what the term actually means, much less how it mechanistically leads to adaptive diversification, is currently debated; whether the term has any predictive value or is a heuristic useful only for post hoc explanation also remains unclear. Recent recognition that evolutionary change can occur rapidly and on a timescale commensurate with ecological processes suggests that it is time to synthesize ecological and evolutionary approaches to the study of community assembly and evolutionary diversification.

1. INTRODUCTION

Ecological opportunity, "loosely defined as a wealth of evolutionarily accessible resources little used by competing taxa" (Schluter 2000, p. 69), has long been thought to be an important—perhaps necessary—prerequisite for adaptive radiation. This view can be traced back to Darwin and was canonized by Simpson (1953); more recently, Schluter (2000) highlighted it as the centerpiece of understanding when and how adaptive radiation occurs. Certainly, the importance of ecological opportunity—as recognized by the absence of ecologically similar species—seems indisputable given the widespread occurrence of adaptive radiations after mass extinction events and on islands, lakes, and mountaintops.

But what actually is ecological opportunity? How is it identified and quantified? How mechanistically does it lead to evolutionary radiation, and why in some cases and not others? And, in cases where radiation has not occurred, can one assess whether the cause was lack of opportunity or some other explanation?

Ecological opportunity: the availability of ecologically accessible resources that may be evolutionarily exploited

Adaptive radiation: evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms (Futuyma 1998)

Diversification: the evolution of phenotypically and reproductively distinct species in a clade

Key innovation: the evolution of a trait that allows a species to interact with the environment in a novel way

1.1. A Historical Perspective: From Conception to Modern Utilization

The notion of ecological opportunity as a prerequisite for adaptive radiation stems from the pioneering work of George G. Simpson (1953), in which he defined ecological opportunity as an environment experienced by an ancestral species that was previously "occupied by organisms for some reason competitively inferior to the entering group or must be empty" (p. 207). Other prominent evolutionary biologists of the time—notably David Lack (1947)—held similar views; namely they supported the idea that a release from the biotic constraints of competing taxa in depauperate environments allows for the proliferation of species, increased ecological specialization, and associated phenotypic diversification.

Simpson (1953) suggested that ecological opportunity could become available in a number of ways. The geographic colonization of isolated areas lacking competitors has provided ample examples of the production of adaptive radiations. Indeed, many classic examples of adaptive radiation, spurred by the ecological opportunity of colonization, are from islands (see Section 2). The absence of mainland species on islands provides opportunities for increased ecological specialization into niches not filled by competing taxa. A similar adaptive landscape may be encountered in a post–mass extinction environment, where ecologically similar competitors may again be absent. Conversely, the appearance of new resources rather than the absence of other species may be the source of opportunity. Finally, Simpson (1953) attached great importance to the evolution of unique phenotypes that allowed a species to interact with the environment in a novel way (i.e., key innovations; Miller 1949, Liem 1973). Simpson suggested that such traits have the potential to allow a species to diversify into a variety of niches not previously accessible and not occupied by competitor species.

Interest in the role of ecological opportunity in adaptive radiation has erupted in the last two decades (**Figure 1**). The term ecological opportunity, which in an evolutionary sense refers to the availability of ecologically accessible resources that may be evolutionarily exploited, was rarely used in the literature prior to 1995, but since then its use has increased almost exponentially. Certainly, a major cause of this increasing interest in ecological opportunity was Schluter's book (Schluter 2000), which emphasized the importance of ecological radiation as a major contributor to evolutionary diversification. Of particular importance to the study of both adaptive radiation and ecological opportunity has been the explosion of molecular phylogenetic studies, a trend that began shortly before Schluter's book was published (e.g., Givnish & Sytsma 1997). The proliferation of densely sampled, time-calibrated phylogenies of many groups has not only set the stage for modern

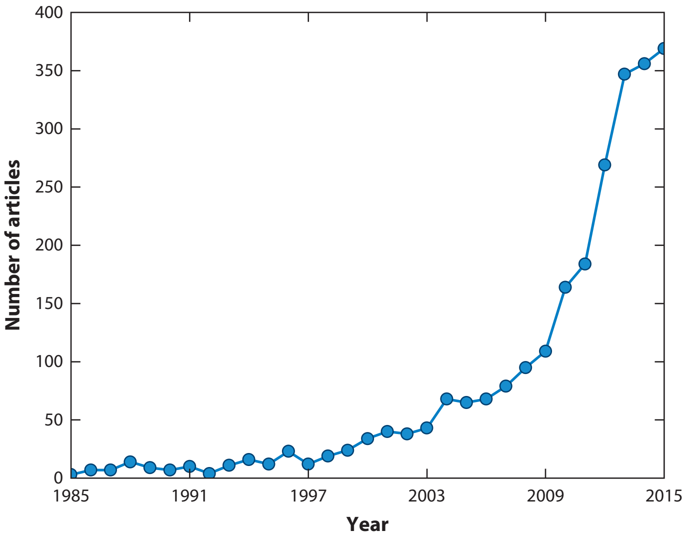


Figure 1

Trends in research on ecological opportunity as reflected in the number of articles published annually. The literature search was conducted using the Google Scholar database on January 20, 2016. To find articles that include "ecological opportunity," the following specifications were used: Find articles with the exact phrases "ecological opportunity" and "adaptive radiation" and with at least one of the words "ecology" or "evolution." Searches were run individually for every year 1950–2015; owing to a lack of studies before 1985, data from only 1985–2015 are shown.

investigation into the causes of evolutionary diversification but has also revealed macroevolutionary patterns consistent with a determinative role for ecological opportunity (discussed in Section 2).

