

REVIEW

Ecological opportunity and the origin of adaptive radiations

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Abstract

Ecological opportunity – through entry into a new environment, the origin of a key innovation or extinction of antagonists – is widely thought to link ecological population dynamics to evolutionary diversification. The population-level processes arising from ecological opportunity are well documented under the concept of ecological release. However, there is little consensus as to how these processes promote phenotypic diversification, rapid speciation and adaptive radiation. We propose that ecological opportunity could promote adaptive radiation by generating specific changes to the selective regimes acting on natural populations, both by relaxing effective stabilizing selection and by creating conditions that ultimately generate diversifying selection. We assess theoretical and empirical evidence for these effects of ecological opportunity and review emerging phylogenetic approaches that attempt to detect the signature of ecological opportunity across geological time. Finally, we evaluate the evidence for the evolutionary effects of ecological opportunity in the diversification of Caribbean *Anolis* lizards. Some of the processes that could link ecological opportunity to adaptive radiation are well documented, but others remain unsupported. We suggest that more study is required to characterize the form of natural selection acting on natural populations and to better describe the relationship between ecological opportunity and speciation rates.

Introduction

Since Darwin (1859) first remarked on the diversity of island species, evolutionary biologists have speculated on the sequence of events that lead to diversification and adaptive radiation following access to new environments. Most theories of adaptive radiation, including Simpson's (1949, 1953) and Schluter's (2000), suppose that the process begins with ecological opportunity. Despite the theoretical role of ecological opportunity as the trigger of adaptive radiation, there have been few focused discus-

sions of how ecological opportunity can generate evolutionary diversification.

The idea of ecological opportunity emerged when ecologists and naturalists noted that certain environmental conditions – such as islands, depauperate habitats, new food resources or antagonist-free spaces – seem to be associated with rapid diversification in some lineages (Mayr, 1942; Lack, 1947; Ehrlich & Raven, 1964). This observation led to hypotheses that some environments may increase diversification. For example, Simpson (1949, 1953) viewed entry into what he termed 'adaptive zones' as the trigger for the process of adaptive radiation. Under Simpson's view, species can enter these adaptive zones in one of three ways: evolution of a key innovation, dispersal into a new habitat or the extinction

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of antagonists. Although influential, these early verbal models do not precisely describe mechanisms by which environments might affect rates of diversification of species and phenotypes.

The terms *ecological release* and *ecological opportunity* are historically associated with the colonization of and subsequent adaptation to island systems (Wilson, 1961; Cox & Ricklefs, 1977). Ecological release refers to an increase in population density, habitat use or morphological or behavioural variation associated with a reduction in interspecific competitive pressures (e.g. Wilson, 1961; Crowell, 1962; Terborgh & Faaborg, 1973; Losos & de Queiroz, 1997). In general, evolutionary or ecological changes leading to ecological release are called ecological opportunities (e.g. Levin, 2004; Nosil & Reimchen, 2005). Recent authors have considered ecological opportunity with respect to its role in diversification – that ecological opportunity may, via the processes of ecological release, result in increased rates of lineage or morphological diversification (e.g. Losos & de Queiroz, 1997; Schluter, 2000; Nosil & Reimchen, 2005; Harmon *et al.*, 2008; Kassen, 2009; Parent & Crespi, 2009).

Ecological opportunity is thus identified with the causes of adaptive radiation proposed by Simpson (1949, 1953). We propose that these changes in the experienced environment have the common effect of relaxing a source of natural selection acting on ecological traits. This suggests a stricter definition of *ecological opportunity* as the relaxation of selection acting on some ecologically important trait. *Ecological release*, then, is the response of populations to that relaxation. In this review, we will show how the demographic and population genetic changes associated with ecological release may be able to promote speciation and adaptive radiation – but the processes by which this could occur are far from inevitable, and in many cases, supported only weakly by existing theoretical and empirical results. By identifying these ‘weak links’ between ecological opportunity and adaptive radiation, we hope to suggest the most profitable avenues for future research in this field.

We first discuss the beginning stages of ecological release and the associated phenomena of relaxed selection, density compensation, expanded habitat or resource use, and increased trait variation (Fig. 1). We present possible mechanisms by which these demographic and population genetic processes can lead to rapid speciation, increased morphological variation and adaptive radiation, evaluating the theoretical and empirical support for each. We follow by considering ecological opportunity from a phylogenetic perspective, discussing methods by which phylogenetic datasets can test for macroevolutionary effects of ecological opportunity. We conclude with a detailed case study of *Anolis* lizards in the Caribbean, for which the proposed relationship between ecological opportunity and adaptive radiation has been extensively described.

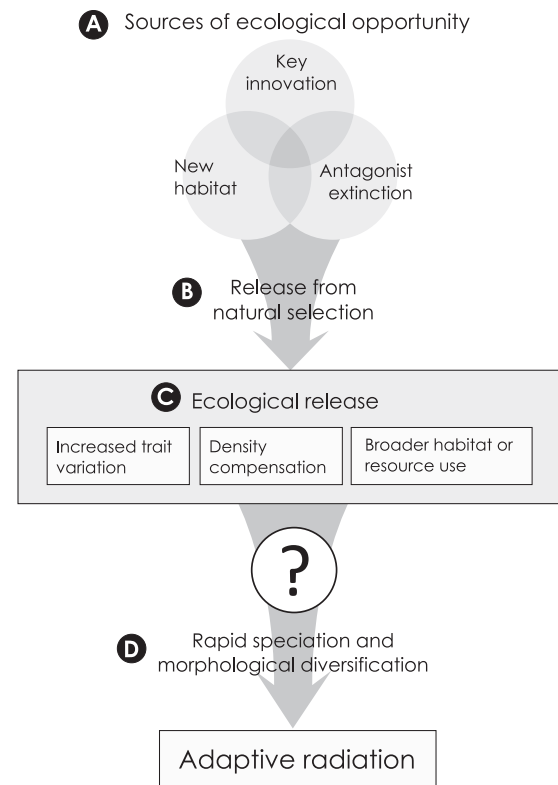


Fig. 1 The series of ecological, demographic and evolutionary processes connecting ecological opportunity to adaptive radiation. Item A: ecological opportunities include colonization of new habitats, evolution of key innovations, extinction of antagonists or a combination of these three events. Item B: ecological opportunities are understood to lead to ecological release, possibly via relaxation of natural selection acting on one or more ecological traits. Item C: ecological release is characterized by increased population size (density compensation), broader habitat use and increased trait variation in released populations. Item D: it is unclear how the phenomena associated with ecological release may ultimately lead to the rapid speciation and increased trait variation that characterize adaptive radiation.

