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Inducible competitors and adaptive diversification

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Abstract Identifying the causes of diversification is central to evolutionary biology. The ecological theory of adaptive diversification holds that the evolution of phenotypic differences between populations and species—and the formation of new species—stems from divergent natural selection, often arising from competitive interactions. Although increasing evidence suggests that phenotypic plasticity can facilitate this process, it is not generally appreciated that competitively mediated selection often also provides ideal conditions for phenotypic plasticity to evolve in the first place. Here, we discuss how competition plays at least two key roles in adaptive diversification depending on its pattern. First, heterogenous competition initially generates heterogeneity in resource use that favors adaptive plasticity in the form of "inducible competitors". Second, once such competitively induced plasticity evolves, its capacity to rapidly generate phenotypic variation and expose phenotypes to alternate selective regimes allows populations to respond readily to selection favoring diversification, as may occur when competition generates steady diversifying selection that permanently drives the evolutionary divergence of populations that use different resources. Thus, competition plays two important roles in adaptive diversification—one well-known and the other only now emerging—mediated through its effect on the evolution of phenotypic plasticity [*Current Zoology* 59 (4): 537–552, 2013].

Keywords Phenotypic plasticity, Competition, Adaptive radiation, Character displacement, Genetic assimilation, Resource polymorphism

1 Competition and Diversification

A central goal of evolutionary biology is to identify the factors that promote diversification. One such factor is competition (throughout this paper, "competition" refers to any direct or indirect interaction between organisms that reduces access to vital resources and so is deleterious—on average—to both parties; *sensu* Odum, 1959; Pianka, 2000). Indeed, evolutionary biologists have long maintained that competition can act as a potent diversifying force. The basic idea—first formulated by Darwin (1859)—is that when species compete for scarce resources, natural selection will favor individuals with phenotypes that allow them to use more abundant underutilized resources, such as those not being exploited by the other species. Consequently, competing species may diverge phenotypically (reviewed in Schluter, 2000; Pfennig and Pfennig, 2012a). In this way, competitively mediated selection promotes diversification.

Trait evolution that arises as an adaptive response to resource competition is dubbed "character displacement" (*sensu* Brown and Wilson, 1956; more precisely, such trait evolution is called "ecological character displacement", while "reproductive character displacement" refers to trait evolution stemming from selection that minimizes deleterious reproductive interactions). Patterns consistent with character displacement have been detected in numerous natural populations (reviewed in Schluter, 2000; Dayan and Simberloff, 2005; Pfennig and Pfennig, 2012a; but see Stuart and Losos, 2013), and character displacement has actually been observed to evolve in both laboratory (Tyerman et al., 2008) and field populations (Grant and Grant, 2006). Moreover, character displacement can promote not only differences between competing species, but also (potentially) ecological speciation (reviewed in Schluter, 2000; Coyne and Orr, 2004; Grant and Grant, 2008; Nosil, 2012; Pfennig and Pfennig, 2012a). Indeed, because character displacement can prompt the rapid proliferation of new species—and foster adaptive diversification of those species into diverse niches—it may play a crucial role in fueling adaptive radiation (see Fig. 1; Schluter, 2000).

Competition's contribution to diversification is not limited, however, to generating diversity between species. Competitively mediated selection also fosters diversity *within* species (Rueffler et al., 2006). Longstanding theory predicts that populations facing intense intraspecific competition can evolve to utilize a wider range of resources (Van Valen, 1965; MacArthur and

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Wilson, 1967; MacArthur, 1972; Roughgarden, 1972), and empirical studies have confirmed this prediction (e.g., Werner and Sherry, 1987; Robinson et al., 1993; Robinson and Wilson, 1994; Dayan and Simberloff, 2005). Essentially, intraspecific competition can depress the fitness of individuals in a population to such a level that some have higher fitness by seeking resources that are less in demand (Rosenzweig, 1978; Rueffler et al., 2006; Svanbäck and Bolnick, 2007). In some cases, competitively induced niche-width expansion may favor individuals that shift and utilize resources that are entirely novel (e.g., Bolnick, 2001; Aubret and Shine, 2009; Bono et al., 2013).