2. WHAT IS THE EVIDENCE THAT ECOLOGICAL OPPORTUNITY PROMOTES ADAPTIVE RADIATION?

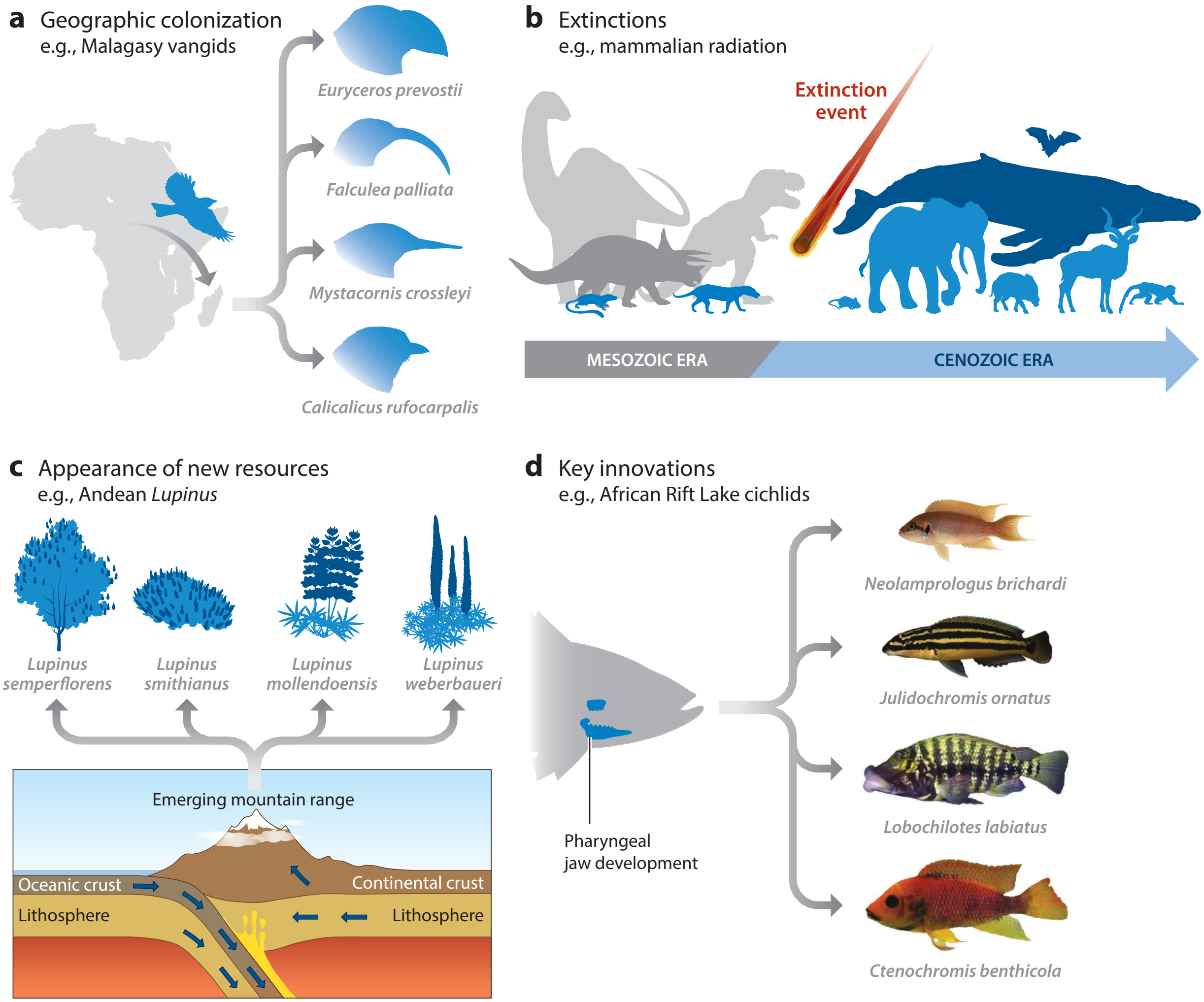
Simpson (1953) suggested that for an adaptive radiation to occur, an ancestral species must have geographical, ecological, and evolutionary access to ecological opportunity. By geographical access, he meant simply that a species must find itself in a location where ecological opportunity occurs. Ecological access requires the availability of resources not usurped by competitively superior species, and evolutionary access means that a species has the ability to utilize the resources. In Simpson's view, adaptive radiation results when the ancestral species already has access along two of these axes and then an event occurs that provides access to the third. For example, adaptive radiation might ensue when a species colonizes an area in which resources are available and it has the evolutionary capability of diversifying to take advantage of them. Alternatively, it may also result when the species is already present in an area but an extinction event removes an ecologically dominant incumbent (see **Figure 2**).

2.1. Geographic Colonization

The fact that many textbook examples of adaptive radiation occur on islands is testament to the importance of geographical access as a precursor to adaptive radiation. The remote Hawaiian archipelago has been particularly fruitful, generating exceptional radiations of birds (Lovette et al. 2002), plants (Givnish et al. 2009), insects (Roderick & Gillespie 1998), and arachnids

(Gillespie 2004, 2015). In landlocked lakes, the aquatic equivalent of islands, the same patterns can be observed: the African Rift Lakes have produced multiple spectacular radiations of cichlid fishes (Sturmbauer et al. 2011, Brawand et al. 2014, Seehausen 2014), and on the Indonesian island of Sulawesi, an adaptive radiation of silversides in Lake Matano has produced exceptional morphological diversity (Pfaender et al. 2010, 2016). One trait that both emergent islands and newly formed lakes have in common is the absence of competitors, such as those that may be present in areas from which an ancestral species has arrived (Carlquist 1974, Givnish 1997a, Leigh et al. 2007). A release from competitors provides the opportunity for radiating species to utilize ecological niches from which they were previously blocked. Similarly, a release from predators may also allow the use of habitats or resources previously inaccessible, thus spurring adaptive diversification (Schluter 1988, Benkman 1991, Heinen et al. 2013, Runemark et al. 2014). As a result of the release from the biotic pressures experienced on the mainland, island radiations often have much higher ecological and phenotypic disparity than their mainland sister clades (Schluter 2000, Lovette et al. 2002). Some have argued that adaptive radiation may primarily be an island phenomenon (Webb et al. 2002); however many extensive evolutionary radiations have also

Disparity: the difference among taxa of a phenotypic trait or traits



occurred in mainland situations when ecological circumstances have permitted (Mouton & Van Wyk 1997, Tanentzap et al. 2015).

2.2. Extinctions and the Appearance of New Resources

In some cases, ancestral species encounter ecological opportunity within the ancestral range. Two ways in which this may occur are in the aftermath of an extinction event and following the appearance of new habitats or resources.

The presence of an incumbent clade usually prevents another clade from diversifying (Rosenzweig & McCord 1991), just as an incumbent species often prevents colonization of an ecologically similar species (the priority effect) (MacArthur 1972, Chase 2007). The evolutionary inhibition of incumbents has been demonstrated in laboratory microbial experiments in which the extent of adaptive radiation was significantly constrained when ecologically similar species were present (Brockhurst et al. 2007).

Given the inhibitory role of incumbents, it is not surprising that the elimination of competing taxa presents an ecological opportunity for those lineages able to survive an extinction event (Erwin 2007, 2015; Chen & Benton 2012). The paleontological record abounds with examples of surviving taxa rapidly radiating after extinction events, sometimes to the extent that the ensuing morphological disparity matches, or even exceeds, that observed in their extinct predecessors (Hull 2015). Surviving lineages of a clade may diversify only into niches that were previously occupied by members of that clade prior to the extinction event (Foote 1996, Ciampaglio 2002), such as in the rapid recovery of ammonoid diversity following the Permian–Triassic mass extinction (McGowan 2004); more commonly, however, lineages may radiate into niches previously filled by competitors that succumbed to extinction (Foote 1999, Friedman 2010).