Sources of ecological opportunity

Simpson's (1949) three sources of ecological opportunity – dispersal to a new environment, acquisition of a key innovation that makes new resources available for exploitation and the extinction of antagonists – are still relevant, and we now have many good examples of each. Paleontological studies (Sepkoski, 1981; Niklas *et al.*, 1983) and sister-group comparisons can retrospectively associate each of these with adaptive radiation (e.g. Farrell, 1998; Sargent, 2004), and microbial evolution experiments directly demonstrate their roles in promoting diversification (reviewed most recently by Kassen, 2009). Two or more of these factors may also interact to generate ecological opportunity.

Organisms often disperse to new environments, such as habitats exposed by glacial retreat (e.g. Ólafsdóttir *et al.*, 2007), newly emerged islands (e.g. Gillespie, 2004; Baldwin, 2007; Givnish *et al.*, 2009; further discussion in Levin, 2003) or habitats created by mountain uplift (e.g. Hughes & Eastwood, 2006). The bacterium *Pseudomonas fluorescens* radiates into multiple niche-specialist forms following experimental 'dispersal' into the spatially structured environments of undisturbed microcosms (Rainey & Travisano, 1998).

Key innovations may create ecological opportunity in the absence of a change to the external habitat. Numerous comparative (Ehrlich & Raven, 1964; Farrell, 1998; Sargent, 2004; Wheat *et al.*, 2007) and paleontological studies (Van Valen, 1971) suggest a role for specific key innovations in the diversification of major groups across the tree of life, including the nectar spurs of columbine (Hodges & Arnold, 1995), glucosinolate detoxification in Pierid butterflies (Wheat *et al.*, 2007), the mammalian hypocone (Hunter & Jernvall, 1995) and metabolic mutualisms between phytophagous insects and microbial endosymbionts (Janson *et al.*, 2008).

Finally, escape from antagonists is likely to facilitate entry into new adaptive zones (Levin, 2004; Ricklefs, 2010). Many paleontological studies demonstrate associations between the extinction of one group and the diversification of another (Sepkoski, 1981; Niklas *et al.*, 1983; Penny & Phillips, 2004), and contemporary studies have attributed the success of invasive species to escape from antagonists in many cases (e.g. Zangerl & Berenbaum, 2005; Blumenthal *et al.*, 2009; reviewed by Keane & Crawley, 2002). In experimental microbial systems, predators and parasites can slow diversification by reducing prey or host densities and thereby competition for shared resources (Buckling & Rainey, 2002; Meyer & Kassen, 2007; reviewed by Kassen, 2009).

Organisms may often experience strong directional selection upon first entering a novel environment or in the course of evolving a key innovation. There are a number of outstanding empirical examples of this process. Marine forms of threespine stickleback (*Gasterosteus aculeatus*) have repeatedly adapted to freshwater conditions following glacial retreat, evolving smaller body size and reduced armour and pelvic spines (Ólafsdóttir *et al.*, 2007; Albert *et al.*, 2008; Barrett *et al.*, 2008). These changes have most likely involved adaptation from standing genetic variation (Albert *et al.*, 2008; Barrett *et al.*, 2008). Similar patterns have been observed in colour adaptation by animals invading novel habitats, such as deer mice on light soils (Linnen *et al.*, 2009) and lizards on white sands (Rosenblum *et al.*, 2004, 2010; Rosenblum, 2006). In his review of adaptive radiation in experimental microbial systems, Kassen (2009) concluded that populations often experience strong directional selection on the way to ecological opportunity. One remarkable commonality among all of these studies is the speed of this adaptation; populations can become

adapted to new environments over comparatively short time scales (Barrett *et al.*, 2008).

From ecological opportunity to adaptive radiation

Figure 1 outlines the conceptual model that connects ecological opportunity (item A) to adaptive radiation (item D), via the phenomena associated with ecological release (items B and C). Although the short-term effects of ecological opportunity are generally well understood, we know much less about the long-term consequences of ecological opportunity for diversification, speciation and adaptive radiation. The immediate outcome of ecological opportunity is the moderately well-studied process of ecological release, which has been variously associated with relaxation of natural selection (Roughgarden, 1972; Lister, 1976a), population increase owing to density compensation (Wilson, 1961; MacArthur *et al.*, 1972), broader habitat or resource use (Lister, 1976b; Robertson, 1996), and increased trait variation (Da Cunha & Dobzhansky, 1954; Nosil & Reimchen, 2005). Most of these phenomena are strongly connected to ecological opportunity, but their relationships to speciation and adaptive radiation are more tenuous.

Release from natural selection

Relaxation of selection acting on one or more ecological traits is expected when new niche space becomes available (Fig. 1, item B; Roughgarden, 1972; Lister, 1976a). Access to new resources created by ecological opportunity should often effectively flatten the adaptive landscape, making a wider range of phenotypes viable (Roughgarden, 1972; Travis, 1989; Lahti *et al.*, 2009). Populations experiencing ecological release are probably most often released from actual or effective stabilizing selection (Roughgarden, 1972; Johnson & Barton, 2005; but see Lahti *et al.*, 2009). Even when populations enter new environments and experience strong directional selection on one or more key traits related to survival in that environment, they might experience a reduction in stabilizing selection on other traits, and even the traits under selection from the new environment would potentially experience weaker selection once a new optimum is achieved.

Despite considerable attention, the form and strength of selection experienced by natural populations remains unclear (Kingsolver *et al.*, 2001; Barton & Keightley, 2002; Johnson & Barton, 2005). Kingsolver *et al.* (2001) found that published estimates of the strength of stabilizing selection are often not statistically distinguishable from zero; but the subset of estimates in the Kingsolver *et al.*'s (2001) dataset that are significant suggest much stronger stabilizing selection than that is typically assumed in theoretical treatments (Johnson & Barton, 2005). Additionally, many of the studies surveyed may

underestimate the strength of stabilizing selection acting on correlations between traits (Blows & Brooks, 2003). The time scale over which selection is measured may also affect assessment of the strength of stabilizing selection; directional selection that fluctuates over short periods (e.g. Grant & Grant, 2002b; Siepielski *et al.*, 2009) may manifest as stabilizing selection over longer periods (Hansen, 1997). Additionally, stabilizing selection owing to multiple antagonistic agents of selection ('effective stabilizing selection,' Johnson & Barton, 2005) may often be missed in studies that examine selection on individual traits or loci (Travis, 1989; Blows & Brooks, 2003; Johnson & Barton, 2005).