Intraspecific competition may even favor the evolution of alternative phenotypes showing differential resource use within a population (e.g., resource polymorphism; reviewed in Smith and Skúlason, 1996; Pfennig and Pfennig, 2012a). Specifically, intraspecific competition can act as a potent agent of negative frequency-dependent disruptive selection that maintains alternative resource-use morphs in a population (for empirical examples, see Smith, 1993; Robinson et al., 1996; Medel et al., 2003; Bolnick, 2004; Calsbeek, 2009; Hendry et al., 2009; Martin and Pfennig, 2009, 2012). These alternative phenotypes are fascinating for at least two reasons. First, they provide dramatic examples of phenotypic diversity within species (Robinson and Wilson, 1994; Smith and Skúlason, 1996; Pfennig and Pfennig, 2012a). Second, because the phenotypic (and ecological) differences between alternative resource-use morphs can be as pronounced as the differences between species (e.g., Liem and Kaufman, 1984; Benkman, 1988, 2003; Hendry et al., 2006; Calsbeek et al., 2007; Wund et al., 2008), the evolution of a resource polymorphism might represent a critical, early stage in the formation of some new species (Fig. 1; West-Eberhard, 1989; Smith and Skúlason, 1996; Robinson and Schluter, 2000; West-Eberhard, 2003, 2005; Mallet, 2008; Nosil, 2012; Pfennig and Pfennig, 2012a).

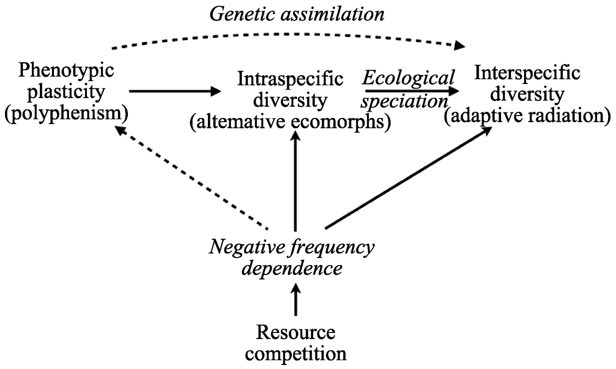

Fig. 1 Competition over resources generates negative frequency dependent selection, which may drive the evolution of different forms of phenotypic diversity (shown across the top of the Figure, including phenotypic plasticity and diversity within as well as among populations and species; extreme manifestations of each form of diversity are shown in parentheses)

Note that trait evolution arising as an adaptive response to competition—i.e., character displacement—can result in the evolution of all these different forms of phenotypic diversity. Horizontal arrows *do not* imply that the evolution of one form of diversity *necessarily* leads to the further evolution of other forms of diversity. Solid arrows represent current and recent attention in evolutionary ecology. Dashed arrows reflect additional causal pathways that are the topic of this paper.

Despite longstanding interest in competition and diversification, the possible proximate mechanisms by which competitively mediated trait evolution arises continue to be explored (Pfennig and Pfennig, 2012b). Traditionally, competitively mediated trait evolution (e.g., niche-width expansion, resource polymorphism, and character displacement) was assumed to only reflect allelic or genotype frequency changes (e.g., see Smith and Skúlason, 1996; Schluter, 2000). This has led to the erroneous view that character displacement can only arise through genetically canalized changes—i.e., changes that reflect allelic or genotype frequency changes and that are relatively insensitive to the environment (*sensu* Pfennig and Pfennig 2012b).

Yet, as we describe in greater detail below, traits that lessen or otherwise mitigate the effects of competition can also arise in individuals through phenotypic plasticity, where a single genotype produces multiple phenotypes in direct response to local environmental heterogeneity (West-Eberhard, 2003; Gilbert and Epel, 2009; Whitman and Agrawal, 2009). Induced responses to competition have historically not been thought of as character displacement, because of an oft-held view that environmentally initiated phenotypic responses cannot mediate evolutionary change (reviewed in Schluter, 2000). However, adaptive responses to competition—which have evolved via character displacement—may often be expressed *facultatively* such that they are only produced when an individual actually experiences competition (Pfennig and Murphy, 2000, 2002; Ernande and Dieckmann, 2004; Svanbäck et al., 2009). Indeed, as we describe in greater detail in the next section, competitively induced plasticity can constitute character displacement under certain circumstances (see also Pfennig and Pfennig, 2012a).