Mass extinction events, which remove entire or large proportions of taxonomic groups, provide ample evidence for the ecological opportunity hypothesis. For example, the Cretaceous–Paleogene mass extinction of the nonavian dinosaurs and other archosaurs resulted in an explosive radiation

Figure 2

(*a*) The colonization of an isolated area (e.g., an island or lake) can provide a release from competition and predation pressures, allowing a clade to diversify into a variety of ecological niches from which they were previously blocked. For example, the colonization of Madagascar resulted in a spectacular adaptive radiation of vangid birds (Yamagishi et al. 2001, Jønsson et al. 2012). Additional examples include Galápagos finches (Grant & Grant 2008), Hawaiian lobeliads (Givnish et al. 2009), African Rift Lake cichlids (Seehausen 2006), Hawaiian spiders (Gillespie 2004, 2015), Sulawesi silversides (Pfaender et al. 2010), and Caribbean *Anolis* lizards (Losos 2009). (*b*) Lineages able to survive extinction events may be presented with access to ecological space previously occupied by members of their own clade or by other competitors. For example, following the Cretaceous–Paleogene mass extinction of the nonavian dinosaurs and other archosaurs, ancestral birds and placental mammals gained access to previously unavailable ecological space and rapidly radiated (Hull 2015); mammals did exist, and some groups originated, prior to the extinction event, but this is simplified for heuristic purposes. An additional example is the Permian–Triassic radiation of ammonoids (McGowan 2004). (*c*) The appearance of new resources may provide ecological opportunities for species that can utilize them. For example, the emergence of the Andean mountains in the tropics provided new cool, high-elevation habitats that spurred adaptive radiations when colonized by ancestral *Espeletia* and *Lupinus* species (Monasterio & Sarmiento 1991, Hughes & Eastwood 2006). Additional examples include flowering plants and phytophagous insects (Labandeira & Sepkoski 1993, Bronstein et al. 2006) and the appearance of grasses and grazing horses (MacFadden 2005). (*d*) The evolution of a feature that allows a lineage to interact with the environment in a novel way may provide the ability to utilize formerly unavailable resources. The evolution of the pharyngeal jaw, for example, allowed African Rift Lake cichlids to diversify into a wide range of trophic specialists (Liem 1973, Mabuchi et al. 2007), although this has recently been debated (Seehausen 2006). Additional examples include the evolution of flight in bats and birds (Cracraft 1990, Sears et al. 2006, Simmons et al. 2008), phytophagy in insects (Farrell 1998), nectar spurs in *Aquilegia* columbines (Hodges & Arnold 1995, Ree 2005), and toepads in lizards (Williams & Peterson 1982). It should be noted that in all panels (*a*–*d*) the structures of all radiating groups are not meant to accurately reflect true phylogenetic relationships.

of birds and placental mammals (Smith et al. 2010, Erwin 2015; see Hull 2015 for a comprehensive review), which took advantage of the release from competitive and predatory pressures.

Access to new ecological opportunity can also occur in situ if new resources appear within an area. The evolution of flowering plants, for example, may have spurred the diversification of phytophagus insects (Labandeira & Sepkoski 1993, Bronstein et al. 2006; however, see McKenna et al. 2009). Similarly, soon after the Miocene appearance of grasslands in North America, horses (family Equidae) radiated rapidly, diversifying in body size, limb morphology, and dentition suitable for grazing on abrasive vegetation (MacFadden 2005). Alternatively, the appearance of novel environmental conditions, such as the emergence of new mountain ranges, can be the catalyst for ecological opportunity. For example, during the uplift of the Andean mountains, high-elevation páramo habitats formed as a type of above-treeline alpine tundra (Madriñán et al. 2013). Elevational tracking of this novel habitat zone by ancestral *Espeletia* and *Lupinus* plant species spurred their diverse radiations (Monasterio & Sarmiento 1991, Rauscher 2002, Hughes & Eastwood 2006, Hughes & Atchinson 2015).

2.3. Key Innovations

In addition to geographical and ecological access, for a clade to radiate, it must have the evolutionary capability to diversify to take advantage of the available resources. Discussion of this topic has focused on the evolution of so-called key innovations—features that allow a lineage to interact with the environment in a novel way and thus may provide the ability, hitherto unavailable, to utilize available resources (Hunter 1998, Galis 2001, Rabosky 2014). For example, the evolution of flight in birds, bats, and pterosaurs presumably provided access to aerial prey resources, leading to subsequent diversification and specialization to different aspects of the aerial realm (Wellborn & Langerhans 2015). In other cases, the key innovation can provide access by minimizing the restricting effect of predators. For example, the evolution of brightly colored phenotypes to advertise toxicity in tropical dendrobatid poison frogs decreased the need for predator-induced hiding behavior and therefore allowed species to utilize habitats and resources that were previously inaccessible (Santos et al. 2003, Summers 2003, Arbuckle & Speed 2015).

Many possible examples of a key innovation leading to adaptive radiation have been suggested, but making a compelling case for a cause-and-effect relationship between the evolution of a trait and subsequent diversification is difficult in any particular instance. One solution is to investigate potential key innovations that have evolved several times to test for a general relationship between evolution of a trait and subsequent diversification (Mitter et al. 1988, de Queiroz 2002): Examples include hypocone dentition in mammals (Hunter & Jernvall 1995), toepads in lizards (Williams & Peterson 1982, Larson & Losos 1996), nectar spurs in *Aquilegia* columbines (Hodges & Arnold 1995, Ree 2005), phytophagy in insects (Mitter et al. 1988, Farrell 1998), and pharyngeal jaws in fish (Mabuchi et al. 2007). Of course, key innovations are often not a single trait but a complex of several traits—the evolution of one trait may set the stage for subsequent evolution of other traits, the combination of which in turn triggers radiation (Donoghue 2005, Marazzi et al. 2012, Werner et al. 2014). For example, features that appeared during the evolution of wings in birds evolved across multiple nodes in the phylogeny; thus, the wing as a key innovation was not a singular evolutionary event but the culmination of many evolutionary changes over millions of years (Cracraft 1990).

Two caveats must be kept in mind when evaluating claims of key innovations relative to adaptive radiation. First, key innovations may not lead to adaptive radiation. Many clades have evolved features that allow them to interact with the environment in a fundamentally different way yet have not diversified to an appreciable extent. For example, archer fish (*Toxotes* spp.) have evolved the ability to shoot water from their mouths up to 3 m to dislodge insects perched on overhanging vegetation (Schuster et al. 2006, Burnette & Ashley-Ross 2015), yet the archer fish family (Toxotidae) comprises only seven morphologically similar species (Allen 2004). Similarly, *Aneides* salamanders evolved a novel foot structure that provides great climbing ability, but *Aneides* contains only six very similar species (Baum & Larson 1991). Among mammals, the elongated digits that evolved in parallel in the Madagascan aye-ayes (*Daubentonia madagascariensis*), Papuan striped possums (*Dactylopsila* sp.), and—although now extinct—the early Tertiary apatemyids (*Heterohyus* sp.) provide the ability to locate and extract prey from crevices in the manner of a woodpecker (Koenigswald & Schierning 1987, Erickson 1991, Rawlins & Handasyde 2002), yet each also failed to radiate to any great extent. The possession of a key innovation may not lead to adaptive radiation because either ecological opportunity is not available—the innovation may provide access to a very narrow spectrum of resources—or the clade does not have the evolutionary flexibility to diversify (see Section 5 for a discussion of the failure for adaptive radiation to occur).