Release from stabilizing selection is an appealing mechanistic link between ecological opportunity and adaptive radiation, as it may explain increased population densities, broader resource use and greater trait variation associated with ecological release. Determining the extent and strength of stabilizing selection in natural populations and examining the effects of putative ecological opportunities on stabilizing selection regimes is therefore a high priority in testing the connection between ecological opportunity and adaptive radiation.

Density compensation

Density compensation occurs when populations in isolated habitats occur at higher densities than in the source population and is thought to result from reduced interspecific competition in species-poor habitats (Fig. 1, item C; MacArthur *et al.*, 1972). Islands and island-like habitat patches often contain fewer heterospecific competitors, and reduced heterospecific competition or predation allows populations to occur at a higher density, and occupy a broader niche, than would otherwise be possible (MacArthur *et al.*, 1972). Increased density can lead to stronger intraspecific competition, which in turn promotes broader habitat use (Svanbäck & Bolnick, 2005). Density compensation has been widely documented in systems including island avifaunas (Wright, 1980; Thiollay, 1993), island lizards (Buckley & Roughgarden, 2006; Buckley & Jetz, 2007), lacustrine fish (Tonn, 1985), primates inhabiting fragmented rainforest (Peres & Dolman, 2000) and marine macroalgae (Eriksson *et al.*, 2009). This phenomenon may be generalized to a lineage experiencing ecological opportunity; the population can expand to higher density owing to access to a new pool of underexploited resources.

Although there is good evidence for density compensation following ecological opportunity, the relationship between density compensation and the form of selection acting on populations remains unclear. For example, release from stabilizing selection might itself lead to increased population size; but density compensation will also almost certainly lead to stronger intraspecific competition (Bolnick, 2004) that could change the shape of the selective landscape to promote broader habitat use

(Bolnick, 2001; Calsbeek & Smith, 2007b). In any case, there is clear potential for feedback between population size and the pattern of natural selection following ecological opportunity. Careful study of these feedbacks is needed to clarify the processes that occur at the beginnings of adaptive radiation.

Expanded habitat or resource use

Following ecological opportunity, and probably in concert with density compensation (Fig. 1, item C; Bolnick, 2004), species may expand their habitat use both in response to the availability of new resources and as a consequence of greater intraspecific competition (MacArthur *et al.*, 1972; Wright, 1980). Some examples of expanded habitat use directly follow from the events associated with ecological opportunity. Removal of heterospecific competitors permits broader habitat use (Lister, 1976b; Connell, 1983; Hearn, 1987; Robertson, 1996). For example, birds in depauperate island communities use broader ranges of habitat and food resources than they do in mainland communities with more competitors (Crowell, 1962; Terborgh & Faaborg, 1973; Cox & McEvoy, 1983).

Introduced species have both expanded their resource use in new ranges and prompted native species to expand their resource use to incorporate new habitats, hosts, prey or food plants (Broennimann *et al.*, 2007; Vellend *et al.*, 2007). Some of the most clear-cut examples of increased variability in habitat use following ecological opportunity are found in human-aided introductions of specialized phytophagous insect species, which frequently feed on host plants found only in the introduced range in addition to whatever ancestral hosts are also present. Such host shifts are most commonly to close relatives of the ancestral host (Pemberton, 2000), as in the case of the thistle-feeding weevil *Rhynocyllus conicus*, which was found feeding on a wide range of thistle species absent in its home range after introduction to California (Turner *et al.*, 1987).

An important component of increased variation in habitat use may be individual-level specialization in the use of habitat or other ecological resources (Bolnick *et al.*, 2003). Individual specialization occurs when individuals within a population subdivide available resources or habitat, so that, in the terms proposed by Roughgarden (1972), the between-individual component of variation in habitat use is large relative to the population's total niche width. Increased population density, such as that which results from density compensation in novel habitats, has been shown to prompt expanded niche use in both theoretical (Svanbäck & Bolnick, 2005) and empirical studies (Bolnick, 2001; Bolnick *et al.*, 2007; Svanbäck & Bolnick, 2007). Heritable individual specialization may provide a critical mechanistic link between the population growth and niche expansion associated with ecological opportunity and macroevolutionary

diversification, as a means by which relaxation of stabilizing selection ultimately leads to disruptive selection (Bolnick, 2006; Bolnick *et al.*, 2007; Snowberg & Bolnick, 2008).

Increases in the range of resource use following ecological opportunity have been documented in a range of empirical systems. This well-supported step does connect ecological opportunity with an increase in diversity, but adaptive radiation involves the formation of new and varied species. More is still needed to translate diversity of resource use into adaptive radiation.

Increased trait variation

Previous models have speculated that one stage in adaptive radiation is an increase in trait variation within populations owing to ecological opportunity (Fig. 1, item C). Empirical studies have sometimes found an increase in phenotypic variation when populations are released from predators, competitors or other sources of stabilizing selection (Roughgarden, 1972; Houle *et al.*, 1994), particularly if such release creates access to new resources (Levene, 1953; Da Cunha & Dobzhansky, 1954; Bolnick *et al.*, 2007). Schluter (2000) suggests that such increases provide indirect evidence for ecological opportunity.

However, increased trait variation is only sometimes observed in natural populations experiencing ecological opportunity (e.g. Lister, 1976a,b; Bolnick *et al.*, 2007). *In-situ* changes in abiotic or biotic environmental factors can sometimes produce novel adapted phenotypes that promote rapid diversification (Nosil & Reimchen, 2005; Landry *et al.*, 2007). Quite often, though, results from natural populations have been inconclusive, with populations showing levels of variation that do not seem to be related to the presence of predators or competitors (reviewed in Schluter, 2000; but see Houle *et al.*, 1994; Duda & Lee, 2009). Indeed, in many studies, populations show expanded habitat use that is not associated with increased levels of phenotypic diversity (Schluter, 2000). For example, Costa *et al.* (2008) found that individual diet variation within lizard populations of the Brazilian Cerrado was positively related to niche width (suggesting ecological release) but failed to find significantly increased variation in morphological characters.