The relationship between competition and phenotypic plasticity has two important ramifications for adaptive diversification. First, as noted by a number of authors (West-Eberhard, 1989; Robinson and Wilson, 1994; Smith and Skúlason, 1996; West-Eberhard, 2003, 2005; Pfennig et al., 2010; Pfennig and Pfennig, 2012a), phenotypic plasticity can facilitate competitively mediated niche and trait evolution (e.g., niche-width expansion, resource polymorphism, and character displacement), which potentially influence the chances of additional diversification taking place (e.g., the evolution of species differences, speciation, and adaptive radiation). Second, and less generally appreciated, competition also potentially generates the selective conditions which favor the evolution of phenotypic plasticity in the first place (Fig. 1). In this paper, we review both forms of adaptive evolution and explore how competitively induced plastic responses may subsequently influence adaptive divergence.

We begin by reviewing the potential for competitively-mediated plasticity to facilitate character displacement (for a more extensive treatment, including a discussion of how character displacement may promote speciation and adaptive radiation, see Schluter, 2000; Pfennig and Pfennig, 2012a). We then discuss how competition may regularly generate heterogeneity in resource use that fosters the selective conditions that favor the evolution of phenotypic plasticity. As we describe, competition potentially plays two important roles in adaptive diversification—one well-known and the other less well known—mediated through its effect on the evolution of phenotypic plasticity.

2 Phenotypic Plasticity and Diversification

It is becoming increasingly clear that phenotypic plasticity may play a key role in driving subsequent diversification (West-Eberhard, 1989; Robinson and Wilson, 1994; Smith and Skúlason, 1996; Robinson and Parsons, 2002; Price et al., 2003; West-Eberhard, 2003; Adams and Huntingford, 2004; Schlichting, 2004; Grether, 2005; West-Eberhard, 2005; Parsons and Robinson, 2006; Lande, 2009; Pfennig et al., 2010; Moczek et al., 2011; Thibert-Plante and Hendry, 2011; Fitzpatrick, 2012). Of course, plasticity does not inevitably facilitate diversification; under some circumstances, it can impede evolutionary diversification (Price et al., 2003; West-Eberhard, 2003; Schlichting, 2004; Pfennig et al., 2010; Fitzpatrick, 2012), or even hide "cryptic" diversification when plastic responses evolve that compensate for maladaptive plastic responses (Grether, 2005). Nevertheless, recent theory and data indicate that phenotypic plasticity can promote diversification at various levels of biological organization—from fostering the origin of novel phenotypes and new species to facilitating adaptive radiation—often through similar processes, such as genetic assimilation (see below; reviewed in West-Eberhard 2003; Pfennig et al., 2010; Moczek et al., 2011). Here, we focus on how phenotypic plasticity potentially promotes adaptive divergence between populations and species—thereby possibly instigating rapid ecological speciation and adaptive radiation—by specifically facilitating competitively mediated trait evolution.

Consider that ecologists have long observed that many species appear to respond adaptively to the presence of competitors by subdividing shared resources and habitats (MacArthur, 1958; Schoener ,1974 1986; Morris, 2003; Losos, 2009). Such "resource partitioning" (*sensu* Schoener, 1974) promotes species coexistence by enabling species to optimize resource acquisition in the face of competition (Pacala and Roughgarden, 1982; Rosenzweig, 1991; Morris, 2003). Importantly, resource partitioning is often expressed facultatively: the individuals of many species respond adaptively to competition by modifying their resource-use traits (examples in supplementary Table 1; see also Mitchell et al. 1990; Morris 2003; Pfennig and Pfennig 2012a, p. 42). In other words, ecologists have long recognized that adaptive responses to competition are often mediated by phenotypic plasticity (Agrawal, 2001; Fordyce, 2006).