The second caveat is that many studies have considered any trait that subsequently leads to species diversification to be a key innovation (e.g., von Hagen & Kadereit 2003, Ree 2005, Erkens et al. 2012, Silvestro et al. 2014). However, the observation that a clade is species rich does not indicate that it is adaptively diverse, much less that the trait allowed clade members to interact with the environment in a new way. More generally, some adaptive radiations contain few species, and some species-rich clades exhibit little diversity in ecological form (i.e., little adaptive disparity) (Givnish 1997b, Losos & Mahler 2010). Consequently, adaptive disparity and species richness are not necessarily related, and different terms are needed for traits that promote one type of diversification or the other (although in some cases, a trait may have both effects). The term key innovations (Miller 1949) refers to those traits that lead to interacting with the environment in a different way; another term is needed to refer to traits that increase the rate of species diversification.

2.4. Testing the Ecological Opportunity Hypothesis with Phylogenies

In several ways, molecular phylogenetics has been instrumental in the resurgence of the study of adaptive radiation and the role that ecological opportunity plays (Glor 2010). For example, molecular studies have revealed that many biotas previously assumed to be comprised of multiple ancestral lineages are the result of diversification of a single clade: Examples include the Malagasy vangas (Vangidae) (Yamagishi et al. 2001, Jønsson et al. 2012, Reddy et al. 2012); Australian, African, and global corvoids (Barker et al. 2004; Jønsson et al. 2011, 2015); Lake Victoria cichlids (Meyer et al. 1990); and Hawaiian lobeliads (Givnish et al. 2009). Molecular phylogenies have also proved useful in clarifying temporal patterns of diversification, which is important for understanding the pace of diversification (Rabosky 2009) and recognizing potential catalysts for adaptive radiation (Donoghue 2005, Glor 2010).

In addition, molecular phylogenies have been used to directly test the hypothesis that rates of adaptive radiation are related to available ecological opportunity. Early studies simply looked at the rate of species proliferation through time as a clade diversified; assuming that as a clade became more species rich ecological opportunity would decrease, these studies tested the prediction that this declining opportunity would lead to a slowdown in the pace of diversification through time[1] (Schluter 2000, Freckleton & Harvey 2006). More recently, researchers have directly tested the

[1]Note that adaptive radiation does not necessarily entail a burst of diversification at the outset; whether such a temporal pattern occurs as part of a radiation is a hypothesis to be tested, rather than part of the definition (Givnish 2015).

relationship between opportunity, estimated as the interspecific morphological variety inferred to have existed at a given time, and the rate of ecomorphological diversification (Mahler et al. 2010). The prediction in these studies is that morphological diversification should decrease as clades become more ecomorphologically diverse (Arakaki et al. 2011, Burbrink et al. 2012, Svensson & Calsbeek 2012, Hughes et al. 2013, Slater 2015). When applying this framework to Greater Antillean *Anolis* lizard radiations, for example, time-calibrated phylogenetic methods revealed both a rapid early accumulation of lineages and bursts of phenotypic evolution (Mahler et al. 2010), a pattern which is common across taxonomic groups and geographic regions [e.g., the fossil record (Foote 1997), birds (Rabosky & Lovette 2008), plants (Agrawal et al. 2009), fishes (Near et al. 2012), and mammals (Schenk et al. 2013)].

Ecological character displacement: the divergence of sympatric species to minimize ecological overlap

3. HOW DOES ECOLOGICAL OPPORTUNITY MECHANISTICALLY LEAD TO ADAPTIVE RADIATION?

Picture a pregnant rodent washing ashore on a lush tropical island full of plant and arthropod life but lacking herbivores, granivores, and carnivores. The many available resources in the form of foods and habitats would constitute a wealth of ecological opportunity, and with luck and avoidance of inbreeding depression, the resulting population would quickly become well established. Scenarios such as this embody the first step in adaptive radiation: A population finding itself in the presence of great opportunity. But how does this ecological cornucopia translate into evolutionary diversification?

Adaptive radiation entails evolution in two dimensions: the proliferation of an initial ancestral species into multiple descendant species and the divergence of these species to adapt to an array of different ecological conditions, which we henceforth refer to as niches (for discussion of this long-lived and contentious term, see Chase & Leibold 2003). Whether speciation and adaptive divergence are a sequential or simultaneous process is an outstanding question in macroevolution.

3.1. The Classic Scenario: Interspecific Competition

The classic scenario postulates speciation occurring first, followed by subsequent divergence. The archipelago model—exemplified by adaptive radiation in Darwin's finches (Grant & Grant 2008, 2014)—is a prime example: An ancestral finch initially colonizes one of the Galápagos Islands, and subsequently individuals from that population colonize another island. In allopatry, the two populations diverge to the extent that they are substantially or completely reproductively isolated (or would be were they to occur in sympatry); such reproductive isolation can evolve for many reasons, such as genetic drift or as an incidental by-product of divergence resulting from different adaptive or sexual selection pressures (Gittenberger 1991, Schluter 2000, Price 2008, Wagner et al. 2012). At the same time, some degree of adaptive divergence occurs as the two nascent species adapt to differences between the islands. Subsequently, colonization from one island to the other brings the two nascent species into sympatry. Once the populations reach their carrying capacities, they may compete for resources. Given the different types of available resources, the two populations may take advantage of this ecological opportunity and diverge in resource use; this resource partitioning permits the species to minimize interspecific competition. Assuming that the populations can coexist long enough (i.e., that competitive exclusion does not lead to the extinction of one; MacArthur & Levins 1967, Slatkin 1980, Gomulkiewicz & Holt 1995), natural selection may then cause the species to phenotypically diverge to adapt to their new resource utilization regime. This is the process of ecological character displacement (Brown & Wilson 1956). Natural selection against hybrids can also lead to the perfection of reproductive isolation if it was incomplete prior to sympatry (the process of reinforcement; Blair 1955). Multiple cycles of such divergence in isolation followed by character displacement in sympatry can lead to a diverse adaptive radiation.