These conflicting results might be resolved by identifying how new variation is created by processes associated with ecological release. The most straightforward explanation for observed patterns of standing heritable trait variation in the face of stabilizing selection is that mutation produces new variation roughly as fast as selection removes it (Kingsolver *et al.*, 2001; Barton & Keightley, 2002; Keightley, 2004; Johnson & Barton, 2005). Under this model, mutation might be expected to create new trait variation within a few generations following release from selection, but the theory underlying this prediction depends somewhat on the genetic

architecture underlying a focal trait or traits (Barton & Keightley, 2002; Johnson & Barton, 2005). Available empirical datasets support some form of mutation-selection balance, showing either sustained response to artificial selection over tens of generations (reviewed by Keightley, 2004) or significant gains of trait variation after just a few generations under relaxed selection (Houle *et al.*, 1994). This suggests that mutation may contribute to the increase in trait variation within a few generations after ecological release. Additionally, even before mutation introduces new variation, the flattening of the fitness surface created by ecological opportunity should also flatten the population trait distribution – increasing trait variation by making formerly rare extreme phenotype values more common. Finally, a purely behavioural expansion of resource or habitat use may actually generate divergent selection in a released population, if there are fitness benefits for individuals exploiting new regions of niche space.

The evolution of increased trait variation is therefore another area where more focused research is needed. Ecological opportunity may only sometimes lead to increased trait variation and, thus, eventually to adaptive radiation. Evidence for this proposition comes from situations where lineages have responded to opportunity by becoming superabundant generalists rather than diversifying. Alternatively, perhaps building up morphological variation within populations is not a necessary step in the process of diversification (Bolnick *et al.*, 2007). Instead, variation could build up among species via speciation, either because reproductive isolation preserves geographical variation that would otherwise be ephemeral (Futuyma, 1987) or because adaptive divergence occurs after isolation is already established (see below). Combining the processes discussed earlier, release from selection frequently results in increased density and variation in habitat use; but this variation is only sometimes associated with increases in levels of trait variation. Increased trait variation associated with ecological release is, therefore, one of the weakest of the possible links between ecological opportunity and adaptive radiation.

Speciation following ecological release

Speciation is the means by which ecological opportunity is translated into the increased rates of lineage diversification associated with adaptive radiation (Fig. 1, item D; Gavrillets & Losos, 2009). The establishment of reproductive isolation can 'lock in' otherwise transient increases in trait variation owing to either relaxed selection or increased disruptive selection arising from intraspecific competition. In this way, speciation can ratchet up diversity with each new ecological opportunity to build adaptive radiations (Futuyma, 1987; Coyne & Orr, 2004). It is also possible that ecological opportunity can promote speciation directly, especially if

ecology plays a key role in reproductive isolation (Nosil *et al.*, 2005; Schluter, 2009).

The classic, and now most widely accepted, view of speciation holds that reproductive isolation usually arises as an incidental by-product of divergence in allopatry (Mayr, 1942; Coyne & Orr, 2004). There is extensive evidence for this mode of speciation in many groups. However, it is difficult to imagine how ecological opportunity could lead to increased rates of speciation under this purely allopatric model. If these were the common mode of speciation in a group, then speciation would represent the rate-limiting step in adaptive radiation. Even when there is ecological 'space' ready to be occupied by new species, lineages would not be able to evolve new forms faster than the rate at which reproductive isolation is imposed by stochastic vicariance events (Coyne & Orr, 2004).

It is easier to imagine a link between ecological opportunity and diversification when natural selection contributes to reproductive isolation (i.e. ecological speciation). A wide variety of ecological processes can be involved in the process of speciation, including competition (Dieckmann & Doebeli, 1999; Abrams, 2006), mutualism (Kiestner *et al.*, 1984), predation (Day *et al.*, 2002), host-parasite interactions (Nuismer, 2006), sexual selection (Gavrilets & Waxman, 2002), fluctuating environments (Abrams, 2006) and environmental gradients (Slatkin, 1973; Doebeli & Dieckmann, 2003). With this abundance of potential mechanisms for ecological speciation, the question for future research seems to be not so much what selective forces *can* mediate speciation, but which ones do most commonly, and how multiple sources of divergent selection may reinforce or interfere with each other in establishing reproductive isolation (Coyne & Orr, 2004; Sobel *et al.*, 2009).

There are copious empirical examples of ecological speciation in adaptively radiating groups (Macleay, 2005; Ryan *et al.*, 2007; Nosil *et al.*, 2008; Egan & Funk, 2009; reviewed in Nosil *et al.*, 2005 and Coyne & Orr, 2004). Hallmark cases include the repeated evolution of ecologically isolated benthic and limnetic forms of threespine sticklebacks (*Gasterosteus aculeatus*) following colonization of freshwater environments (Schluter & McPhail, 1992; Rundle *et al.*, 2000; Vines & Schluter, 2006) and the strong connection between population-level specialization on different seed sizes and rates of gene flow between species of Darwin's finches in the Galapagos (Schluter & Grant, 1984; Grant & Grant, 2002b, 2008). In one well-studied pair of Lake Victoria cichlid species, reproductive isolation arises from interactions between water clarity and male nuptial colouration (Seehausen *et al.*, 2008; Seehausen, 2009). Finally, laboratory studies of mutant strains of the bacterium *Pseudomonas fluorescens* found that ecological opportunity caused an increase in both phenotypic variance and lineage diversification (Rainey & Travisano, 1998), with the resultant pair of genetically and ecologically distinct morphs typically

understood as analogous to new species (e.g. Meyer & Kassen, 2007; Kassen, 2009).

Even though there are a few examples of speciation associated with ecological release, this step remains a fairly weak link in the chain of events from ecological opportunity to adaptive radiation. The main problem is that, even in taxa clearly undergoing what we would label as 'adaptive radiations,' most speciation appears to be associated with geographical separation of populations. The challenge for theory is to identify and test mechanisms by which resource availability can directly influence speciation rates.