Yet, as noted above, competitively induced plasticity, such as adaptive resource/habitat switching (Robinson and Wilson, 1998; Svanbäck and Bolnick, 2007) and character release (Diamond et al., 1989; Robinson and Wilson, 1994), have not traditionally been considered by evolutionary biologists as a mechanism of character displacement. This is primarily because phenotypic plasticity is frequently regarded as a "nongenetic" response incapable of mediating adaptive evolution (e.g., see Arthur, 1982; Schluter and McPhail, 1992; Taper and Case, 1992). However, there are two ways in which competitively induced plasticity may constitute character displacement (Pfennig and Pfennig, 2012a, pp. 44–45).

First, populations often harbor genetic variation in the degree to which individuals respond to environmental cues, including cues associated with competition. Specifically, different genotypes typically produce different phenotypes under different environmental conditions (i.e., different genotypes typically differ in their "norms of reaction"; reviewed in Schlichting and Pigliucci, 1998). Moreover, because some of this variation may be "cryptic" (i.e., genetic variation that is not normally expressed as phenotypic variation under an organism's standard conditions but is expressed under unusual conditions; Gibson and Dworkin, 2004), competitively induced plasticity may expose standing genetic variation to selection, thereby potentially enabling traits that minimize competition to *evolve* in a population (e.g., Nussey et al., 2005; Svanbäck and Bolnick, 2007; Ledón-Rettig et al., 2010). Essentially, variation in both the tendency to respond to competitors and the phenotypes produced by individuals that express these responses can constitute an alternative axis of heritable variation (in contrast to alleles encoding "fixed" traits) on which selection can act to promote competitively mediated trait *evolution*. In other words, competitively mediated selection acting on underlying reaction norms can serve as a mechanism of trait evolution and, therefore, character displacement (for possible empirical examples, see Pfennig and Murphy, 2002; Parsons and Robinson, 2006).

Second, phenotypic plasticity may also promote character displacement if the environmentally induced trait is transmitted reliably across generations *even in the absence of genetic specification of that trait* (Pfennig and Pfennig, 2012a). Such inherited environmental effects—"transgenerational plasticity"—can potentially form the basis of an alternative inheritance system on which adaptive evolution can unfold (i.e., an inheritance system that does not involve changes in DNA sequence; see Jablonka and Lamb, 2010). For example, in many species of animals, learning can influence an individual's choice of food and/or habitat (Werner et al., 1983; Papaj and Prokopy, 1989; Price, 2008, pp. 129–135). Once members of a population acquire such a new, learned food or habitat preference (as might occur, e.g., following exposure to a new competitor) these preferences can be transmitted across generations and even reinforce differences between species, thereby mediating character displacement (e.g., see Price, 2008, pp. 293-296). Additionally, acquired information or materials (e.g., RNA transcripts, cytoplasm, hormones) can be transmitted via maternal effects, which occur when a female's phenotype influences her offspring's phenotype, independent of the direct effects of her coding sequences on offspring phenotype (Donohue and Schmitt, 1998; Mousseau and Fox, 1998; Räsänen and Kruuk, 2007). Empirical studies have demonstrated that maternal effects can be triggered by interspecific competition (Allen et al., 2008; Pfennig and Martin, 2009), that they can mediate adaptive phenotypic change (Badyaev et al., 2002; Galloway and Etterson, 2007; Allen et al., 2008; Pfennig and Martin, 2009), and they can be transmitted reliably across generations (Plaistow et al., 2006). Indeed, environmentally mediated maternal effects may play an under-appreciated role in driving character displacement between interacting species (Pfennig and Martin, 2009).