Reinforcement: the evolution of traits that minimize hybridization between incipient species

Not too long ago, both character displacement and reinforcement were thought by some to be unlikely on both theoretical and empirical grounds, but in recent years, these concerns have diminished and both are now generally considered to commonly occur (Schluter 2000; Dayan & Simberloff 2005; Grether et al. 2009; Pfennig & Pfennig 2012a,b; Stuart & Losos 2013). Evidence from both laboratory studies of microorganisms (Rainey & Travisano 1998, Tyerman et al. 2008, Bailey & Kassen 2012, Le Gac et al. 2012) and field studies of trait shifts in nature (Grant & Grant 2006, Pfennig et al. 2006, Goldberg et al. 2012, Stuart et al. 2014) continue to provide compelling evidence for character displacement when ecological opportunity is present. Additionally, an increased movement of species to regions outside of their native range in the Anthropocene is providing ample opportunities to observe species in the early stages of secondary contact and coexistence, setting the stage for many new observational studies of character displacement (Weber & Strauss 2016).

3.2. Predation

Traditionally, interspecific competition has been considered the driving force behind adaptive radiation in the presence of ecological opportunity, but other mechanisms may be important as well. In particular, predation (defined here as consumption of one individual by another, thus including herbivory and parasitism) can cause populations to shift their resource use; in the presence of ecological opportunity, predation, in theory, may be a potent force driving adaptive radiation (Langerhans 2007).

Predation can play a role at several different stages of adaptive radiation. On one hand, allopatric populations may diverge adaptively not due to differences in resource availability but as a result of experiencing different predation pressures. Damselfly larvae, mosquitofish, sticklebacks, and zooplankton, for example, exhibit divergence in behavior, habitat use, and morphology depending on the types of predators to which they are exposed (Marchinko 2009, Strobbe et al. 2011, Walsh & Post 2011, Giery & Layman 2015, Giery et al. 2015).

On the other hand, divergence can also occur between sympatric species as they adapt in different ways to predation by a common predator (Allen et al. 2013). Such predator-driven divergence can be particularly potent when it drives species into different niches and lifestyles that also lead to differences in resource use. For example, the evolution of body armor can affect locomotion, which in turn may alter how animals can forage and acquire resources (Langerhans 2009, Broeckhoven et al. 2015).

Predator-driven prey divergence can result in evolutionary patterns similar to those resulting from interspecific competition. When prey species share a predator, an increase in the population size of one prey species may lead to a larger population of the predator, which in turn would lead to a reduction in the population of the second prey species. The result is that the population sizes of the two species would be negatively related, just as occurs with interspecific competition (Holt 1977). And just as with interspecific competition, prey species may diverge in habitat or resource use to minimize vulnerability to the shared predator, leading to the same pattern of character displacement as produced by interspecific competition. The process by which predation may lead to the same types of ecological and evolutionary response as competition has been termed competition for enemy free space (Jeffries & Lawton 1984) or apparent competition (Holt 1977).

In these ways, predation-driven divergent selection could lead to adaptive radiation in the presence of ecological opportunity. However, the extent to which predation drives adaptive radiation remains unresolved, and few examples have been documented (Vamosi 2005, Langerhans 2007, Anderson & Langerhans 2015).

In addition to predation, other interspecific interactions may be important in stimulating adaptive radiation. For example, mutualisms can promote the coexistence of closely related species and may also lead to new ecological opportunities (Anacker & Strauss 2014, Weber & Strauss 2016).

3.3. Sympatric Speciation

The archipelago model of adaptive radiation by allopatric speciation, as described earlier for Darwin's finches, is easy to envision. Speciation may occur on different islands, with species subsequently coming into contact via dispersal. However, any biogeographic or historical setting in which populations become geographically isolated may produce allopatric speciation and serve as the first stage in the adaptive radiation process. Allopatric speciation has historically been considered the predominant process by which speciation occurs, at least in animals if not plants, and is one reason that the traditional view of adaptive radiation invokes speciation in allopatry followed by divergence in sympatry.

The alternative view of the relationship between ecological opportunity and adaptive radiation envisions speciation and adaptive diversification occurring in concert in one place without an allopatric stage. In this view, the ancestral population first expands its resource use, taking advantage of the variety of available resources, the lack of predators, or a combination of both (Parent & Crespi 2009, Yoder et al. 2010, Wellborn & Langerhans 2015). This niche expansion in the absence of other species is referred to as ecological release[2] (Yoder et al. 2010, Wellborn & Langerhans 2015). Subsequent to niche expansion, disruptive selection operates on the population, favoring individuals better suited to utilize specific resources but working against those intermediate individuals not well adapted to any particular resource (Wellborn & Langerhans 2015). As subpopulations become well adapted to specific resources, the relative fitness of intermediate phenotypes decreases. As a result, strong selection favors individuals that mate assortatively, leading to increasing reproductive isolation between the subpopulations, which may eventually become different species (Dieckmann & Doebeli 1999, Kondrashov & Kondrashov 1999, Doebeli & Dieckmann 2000). This represents one model of sympatric speciation, now often studied under the rubric of ecological speciation (Nosil 2012).

For much of the latter half of the twentieth century, sympatric speciation was theorized to be very unlikely, the primary criticism being that interbreeding between diverging subpopulations would tend to homogenize the populations and prevent the establishment of assortative mating (Mayr 1963, Felsenstein 1981, Coyne & Price 2000, Coyne & Orr 2004). However, in recent years the development of new theoretical frameworks and the discovery of a slew of suggestive examples have caused the pendulum to swing in the opposite direction, and such sympatric ecological speciation is now considered a likely phenomenon by many (e.g., Bolnick & Fitzpatrick 2007, Givnish 2010, Bird et al. 2012, Nosil 2012, Mullen & Shaw 2014). In some respects, a model of adaptive radiation via sympatric speciation is more parsimonious than invoking the existence of an intermediate allopatric stage for speciation, for which there often is no independent evidence. This argument has been made particularly forcefully for adaptive radiations occurring on small islands or in lakes where the opportunity for allopatry is not obvious (Schliewen et al. 1994, Barluenga et al. 2006, Kautt et al. 2012, Martin & Feinstein 2014; but see Martin et al. 2015). Nonetheless, whether adaptive radiation often proceeds by sympatric speciation remains much

[2] Ecological release can occur in the classic allopatric scenario as well but is not a necessary part of it.

debated (Schluter 2009, Nosil 2012, Henning & Meyer 2014, Martin et al. 2015), and the number of putative cases of adaptive radiation via this mechanism of speciation remains low.

4. IS ECOLOGICAL OPPORTUNITY NECESSARY FOR ADAPTIVE RADIATION?

Clearly, ecological opportunity often leads to adaptive radiation. But is it a necessary prerequisite? Can adaptive radiation occur in the absence of preexisting ecological opportunity by members of a diversifying clade either by wresting previously unavailable resources away from other taxa that had been using them or by creating their own opportunity?