Adaptive radiation into many forms

So far, we have described how ecological opportunity leads to ecological release, diversification and speciation – adaptive radiations are simply aggregates of many instances of adaptive divergence and speciation, occurring rapidly (Schluter, 2000). Adaptive radiations have been identified at all levels in the tree of life and in taxa ranging from angiosperms (Stebbins, 1970; Davies *et al.*, 2004) to tetrapods (Guyer & Slowinski, 1993), and in island examples including Hawaii (Zimmerman, 1970; Witter & Carr, 1988), the Caribbean (Losos, 1994) and the Galapagos (Grant & Grant, 2002a). Levels of phenotypic variation among species in these radiating clades are comparatively easy to explain given known levels of trait heritability and the strength of selection in natural populations (Harmon *et al.*, 2010). Increased rates of speciation, on the other hand, require special explanation, which may be provided by ecological opportunity.

Ecological opportunities vary in both the number of species they ultimately produce and the rate at which they produce them. The most obvious candidate for determining an ecological opportunity's 'size' are the resources it makes accessible and the total population they can sustain. Perhaps larger populations are better able to persist as they are subdivided by adaptive speciation or vicariance. For example, the benthic and limnetic zones of glacial lakes support only two stickleback ecotypes (Vamosi, 2003; Vines & Schluter, 2006), but the substantially larger resource base and more diverse environments present in African rift lakes support the much more diverse cichlid radiation (Seehausen, 2006, 2009). Within the single system of Caribbean anoles, Losos & Schluter (2000) identified a minimum island area necessary for intra-island speciation, a 'speciation-area relationship' not fully explained by the greater habitat diversity on larger islands; and Kisel & Barraclough (2010) recently found evidence extending this relationship between island area and the probability of speciation to mammals, birds, flowering plants, insects and molluscs.

If speciation is primarily allopatric, the role of ecological opportunity in promoting adaptive radiation beyond an initial ecological release must be by increasing the

opportunities for reproductive isolation or by reducing the probability of extinction, rather than creating new species directly (Schluter, 2000). As the most obvious case, a population that has grown larger as a result of ecological opportunity is more likely to persist as it is subdivided by stochastic vicariance events. Adaptations that allow exploitation of new niche space may also make reproductive isolation more probable without directly causing it. For instance, seed dispersal by ants (myrmecochory) is associated with reduced seed predation and better seed placement, both of which allow plants employing this strategy to produce fewer seeds (Giladi, 2006); but because ants do not disperse seeds very far from the source plant, myrmecochorous species are more prone to allopatric speciation (Lengyel *et al.*, 2009). Key innovations that indirectly increase the probability of speciation in this manner will often be 'magic' traits with functions related both to survival and to mate choice or attraction (e.g. the beaks of Galapagos finches; Grant & Grant, 2008). Species newly formed by ecological opportunity may encounter entirely different ecological opportunities made accessible by adaptive evolution or created by the presence of a new sister species ('niche construction'; Rozen & Lenski, 2000). It may also be that the majority of ecological opportunities never lead to adaptive radiation. These cases of 'failed radiation' are of great interest in their own right (Vamosi, 2003; Seehausen, 2006; Nosil *et al.*, 2009), as we discuss below.

As adaptive radiation proceeds, lineages are expected to rapidly fill unoccupied niche space as they diversify (Gavrilets & Losos, 2009). If this process is truly driven by ecological opportunity, then eventually unoccupied niches should run out, causing the rate of diversification to decrease through the course of an adaptive radiation (Walker & Valentine, 1984; Schluter, 2000; Freckleton & Harvey, 2006; Rabosky & Lovette, 2008). This process should have a marked effect on the rates of lineage diversification through time, causing the apparent lineage diversification rate to decrease through time, which can be observed in phylogenetic analyses (Schluter, 2000; Rabosky & Lovette, 2008).

Additionally, declining rates of lineage diversification can result from processes other than ecological opportunity (von Hagen & Kadereit, 2003). For example, woodland salamanders of the genus *Plethodon* show a pattern of early diversification but very limited morphological divergence, suggesting that the pattern is attributable to allopatric speciation facilitated by poor dispersal, not ecological opportunity (Kozak *et al.*, 2006). Diversification analyses that aim to detect instances of ecological opportunity should therefore incorporate a measure of occupied niches. Harmon *et al.* (2003) correlated a measure of lineage diversity (based on lineage-through-time plots) and a proxy for niche space (morphological disparity, based on disparity-through-time plots) to test for an effect of ecological

opportunity in the diversification of four clades of iguanian lizards. The authors found that lineages that diversified early had lower morphological disparity within subclades, findings consistent with a role for ecological opportunity. We discuss emerging efforts to detect ecological opportunity using phylogenetic patterns in detail below.

Thus, the demographic and population genetic processes associated with ecological release may be able to link ecological opportunity to adaptive radiation, as conceived by Simpson (1949, 1953) and Schluter (2000); but it is unclear how general these processes are and how regularly they result from the various possible causes of ecological opportunity (Fig. 1). Adaptive radiation following ecological opportunity is clearly not inevitable or deterministic. Some lineages will experience only some of results of ecological opportunity, and many lineages may experience ecological release in differing ways. In particular, relaxation of stabilizing selection, density compensation and expanded habitat use are closely connected, and it seems probable that they may occur in many possible orders or virtually simultaneously (Fig. 1, items B and C). Additionally, the strength of evidence for each process involved varies greatly. Three major gaps remain in our understanding of adaptive radiation. First, what are the factors that increase morphological or genetic variation following the onset of ecological opportunity, and why do we not always see such a pattern? Second, is there a direct relationship between ecological opportunity and rates of speciation? Finally, what is the relationship between the filling of adaptive zones, rates of speciation and rates of phenotypic diversification in clades (Fig. 1, item D)?

Phylogenetic signals of ecological opportunity

Phylogenetic comparative methods provide a promising avenue for testing the long-term predictions of models of ecological opportunity. We focus in particular on two characteristics of adaptive radiation driven by ecological opportunity that should leave a signature in comparative data. First, adaptive radiation into new forms should be reflected as an increased rate of diversification during some time period in the history of a group. Second, as accessible niches become occupied, opportunity for ecological speciation should become increasingly limited, and rates of diversification should slow through time (Simpson, 1953; Valentine, 1980). Numerous phylogenetic comparative methods to quantify patterns of lineage accumulation and trait evolution can be brought to bear on these questions.