Not only *can* competitively induced plasticity constitute character displacement, but it likely *does* frequently mediate character displacement. This is because phenotypic plasticity can potentially produce rapid and population-wide phenotypic responses, thereby overcoming a major impediment faced by rare mutations (Lande, 2009; Pfennig et al., 2010). In particular, environmentally induced change typically occurs in numerous individuals simultaneously, a situation that contrasts markedly with the production of new genetic variants, which typically arise in only a few, or even just one, individual (West-Eberhard, 2003). Moreover, unlike genetic mutations that can only affect performance across generations, plastic responses to competition are produced within the lifetime of each individual. Such induced responses that can rapidly ameliorate the negative effects of competition are likely to be favored because character displacement can be a time-limited process: if character displacement unfolds too slowly, a population runs an increased risk of extinction via competitive exclusion (Rice and Pfennig, 2007). Thus, because it potentially enables many individuals to rapidly mitigate the effects of competition, competitively induced plasticity may be a general and important mechanism for instigating character displacement.

An additional reason why phenotypic plasticity should be especially effective at promoting rapid character displacement is that the ability to facultatively respond to *inter*specific competition may pre-exist in many populations, having previously evolved as an adaptive response to *intra*specific competition. As alluded to above, and as we discuss below, many species respond to intraspecific competition through facultative shifts in resource use and associated traits (Rosenzweig, 1991; Morris, 2003). The presence of pre-existing competitively induced responses, and any underlying genetic variation in those responses, means that pre-existing genetic pathways and developmental mechanisms can evolve under selection arising from heterospecific competitors and thereby drive their adaptive evolution. Indeed, empirical evidence suggests that intraspecific variation generated by plasticity may often form the basis for interspecific variation during character displacement (reviewed in Pfennig and Pfennig, 2012a, pp. 98–102).

Competitively induced phenotypic plasticity and genetically canalized change are not mutually exclusive mechanisms of character displacement, and may even be complementary under certain conditions (Fig. 2). Character displacement may often proceed through an initial phase in which trait divergence is environmentally induced to a later phase in which divergence becomes genetically differentiated in different populations and species (Pfennig and Pfennig, 2012a). Evolutionary biologists have long recognized that an originally inducible phenotype can lose environmental sensitivity over evolutionary time and eventually become "fixed" or produced constitutively through "genetic assimilation", for example depending on environmental frequency and plasticity costs (Baldwin, 1896; Morgan, 1896; Baldwin, 1902; Waddington, 1953, 1957; Pigliucci and Murren, 2003; West-Eberhard, 2003; Lande, 2009; Moczek et al., 2011).

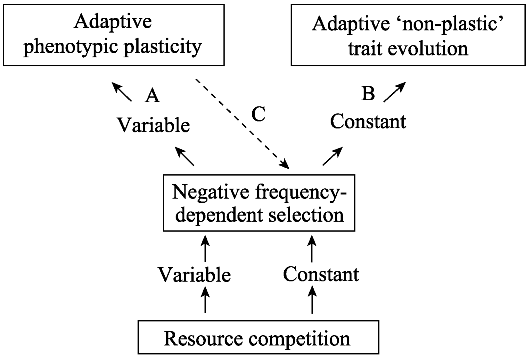

Fig. 2 When individuals compete for scarce resources, natural selection can be negatively frequency dependent and favor individuals with phenotypes that allow them to use more abundant underutilized resources, such as those not being exploited by other conspecifics or by heterospecifics

Ecological character displacement—adaptive evolution in a population that minimize the negative consequences of competition—can favor (A) adaptive plastic responses to the effects of variable competitors, or (B) adaptive non-plastic traits to effects from constant competitors. Character displacement has occurred in either population (A or B) relative to a population that has not experienced competition (e.g., in allopatry). The evolution of competitively mediated plastic responses (A) can sometimes trigger further rapid adaptive divergence (C) in a plastic population that now encounters persistently strong competition leading to (B). Variable plastic responses by many individuals in the population reduce the risk of competitive exclusion. Furthermore, by enhancing the breadth of resource use, such variable plastic responses can also strengthen frequency-dependent interactions.