4.1. Competitive Replacement

The paleontological literature is replete with proposed examples of one clade diversifying at the expense of an existing clade, outcompeting the extant species, and forcing the clade into evolutionary decline—a process known as active clade replacement (see discussions in Benton 1996, Jablonski 2008). The paleontological signal of such a situation would be negatively correlated species diversity patterns, one clade rising in diversity while the other diminishes. Perhaps the most convincing examples are those observed among post-Paleozoic cyclostome and cheilostome bryozoans (Lidgard et al. 1993, Sepkoski et al. 2000) and the multiple diversifying clades of canids and felids driving two canid subfamilies extinct in North America (Silvestro et al. 2015).

However, most purported examples of competitive clade replacement have fallen out of favor (Wilson et al. 2012, Benton et al. 2014) and have been replaced with a scenario whereby the incumbent taxon declined prior, and for reasons unrelated, to the diversification of a second group (Rosenzweig & McCord 1991; Benton 1996, 2009; Van Valkenburgh 1999; Brusatte et al. 2008). Subsequent diversification of the second clade after extinction of the first exemplifies postextinction radiation driven by new ecological opportunities, an alternative process known as passive clade replacement (Alroy 1999, Archibald 2011). For example, the idea that the rise of the dinosaurs came at the expense of other archosaurs has lost support, replaced by the idea that the process represented an extended passive replacement facilitated by dramatic changes in the global environment (Brusatte et al. 2008, 2010; Benton et al. 2014).

Moreover, the scenario of one clade competitively diversifying and eliminating a second clade is called into question by the rarity in which even a single species competitively eliminates another throughout its range today. The vast number of human introductions of species to areas outside their native ranges has brought together countless numbers of competitively similar species with no prior history of interaction (Sax et al. 2007). Nonetheless, few examples exist of one species causing the global (as opposed to local) extinction of another species as a result of interspecific competition (Davis 2013). By contrast, exposure to novel predation and disease from introduced species has led to the global extinction of many native species (Sax et al. 2007, Roy et al. 2012, Kraus 2015). Although novel competition can cause rapid reductions in population sizes of native species and may result in extinctions over a longer temporal scale than those caused by predation or disease (McCune et al. 2013), given the relative rarity of documented competition-caused extinctions of even single species, the possibility of an adaptively radiating clade eliminating an entire clade of established species by way of resource usurpation appears unlikely.

4.2. Self-Propagating Radiations: Niche Construction

Ecological opportunity thus seems usually necessary as a prerequisite for adaptive radiation. In most well-studied cases, such opportunity exists prior to adaptive radiation, but an alternative is that clades create their own opportunity as they radiate (for extensive discussion, see Odling-Smee et al. 2003, 2013). Ecological opportunity may be generated through the creation of novel niches, whereby the environment is modified in some way—either biotically or abiotically—such that access to newly created resources results (Matthews et al. 2014).

This process of niche construction may occur in three ways. First, as a clade radiates, the presence of multiple species provides ecological opportunities that other clade members can exploit (which we term intraclade niche construction). The traditional view is that as a clade diversifies, ecological resources become increasingly limited, and the rate of diversification slows down. But an alternative possibility is that the more species there are in a clade, the more opportunities there are for predators or mutualists (Whittaker 1977, Tokeshi 2009, Erwin 2015, Wellborn & Langerhans 2015). Most ecological communities comprise species from many clades; however, when members of a single radiation are extremely diverse ecologically (usually on islands or in lakes), this accelerating effect of species richness may have an evolutionary component: As the clade radiates, it may create additional opportunities, spurring further radiation, thus creating further opportunities, and so on.

This scenario is most likely when adaptive radiations transcend trophic levels, producing radiation members that consume other members of the same clade (Schluter 2000). Indeed, the evolution of a species that preys on other members of a clade has been observed in a diversity of taxa. For example, freshwater fishes specialized to feed on the scales of other species in its clade have evolved in both Bahamanian pupfish (*Cyprinodon* sp.) (Martin & Wainwright 2013a, Martin & Feinstein 2014) and African Rift Lake cichlid (Koblmüller et al. 2007, Takahashi et al. 2007, Seehausen 2014) radiations. Additionally, intraclade niche construction has also been demonstrated experimentally in microbial laboratory systems. For example, by manipulating the spatial complexity of the structural environment available to an ancestral population of *Escherichia coli*, initial colonizers of uninhabited fragment patches modified the environment such that divergence occurred when subsequent colonizers were able to exploit a different, previously unavailable niche, and adaptive radiation ensued (Habets et al. 2006). Similarly, several microbial studies have shown the evolution of a trophic specialist able to metabolize the waste product of an ancestral species (Kassen 2009). Though these examples demonstrate that adaptive radiations may create additional opportunity during diversification, the general pattern in adaptive radiations of decreasing diversification and ecomorphological adaptation rates through time (e.g., Agrawal et al. 2009, Mahler et al. 2010; but see Slater 2015) suggests that the creation of additional ecological opportunities within a clade during radiation is rare.

Second, concurrent radiation of two clades may create opportunities for ecological diversification in one or both clades (which we term interclade niche construction). For example, a radiation driven by competition or predation may create new ecological opportunities for a coexisting clade that may adapt and use constituent members of the first as a resource. This may spur further complementary radiation of the first clade as members seek to avoid being exploited by the second. The diversification of apple maggot flies, for example, is paralleled by radiation of the parasites that prey upon them (Forbes 2009), much like the diversification of herbivorous weevils occurring in concert with that of flowering plants (McKenna et al. 2009). In some cases, coevolutionary dynamics are more complicated, involving one clade escaping harmful biotic pressures of another and diversifying as selection is relaxed, thus providing the basis of the escape and radiation theory of plant–herbivore coevolution (Ehrlich & Raven 1964) and Vermeij's (1987) theory of evolution and escalation.

A third way in which radiations may create their own ecological opportunity is through the construction of new ecological opportunities via alterations to the physical environment: so-called ecosystem engineering (Jones et al. 1994, 1997; Wright & Jones 2006; Odling-Smee et al. 2013).

Ecosystem engineers affect resource availability for other species by physically modifying the abiotic or biotic characteristics of an environment (Jones et al. 1994, Erwin 2008). Ecosystem engineering could lead to adaptive radiation if an ecosystem engineer (or clade of ecosystem engineers) creates new environments that prompt adaptive radiation in another clade. For example, the unique and complex habitat structure built by coral reefs provided ecological opportunities for specialization and subsequent diversification of tetraodontiform fishes (Alfaro et al. 2007), just as the evolution of burrowing led to increased bioturbation and subsequent diversification of marine animal lineages able to exploit the newly constructed habitat zone during the Cambrian explosion (Erwin 2008). These examples, of course, do not illustrate a clade creating its own ecological opportunities. However, the possibility exists that a radiating clade could take advantage of opportunities created by an ecosystem-engineering clade member. One example may be the exceptional adaptive radiation of lobeliad plants in Hawaii. After initial radiation by a colonial species, forest plants that evolved to withstand hot, unshaded habitats may have acted as ecological engineers by subsequently providing suitable environmental conditions, which allowed for the evolution of shade-tolerant subcanopy species (Givnish et al. 2004, 2009).