First, one can test whether rates of lineage, habitat use or morphological diversification are elevated by ecological opportunity (e.g. following the evolution of a key innovation). A few methods have been advanced to detect the rapid diversification thought to be character-

istic of adaptive radiation. For lineage diversification, one can compare rates of net diversification across clades (reviewed in Schluter, 2000). Some recent studies have used this approach to highlight clades that have diversified at rates higher than the 'background' rates of their close relatives (e.g. Roelants *et al.*, 2007; Alfaro *et al.*, 2009; Moore & Donoghue, 2009). A similar approach can be used to identify rapid evolution of traits related to habitat use. Studies have compared either rates of morphological evolution (e.g. O'Meara *et al.*, 2006) or the extent of morphological disparity (e.g. Losos & Miles, 2002) between putative adaptive radiations and other groups. A few studies have combined both of these approaches (e.g. Harmon *et al.*, 2003, 2008). These studies have generally found elevated rates of both lineage diversification and trait evolution in groups of interest (Collar *et al.*, 2009; Roelants *et al.*, 2007; but see Pinto *et al.*, 2008).

Second, one can test whether these initially high rates of evolutionary diversification slow through time. Most studies have focused on detecting declining rates of lineage diversification; fewer studies have looked for declining rates of trait evolution. Lineage-through-time (LTT) plots (Nee *et al.*, 1992, 1994; Harvey *et al.*, 1994; Nee, 2001) can be used to test for changes in speciation and extinction rates for a given clade, and therefore, present diversification in a historical context. The most common measure of this slowdown is the gamma statistic of Pybus & Harvey (2000), which compares observed sets of waiting times (i.e. 'lag' times between speciation events) to those expected under a uniform process of diversification. Alternative methods use model-fitting approaches based on maximum likelihood (e.g. Rabosky *et al.*, 2007; Rabosky & Lovette, 2008). Most recent studies using these approaches have suggested that the rate of lineage diversification in evolving clades slows through time (Schluter, 2000; Harmon *et al.*, 2003; Phillimore & Price, 2008; Rabosky & Lovette, 2008; Gavrillets & Losos, 2009). One caveat to this finding is that diversification models with strikingly different ecological assumptions, even models involving no ecological differences among species at all, may nevertheless produce very similar patterns of diversification (e.g. Mooers & Heard, 1997; Hubbell, 2001; McPeck, 2008; Rabosky, 2009a). Some quantitative model comparisons that would be very useful to sort out these competing explanations are currently not possible (Rabosky, 2009a). More work is desperately needed in this area.

In contrast to the large body of work on reduced rates of lineage accumulation through time, comparatively a few studies have looked for an analogous slowdown in the rate of trait evolution in a comparative context. Recently, Harmon *et al.* (2010) used methods first proposed by Blomberg *et al.* (2003) to test for slowdowns in body size and shape evolution across a large data set of phylogenies, including many canonical examples of adaptive radiation.

Perhaps surprisingly, this study found little evidence for a decreased rate of trait evolution. The lack of a slowdown in trait evolution stands in stark contrast to the finding of many studies, cited earlier, that rates of lineage accumulation slow through time in adaptive radiations – it implies that adaptive divergence continues even after an adaptive radiation has reached some equilibrium level of species diversity. This pattern is hard to reconcile with suggestions that ecological opportunity leads to brief, rapid diversification of both lineages and ecologically important traits (e.g. Harmon *et al.*, 2003). Instead, it suggests that the tempo of adaptive radiation is limited more by the formation of new species than by the evolution of new traits (see also Schluter, 2000; Gavrillets, 2004). This might mean that adaptive divergence requires reproductive isolation in the first place (Venditti *et al.*, 2010) or that the establishment of reproductive isolation is necessary to preserve diversity as it is created by ecological opportunity (Futuyma, 1987); more work is needed to disentangle the causal relationship between adaptation and speciation in adaptive radiation.

A fruitful direction in the development of new comparative methods will be to incorporate actual microevolutionary parameters (e.g. changes in population trait variance, population size, shapes of fitness functions and habitat usage; see steps 2–5) into models of evolution that can be fit to empirical data (e.g. Estes & Arnold, 2007; see also Harmon *et al.*, 2010). Whereas population genetic processes have explicitly been incorporated into phylogeny estimation (e.g. Maddison, 1997; Maddison & Knowles, 2006; Drummond & Rambaut, 2007; Kubatko *et al.*, 2009; Liu *et al.*, 2009), little has been made in this regard for comparative methods (but see Estes & Arnold, 2007). Some currently available methods can test for changes in population sizes (Drummond *et al.*, 2005; Opgen-Rhein *et al.*, 2005) and trait variance (e.g. Felsenstein, 2008), although these methods require extensive sampling both within and across species.

Case study: *Anolis* lizards in the Caribbean

In a few well-studied natural systems, ecological, population genetic and phylogenetic evidence exists to evaluate the entire process from ecological opportunity to adaptive radiation (e.g. Grant & Grant, 2008). Perhaps the most compelling such case is that of Caribbean anole lizards (genus *Anolis*), which have repeatedly evolved habitat specialist types, or ecomorphs, on islands in the Greater Antilles. The extensive body of research on the ecology and evolution of this group has been recently compiled by Losos (2009); below, we review the evidence for the components of our proposed model that have been documented in island *Anolis* radiations. Four to six ecomorphs with distinct behaviours, morphology and microhabitat usage occur on the islands of the Greater Antilles (Puerto Rico, Jamaica, Hispaniola, and

Cuba). For example, trunk-ground anoles live on the base of tree trunks, scurrying to the ground to capture food, whereas twig anoles are typically found moving slowly on narrow twigs.

Phylogenetic studies have shown conclusively that each ecomorph evolved more than once following the colonization of new islands, so that species of the same ecomorph on different islands represent cases of convergent evolution (Losos *et al.*, 1998). Interestingly, the ecomorphs present on each island represent a nested series; the smallest island, Puerto Rico, is missing one ecomorph, whereas the next largest, Jamaica, is missing two (Losos, 2009). This repeated evolution into the same set of outcomes – which is not seen in related *Anolis* species on mainland Central and South America (Pinto *et al.*, 2008) – suggests that anoles evolved to fill a set of niches that are widely available on Caribbean islands. The predictability of this process, at least in the Greater Antilles, further suggests that ecomorph evolution was driven by ecological opportunity.