Genetic assimilation may be a common route to character displacement (Wilson, 1992, p. 174; Pfennig and Pfennig, 2012a, pp. 94–102). Under this hypothesis, competing species may initially respond to each other's presence through the evolution of beneficial facultative adjustments in resource-use traits (pathway A in Fig. 2). One or both species may ultimately lose this plasticity and become fixed for alternative phenotypes (modeled by Price et al., 2003 and Lande, 2009; for possible empirical examples, see Schwander and Leimar, 2011; Pfennig and Pfennig, 2012a, pp. 94-102). Thus, when a strong competitive interaction arises that generates persistent selection for traits that minimize interspecific competition, ecologically relevant traits that are initially environmentally induced may become genetically canalized, and thereby mediate character displacement (pathway B in Fig. 2; Pfennig and Pfennig, 2012a). In short, phenotypic plasticity may enhance diversification by facilitating character displacement, thereby promoting adaptive divergence and possibly even adaptive radiation.

Having discussed how phenotypic plasticity promotes diversification between competing populations and species, we now turn to the important issue of how competition can generate heterogeneity in resource use that fosters the selective conditions that initially favor adaptive plasticity.

3 Competition and Phenotypic Plasticity

Above, we hypothesized that the ability to respond to *inter*specific competition through phenotypic plasticity may already exist in many populations if it had previously evolved as an adaptive response to *intra*specific competition. We further noted that many organisms can facultatively respond to either form of competition (see supplementary Table 1). In this section, we consider how competitively-induced phenotypic plasticity may evolve.

Phenotypic plasticity is thought to evolve as an adaptive response to contrasting selection arising from unavoidable environmental heterogeneity (reviewed in Berrigan and Scheiner, 2004). Variation in local environment can destabilize an organism's homeostasis and development and thereby disrupt the match between the organism's phenotype and its environment (Whitman and Agrawal, 2009). Phenotypic plasticity can lessen such mismatches and thereby enhance fitness. Although some forms of plasticity represent unavoidable and stressful responses to adverse conditions (Ghalambor et al., 2007), many examples appear to be beneficial responses by specific traits that contribute to individual fitness; i.e., “adaptive plasticity” (Gotthard and Nylin, 1995; Travis, 2009). Generally, adaptive plasticity is favored when organisms confront environmental variation, when no fixed trait is best suited for all environmental conditions, when cues are available that reliably signal change in local conditions, and when the fitness benefits outweigh the costs of expressing plasticity (Berrigan and Scheiner, 2004; Travis, 2009; Whitman and Agrawal, 2009).

Competition may be especially likely to promote the evolution and refinement of adaptive plasticity. For one thing, competition is a potentially potent agent of selection for all organisms (Connell, 1983; Schoener, 1983; Goldberg and Barton, 1992; Morris, 2003). In the case of exploitative competition, the amount (and/or quality) of resources that an individual can acquire is reduced, which can, in turn, negatively impact organismal growth, reproductive success, and survival. In the case of interference competition, an individual may incur additional costs from direct interactions with competitors (e.g., injury or death). Given that competition is a potentially important agent of selection, does it foster the conditions that favor the evolution of adaptive plasticity?

Recall that adaptive plasticity is favored when organisms confront environmental variation and when no fixed trait is best suited for all environmental conditions. Competition causes consumers to experience unavoidable heterogeneity in environmental conditions. This is because competition invariably leads to heterogeneity in resource availability (Yang et al., 2010). Although some such heterogeneity may stem from variability in abiotic factors (e.g., Weatherhead, 1986; Grant and Grant, 1992; Yang et al., 2008), much of it may be generated by consumer-resource dynamics (e.g., Ernande Dieckmann, 2004; Svanbäck and Persson, 2009; Svanbäck et al., 2009). Ecological theory suggests that persistent low competition will tend to mute the effects of externally generated resource fluctuations, whereas intermittent strong competition will enhance their effects (McCann et al., 1998; Andersson et al., 2007). Thus, competition and other factors that regulate consumer and resource densities individually and interactively generate variation in competitive environment at a variety of scales experienced by the individual. The interplay between competitive interactions and abiotic factors in generating variation in resource availability may make it impossible to disentangle their respective effects on the evolution of adaptive plasticity in many systems. But such disentangling is not actually required, because it is sufficient to show evidence of resource competition among similar phenotypes (Diamond et al., 1989; Schluter and McPhail, 1992) and that this varies. Although empirical studies of heterogeneity in competitive conditions are difficult to study and therefore are rare (Schoener, 1983; Goldberg and Barton, 1992), an increasing number of studies have demonstrated such effects (Donohue et al., 2000; Nussey et al., 2005; Olsson et al., 2007; Yang et al., 2010).