5. WHY DOES ECOLOGICAL OPPORTUNITY NOT ALWAYS RESULT IN ADAPTIVE RADIATION?

Although ecological opportunity is the usual stimulus for adaptive radiation, some clades fail to radiate in the presence of an apparent ecological opportunity (Wilson 1992, Losos 2010, Losos & Mahler 2010; depauperons, sensu Donoghue & Sanderson 2015, Weber & Strauss 2016). For example, in the Galápagos, Darwin's finches are the only clade of birds that radiated to any appreciable extent (Valente et al. 2015). Similarly, on Caribbean islands, *Anolis* lizards have repeatedly and independently diversified on separate islands, yet few other clades of lizards have followed suit, despite having had the same temporal opportunity to do so (Crother & Guyer 1996, Thorpe et al. 2008). The presence of ecological opportunity, therefore, does not guarantee that a clade will radiate.

A clade might fail to radiate in the apparent presence of ecological opportunity for several reasons. One explanation is that ecological opportunity is not actually present. For example, the failure of some clades to radiate on islands may be because earlier-arriving clades already usurped available resources. This can be observed in the case of muroid rodents, in which early colonizers had inhibitory effects on the ultimate diversity of later colonizers within independent radiations around the world (Schenk et al. 2013). Alternatively, ecological opportunity itself may have been misidentified. The spectrum of available resources that constitutes an ecological opportunity for one species may not be the same as that required by a different species. For example, the diversity of seed sizes and shapes available on the Galápagos may have constituted opportunity to an ancestral finch species, but the range of insects may not have provided diverse opportunities for insectivorous birds, thus explaining differences in evolutionary diversification among Galápagos birds (Arbogast et al. 2006, Grant & Grant 2008, Rundell & Price 2009, Valente et al. 2015).

Even in the presence of ecological opportunity, however, adaptive radiation may not occur for two reasons. First, as discussed previously, adaptive radiation requires both proliferation of species and diversification in resource use to fill different ecological niches. Consequently, if a species is unable to speciate then adaptive radiation cannot occur (Wellborn & Langerhans 2015). For example, many types of organisms—e.g., birds, lizards, snails, and snakes—almost never speciate on islands smaller than a threshold size (Coyne & Price 2000, Losos & Schluter 2000, Losos & Parent 2009, Kisel & Barraclough 2010, Pyron & Burbrink 2014). Failure of these species—such as *Pinaroloxias inornata*, the single species of Darwin finch on Cocos Island, or *Anolis* lizards in the

Lesser Antilles—to radiate on these ecologically diverse islands may be a result of their inability to speciate.

Evolvability: the capacity to generate heritable phenotypic variation

The second reason that a clade may fail to radiate in the presence of ecological opportunity is that it does not have the ability to evolve readily into diverse forms (Schluter 2000): Clades that lack such evolvability will change more slowly or not at all, whereas those that can readily change will be capable of adapting to new circumstances (Arbogast et al. 2006, Adamowicz et al. 2008, Wellborn & Langerhans 2015). Several factors could account for differences in evolvability. For example, species with greater modularity—i.e., in which different aspects of the phenotype can evolve independently—may be able to diversify to a greater extent than species in which phenotypic components are less independent (Vermeij 1973, Kirschner et al. 1998, Rutherford & Lindquist 1998, Clune et al. 2013). Phenotypic and behavioral plasticity may also be important factors in determining levels of evolvability (Baldwin 1896, Draghi & Whitlock 2012, Snell-Rood 2013). Plasticity may allow a species to exist in conditions that otherwise would be unsuitable, possibly providing sufficient time for subsequent genetic adaptations to the new ecological environment (reviewed in West-Eberhard 2003). However, identifying the evolutionary role of evolvability may be difficult as evolvability itself may evolve rather than being characteristic of entire clades (Zaman et al. 2014). For example, hybridization events increased evolvability in populations of African Lake Malawi cichlids (Parsons et al. 2011).

The observation that some clades radiate more than others (Carlquist 1974) suggests that evolvability and propensity to speciate may be important in determining whether adaptive radiation occurs. Some clades appear to have high evolvability and propensity to radiate regardless of the environment: Examples include the Hawaiian honeycreepers and Darwin's finches, which have both radiated extensively on their respective archipelagos, as have their sister taxa on the mainland (Burns et al. 2002, Lovette et al. 2002). By contrast, the Hawaiian thrushes and the Galápagos mockingbirds have not radiated on either islands or the mainland despite existing there for the same length of time (Lovette et al. 2002, Arbogast et al. 2006, Grant & Grant 2008). Cichlid fishes show a similar pattern, with some clades frequently radiating and others not (Seehausen 2014). These consistent differences among clades suggest either intrinsic differences in evolvability or speciation propensity may exist among taxa.

Alternatively, some clades that appear to readily radiate on islands remain relatively depauperate elsewhere. For example, *Tetragnatha* spiders and aglycyderid weevils radiated to a greater extent on Hawaii than on the mainland (Paulay 1994, Gillespie 2015), and cichlid fish diversity in Africa is much higher in lakes than rivers (Genner et al. 2015). In these cases, extrinsic circumstances appear to be more important than intrinsic propensities in determining whether radiation results.

6. CAN ECOLOGICAL OPPORTUNITY BE IDENTIFIED AND QUANTIFIED A PRIORI OR IS IT ONLY OF HEURISTIC VALUE?

Ecological opportunity is usually recognized after it has occurred: A clade that has experienced an adaptive radiation is identified and then its history is assessed to see whether ecological opportunity was present early on. Alternatively, an event that generates ecological opportunity—such as a mass extinction event or creation of a new island or mountain range—is identified, and clades are studied to see if any have subsequently radiated. The consensus is clear that ecological opportunity usually precedes adaptive radiation.

Nonetheless, two key questions remain. First, as discussed in the previous section, in those cases in which a clade did not radiate, is a lack of ecological opportunity the explanation? Second, looking forward, can we identify species or clades currently experiencing ecological opportunity and thus might radiate in the future? In other words, can ecological opportunity be identified independently of the occurrence of adaptive radiation? Can ecological opportunity be measured? Does the concept have predictive value, or is it just a useful heuristic for explaining adaptive radiation after the fact (Losos 2010)?

Answering these questions requires a means of measuring ecological opportunity, which is not straightforward. In this respect, the concept of ecological opportunity is plagued by the same difficulties as the empty niche concept (Chase & Leibold 2003, Losos & Mahler 2010). Not only are both hard to identify in the absence of species that fill or take advantage of them but also it is difficult to demonstrate that resources are ever truly underutilized by some member of a community, even if not by a member of a focal clade.