Sources of ecological opportunity for island anoles

Because mainland *Anolis* species have not evolved the distinct ecomorphs seen in island populations, it seems clear that migration to the new island habitat is the ultimate source of ecological opportunity for this group. However, we do not know how the environments available on Caribbean islands create selective regimes differing from mainland environments. Habitat types occupied by Caribbean anole ecomorphs are also available on smaller islands and on the mainland of South America, but ecomorphs have not evolved in these places, in spite of character evolution rates comparable to those of the island species (Pinto *et al.*, 2008). One likely possibility is that reduced predation pressure on islands allowed the structured radiation of Caribbean anoles (Losos, 2009).

Relaxation of selection

Although no study has compared the strength of stabilizing selection acting on island *Anolis* populations with mainland populations, selection gradient analyses provide considerable evidence for the hypothesis that the diversification of these lizards is the result of changes in selective regimes. Many studies have documented ongoing selection on ecologically meaningful traits (Arnold & Wade, 1984; Losos *et al.*, 2004; Thorpe *et al.*, 2005; Losos *et al.*, 2006; Calsbeek & Smith, 2007a; b). The form of selection on anoles can be quite labile, changing from one environment to another (Thorpe *et al.*, 2005; Calsbeek & Smith, 2007b) and over short periods of time (Losos *et al.*, 2006; Calsbeek & Smith, 2007b). One study has specifically documented that the strength of stabilizing selection varies in different environments (Calsbeek & Smith, 2007b).

Density compensation

There is good evidence for density compensation in anoles, such that species on small islands occur at higher densities than populations on the mainland or larger islands. A recent meta-analysis of lizard density across the globe indicates that lizards tend to be much more abundant on islands, even accounting for differences in resource availability (Buckley & Jetz, 2007). In anoles specifically, survey data indicate that anoles are most abundant on islands of intermediate size (area $\sim 1 \text{ km}^2$) and that their abundance declines with increasing numbers of heterospecific competitors (Buckley & Roughgarden, 2006). This observation of density compensation on islands of intermediate size strongly supports the model we describe: smaller islands apparently do not provide the resource base to spur density compensation (i.e. they lack ecological opportunity); and populations on larger islands have proceeded from density compensation to adaptive radiation into many species, creating inter-specific competition that reduces individual species' densities.

Expanded resource use

Anoles broaden their habitat use following release from competitors, but there is little evidence that variance in morphological characters also increases. Several studies have measured perch choice in anoles in the presence and absence of congener lizard species, showing that many species of anoles increase their realized habitat breadth when competitors are absent (Schoener, 1975; Lister, 1976b; Rummel & Roughgarden, 1985). More recent studies demonstrated directional selection after introduction to a novel environment void of interspecific competition (Losos, 1994; Losos & de Queiroz, 1997).

Increased trait variation

Evidence for increased trait variation following island colonization has not been found in anoles. Artificial introductions of anoles to competition-free environments showed no increase in trait variation (Losos, 1994; Losos & de Queiroz, 1997). Comparison of island anoles to continental populations reveals that, although continental anoles have not evolved either the island ecomorphs or a different but similarly structured set of discrete forms, they are approximately as diverse as the island populations (Pinto *et al.*, 2008).

Speciation and adaptive radiation

Anoles show remarkable ecological diversity and specialization on different environments and are significantly more diverse than related lizards, which has been offered as evidence that they constitute an adaptive radiation (Losos & Miles, 2002). Both biogeographical

and phylogeographical data suggest that the majority of speciation events occurred in allopatry (Losos, 2004). Often, speciation in anoles is associated with overwater dispersal and colonization (Glor *et al.*, 2005). Speciation can occur within islands, but apparently only when those islands are at least as large as Puerto Rico (Losos & Schluter, 2000). Even within islands, speciation in anoles seems to require some form of geographical isolation of populations (Glor *et al.*, 2004). There is little evidence, thus far, that adaptation plays a direct role in anole speciation, although there are likely indirect links between the two processes (Losos, 2004). Just as there is no evidence that the extent of island anoles' morphology diversity exceeds that of continental populations, so rates of diversification of anoles on Caribbean islands are no greater than rates of diversification on the mainland (Pinto *et al.*, 2008). The role of ecological opportunity in the radiation of Caribbean anoles has probably been to allow the coexistence of multiple reproductively isolated anole populations within the same community, rather than to spur adaptive divergence as a prelude to speciation.

Slowing diversification as niche space fills

There is some evidence that speciation rates in anoles were fastest at the origin of the Caribbean radiation. Harmon *et al.* (2003) found a significant slowdown in net diversification rates in a chronogram of Caribbean species. There is also evidence that the evolution of ecomorph categories is concentrated reasonably deep in the anole tree; few ecomorphs have evolved recently (Losos *et al.*, 2006). Furthermore, ecomorph types rarely evolve more than once within islands, suggesting that there is some incumbency effect as a result of resource competition (Losos *et al.*, 2006). However, in terms of other morphological and ecological characteristics, there is little evidence for an overall slowdown in anole evolution (Harmon *et al.*, 2003). As we have noted earlier, this slowdown in lineage accumulation but not morphological diversification is observed in most systems for which a comparison is possible and is consistent with the hypothesis that diversification spurred by ecological opportunity facilitates allopatric speciation rather than causing adaptive speciation directly.

Many of the weak points identified in previous sections for anoles are, in general, weak points for the connection between adaptive radiation and ecological opportunity in general. Even in well-studied systems, there are not clear connections between increased resource use, decreases in stabilizing selection, increased trait variance within populations and speciation.

Discussion

One of the central insights into evolutionary ecology is that processes taking place over a single generation ultimately determine patterns of diversification and

extinction over millions of years (Darwin, 1859; Huxley, 1942; Simpson, 1953; Van Valen, 1971; Schluter, 2000; Kinnison & Hendry, 2001). We attempt to apply this principle to connect ecological opportunity, any change in the experienced environment that relaxes a source of natural selection and adaptive radiation. We emphasize that the testable, empirically documented demographic and evolutionary processes associated with ecological release are the means by which ecological opportunity may give rise to divergence, speciation and, ultimately, adaptive radiation. However, we also identify some weak points in both theory and empirical data connecting ecological opportunity to adaptive radiation. We do not advocate abandoning the idea that ecological opportunity leads to adaptive radiation but suggest that future studies focus on the weaker links in the chain of processes connecting ecological opportunity to the formation of many and varied species.

Upon encountering ecological opportunity, we expect that a population will experience a relaxation of selection acting on one or more ecological traits, increase in size owing to density compensation (MacArthur *et al.*, 1972), expand its habitat use to take advantage of new resources and show increased variation in ecologically important traits (Kimura, 1965; Keightley & Hill, 1990; Houle *et al.*, 1994). If speciation follows, variation acquired via ecological opportunity will be preserved in macroevolutionary time (Futuyma, 1987), and newly formed species can enter new ecological opportunities to eventually build an adaptive radiation (Schluter, 2000). Finally, as available niche space becomes filled, we expect rates of lineage accumulation to decrease (Rabosky & Lovette, 2008).

Some of the processes we implicate in the link between ecological opportunity and adaptive radiation are individually well documented, and many are fully described for a few well-studied systems, such as Caribbean *Anolis* lizards. New phylogenetic analyses allow us to test for the patterns of lineage diversification and niche evolution expected when adaptive radiations are driven by ecological opportunity (Rabosky, 2009b). In spite of consensus – and not inconsiderable evidence – that ecological opportunity is the seed of adaptive radiation, key questions remain. Below, we address three of these.

How widespread is stabilizing selection?

As we discuss earlier, the central component of many models of ecological opportunity is the relaxation of natural selection – most often stabilizing selection – acting on natural populations. Thus, the feasibility of the link between these models and adaptive radiation depends on the strength and ubiquity of stabilizing selection. Extensive examples of stasis in the fossil record are thought to indicate strong stabilizing selection (Charlesworth *et al.*, 1982; Hansen, 1997), and stabilizing selection should – by definition – operate on populations that occupy fitness maxima (Lande, 1976). Effective

stabilizing selection may result from directional selection on multiple genes with pleiotropic effects (Barton, 1990) or on correlated quantitative traits (e.g. Brooks *et al.*, 2005). Strong stabilizing selection has been documented in some natural populations using standard regression analyses (e.g. Brooks *et al.*, 2005; Johnson & Barton, 2005; Calsbeek & Smith, 2007b); but published estimates of stabilizing selection terms are frequently not statistically distinguishable from zero (Kingsolver *et al.*, 2001). This is likely an effect of both bias in the selection of study systems (Conner, 2001) and the large sample sizes necessary to rigorously detect stabilizing selection using multiple regression approaches (Lande & Arnold, 1983; Hersch & Phillips, 2004). Additionally, the methods most commonly used to estimate quadratic regression terms, which indicate either stabilizing or disruptive selection, may underestimate the strength of selection acting on correlations between traits (Blows & Brooks, 2003; Brooks *et al.*, 2005), which may often be under effective stabilizing selection (Johnson & Barton, 2005). Thus, although intuition, theory and broad-scale patterns suggest that stabilizing selection is widespread, this hypothesis has not been rigorously tested.

This ambiguity suggests a programme of research to test the role of ecological opportunity in ecological release and adaptive radiation, in which the variation of one or more ecological traits and the strength of the stabilizing selection acting on those traits are compared in an ancestral population and a population recently having experienced ecological opportunity (e.g. through introduction to a new range or extirpation of antagonists). The frequency with which this pattern is observed in introduced species – which are already recognized as inadvertent experiments in evolutionary ecology (Levin, 2003; Vellend *et al.*, 2007) – may be one effective test of the link between ecological opportunity and adaptive radiation.

When does radiation fail to follow ecological opportunity?

Some groups fail to diversify despite apparent ecological opportunity. Two factors that could prevent adaptive radiation despite access to ecological opportunity are genetic constraints and failure to establish reproductive isolation. First, some lineages may have patterns of genetic variances and covariances (G-matrices) that make it difficult or impossible to exploit natural discontinuities in the environment or in niche space. Organisms tend to evolve along genetic 'lines of least resistance' (Schluter, 1996), and if these lines do not coincide with axes of habitat or resource availability provided by ecological opportunity, diversification will be much more difficult (Seehausen, 2006).

Second, theory suggests that speciation in general can be difficult, especially in the face of gene flow (Felsenstein, 1981), which can prevent populations in novel

environments from becoming isolated from source populations and thus slow the rate of speciation within a new habitat. Particular genetic mechanisms, strong selection on a single trait or weaker 'multifarious' selection on multiple traits can promote speciation (Nosil *et al.*, 2008, 2009; Nosil & Harmon, 2009). When none of these are present, speciation and not ecological opportunity is the rate-limiting factor for adaptive radiation (Schluter, 2000). Additionally, geography may play a key role in speciation. For example, if environmental gradients are gradual, many intermediate environments may be present, fostering high levels of gene flow among populations and inhibiting speciation (Schilthuizen, 2000). Similarly, by providing more physical barriers to gene flow, archipelagos may promote speciation more than large single islands of the same total area.

How do the results of ecological opportunity alter the chances for future ecological opportunity?

When an ecological opportunity is encountered and a population undergoes divergence and speciation as a result, further diversification need not follow. A single ecological opportunity presumably opens up a finite new volume of niche space; as we have discussed earlier, this should create a pattern of slowing diversification over time as an adaptive radiation progresses (Freckleton & Harvey, 2006; Harmon *et al.*, 2008; Rabosky & Lovette, 2008; Bokma, 2009). This is simply the most direct way in which diversification created by ecological opportunity may feed back – negatively in this case – to change the future availability of ecological opportunity. Adaptive evolution can alter environmental sources of selection (Arnold *et al.*, 2001; Gandon & Day, 2009), and new species created by ecological opportunity can change community diversity and resource bases (Harmon *et al.*, 2009); such processes may eliminate ecological opportunities or create new ones. This feedback may often be mediated by interactions with lineages unrelated to the growing radiation, as in Ehrlich & Raven's (1964) classic model of alternating diversification in plants and herbivorous butterflies or in more nearly simultaneous co-diversification (Benkman *et al.*, 2001; Machado *et al.*, 2005; Godsoe *et al.*, 2008).

Conclusion

In this study, we review the substantial evidence for the demographic and evolutionary changes that can connect ecological opportunity to macroevolutionary diversification. Some components of the mechanism we outline are individually supported by an array of empirical and theoretical work, but others have little or inconsistent support from empirical data; in a few study systems, much of the link between ecological opportunity and adaptive radiation is well documented. The years since the publication of Schluter's (2000) opus have seen

unprecedented progress towards a general description of the link between ecological processes and evolutionary patterns, and we hope that what we present here will serve as a useful guide for future work towards this goal.

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