Ecological opportunity represents an adaptive landscape with many vacant peaks (Simpson 1953). An approach to testing for the existence of ecological opportunity might involve estimating selection on an adaptive landscape (Fear & Price 1998, Schluter 2000, Arnold et al. 2001; the concept of adaptive landscapes is extensively reviewed in Svensson & Calsbeek 2012). If it is possible to generate a variety of phenotypes (e.g., through hybridization), it may be possible to detect unoccupied adaptive peaks, which suggests the existence of ecological opportunity. In other words, an alternative way of making a living may exist but awaits the evolution of a species able to utilize that ecological space.

Of course, estimating the adaptive landscape, particularly in the context of evolutionary radiation, is fraught with difficulty. In particular, the presence of other species—e.g., competitors and predators—will alter the shape of the landscape, potentially causing peaks to appear or vanish compared with a landscape estimated in their absence. Consequently, in the context of investigating whether ecological opportunity exists, the landscape will need to be investigated in the presence of other species. This approach, however, will only suffice to identify currently existing opportunity. Once speciation occurs, the landscape may shift as a result of the presence of a new species. Hence, estimating how long opportunity persists during the course of a radiation will be very difficult and is beyond any work that has been conducted to date.

Only a few studies have quantified the adaptive landscape experienced by the constituent species of a given adaptive radiation (e.g., Case 1979, Schluter & Grant 1984, Pfaender et al. 2016). For example, Martin &Wainwright (2013b) estimated the adaptive landscape by measuring selection on a variable population produced by hybridizing three sympatric Bahamian pupfish species (*Cyprinodon* sp.). Their study confirmed the existence of two peaks corresponding to the phenotypes of two of the three species. Similarly, Arnegard et al. (2014) explored the adaptive landscape of threespine stickleback fish (*Gasterosteus aculeatus* complex) using hybrids of two species adapted to different habitats. Hybrids were distributed across a great range of morphologies, with subsequent fitness (using growth rate as a proxy) highest at two adaptive peaks corresponding to morphologies most similar to those of the two parental species. Extending this approach to test for the existence of unoccupied adaptive peaks available to species potentially experiencing ecological opportunity is a logical next step in this research direction.

FUTURE ISSUES

Simpson's (1953) suggestion that ecological opportunity is the impetus for adaptive radiation is well supported. Now would seem to be the time for the field to move beyond documenting whether a relationship exists between ecological opportunity and adaptive radiation and to investigate the underlying mechanistic basis for the relationship. Additionally, investigations should assess when and why the two are sometimes uncoupled, either because adaptive radiation can occur without preexisting opportunity or, conversely, because radiations sometimes fail to follow from the existence of opportunity.

New tools—from comparative genomics to the ability to estimate adaptive landscapes and conduct evolutionary experiments in the field—now provide the means to further refine these questions. However, at the most fundamental level, a detailed understanding of the natural history of study organisms will remain crucially important to the development and interpretation of studies attempting to synthesize ecological and evolutionary processes (Greene 1986; Grant & Grant 2008, 2014). We expect the study of ecological opportunity to continue to blossom in the near future.

1. Adaptive landscapes. Recent empirical studies have estimated the shape of adaptive landscapes with multiple coexisting species in an adaptive radiation. Further studies attempting to quantify ecological opportunity (i.e., the presence of multiple adaptive peaks on a landscape) will continue to develop our understanding of the nature of ecological opportunity and will allow us to see how opportunity varies among taxa, among areas, and through time. Further, a more detailed macroevolutionary theory of how the adaptive landscape itself evolves will be important to further bridge the pattern–process divide (Arnold et al. 2001, Svensson & Calsbeek 2012, Wellborn & Langerhans 2015).
2. Genomics. Investigations into the genomic structure of several well-studied adaptive radiations have already begun [e.g., Darwin's finches (Almen et al. 2015), African Rift Lake cichlids (Wagner et al. 2013, Brawand et al. 2014), *Heliconius* butterflies (Heliconius Genome Consort. et al. 2012, Supple et al. 2013)]. Studies that synthesize research on adaptive landscapes with genomics will have the potential to present a clearer understanding of the phenotype–fitness and genotype–phenotype relationships and will be instrumental in understanding the genetic basis of how and why ecological opportunity is exploited and adaptive radiation occurs.
3. Niche construction. As a better understanding of eco-evolutionary feedback relationships continues to develop, opportunities to provide empirical tests for hypotheses of niche construction will arise. Although long supported in the paleontological literature (Odling-Smee et al. 2013), and more recently by microbial laboratory studies (Rainey & Travisano 1998, Habets et al. 2006), little evidence from contemporary ecological studies exists (although see Matthews et al. 2016).
4. Species introductions. The global movement of species in the Anthropocene has provided unparalleled opportunities to observe novel ecological and evolutionary scenarios (Wellborn & Langerhans 2015, Weber & Strauss 2016). For example, movement of species to areas with no, or few, ecological competitors may provide situations analogous to conditions first experienced by ancestral species in an adaptive radiation, potentially presenting the introduced species with ecological opportunity. It may be particularly valuable to compare introduced species from clades that have radiated elsewhere with those from clades that have failed to radiate to examine the role of inherent evolvability of a clade when responding to ecological opportunity. Advances in methods for predicting areas vulnerable to invasion may also provide opportunities to identify ecological opportunity a priori. For example, the identification of young diversifying clades—particularly those in areas strongly associated with the production of adaptive radiations such as islands—may suggest that ecological opportunity is still present and therefore more vulnerable to ecological and evolutionary exploitation by novel colonists.

5. Global extinctions. As we enter the Sixth Mass Extinction in the Anthropocene (Ceballos et al. 2015), we are being presented with the first large-scale opportunity to study ecological and evolutionary responses to biodiversity loss (Wellborn & Langerhans 2015). Despite an undoubted catastrophe for global biodiversity, this evolutionary research opportunity is unprecedented. For example, current global amphibian rates of extinction are four orders of magnitude higher than expected background rates (Alroy 2015). The IUCN Red List currently classifies >30% of frogs and toads (Anura) and >49% of newts and salamanders (Urodela)—representing a wide range of ecological diversity—as either extinct or threatened with extinction (Catenazzi 2015). Their loss may present ecological opportunities for lineages able to exploit resources vacated by the loss of a large proportion of an entire taxonomic group. Of course, this discussion assumes that whatever is causing extinction—often habitat loss—would not preclude the addition of new species to a community. In many cases, this will not be true.
6. Latitudinal diversity gradient. The latitudinal gradient in species diversity is well supported (Hillebrand 2004); however, the underlying mechanisms which have led to it remain unclear. Given the existence of a positive relationship between ecological opportunity and speciation rates, identifying a relationship between ecological opportunity and latitude may present one way to understand the evolution of the latitudinal diversity gradient (Schluter 2016). A more comprehensive understanding of the geographic nature of ecological opportunity would help us understand how it may be important in shaping global patterns of species diversity.

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