If individuals cannot avoid such environmental heterogeneity (in resources or competitors), and if they experience contrasting selection pressures in which no one fixed trait is best suited for all environmental conditions because of severe trade-offs in foraging performance, then selection will tend to favor phenotypic plasticity (Via and Lande, 1985; Callaway et al., 2003; Whitman and Agrawal, 2009). When there is an array of possible resources, competition can generate negative frequency dependent selection that is diversifying (Rueffler et al., 2006). Although persistent competition favors diversification of “fixed” phenotypes (pathway B, Fig. 2), when the strength of competition varies (as may frequently occur in the wild; Schoener, 1983; Goldberg and Barton, 1992; Andersson et al., 2007), the mode or direction of selection fluctuates. Such fluctuations in selection will tend to favor genotypes that can detect and beneficially respond to changes in the intensity of competition (pathway A, Fig. 2); in other words, it will tend to favor phenotypic plasticity (Ernande and Dieckmann, 2004; Svanbäck et al., 2009).

A second key condition that is thought to favor the evolution of adaptive plasticity—the availability of cues that reliably signal change in local conditions—is also likely to be present during resource competition. However, the nature (and reliability) of cues that signal competition may differ between interference and exploitative competition. Under interference competition, the density of other consumers can reliably be assessed from direct physical interactions or visual and chemical cues that indicate consumer presence (e.g., Dill, 1983; Hoffman and Pfennig, 1999). By contrast, cues indicating exploitative competition may be less reliable if they are based on resource abundance, given that (as noted above) resources can be depleted for reasons other than competition (e.g., due to climatic or seasonal variation; Weatherhead, 1986; Grant and Grant, 1992; Yang et al., 2008). Moreover, cues indicating the intensity of *intraspecific* exploitative competition may be more reliable than those indicating the intensity of *interspecific* exploitative competition, if the former involve direct cues related to conspecific density during feeding and non-feeding contexts (involving any aspect of sociality, reproduction, etc.).

The utility of cues related to competitive conditions is also influenced by an interaction with plastic response time (Grime and Mackey, 2002; Stomp et al., 2008; Novoplansky, 2009; Whitman and Agrawal, 2009). Cues must provide sufficient time to allow effective responses to changes in competition because mismatches between induced phenotype and local condition reduces fitness (Stomp et al., 2008). Thus, the periodicity of fluctuating competition relative to phenotypic response time may be an important determinant of inducible competitors. However, a variety of mechanisms may also mitigate some of these costs. Many behavioral and physiological traits functionally related to resource use can change rapidly and are reversible and therefore reduce the risk of mismatch costs even in quickly changing competitive conditions (e.g., Piersma and Lindström, 1997; Stamps, 2003; Snell-Rood, 2013). Morphological and life history plasticity generally require longer developmental response times and so may evolve under slower changes in competition (e.g., Andersson et al., 2007). Different competitively induced traits may also interact in ways that reduce mismatches. Persistent competitive avoidance initiated by rapid behavioral changes in diet or habitat use in coarse-grained environments (e.g., Morris, 2003) can subsequently induce morphological responses that further enhance resource acquisition on alternative resources, and also alter life history and development (Smith and Skúlason, 1996; Stamps, 2003). Finally, the costs of slow response times may be reduced if continuously increasing responses represent a spectrum of intermediated phenotypes with increasing benefits (Stomp et al., 2008) much like the beneficial effects of learning (Werner et al., 1981; Dill, 1983; Papaj and Prokopy, 1989; Price, 2008).

The evolution of adaptive plasticity also necessitates that the benefits of induced responses outweigh any costs associated with phenotypic plasticity (Auld et al., 2010). Induced responses to competition are beneficial to the extent that they mitigate the negative effects of competition when it occurs while maximizing the advantage of optimal resource surplus in the absence of competition. Different kinds of beneficial responses are possible and fall into three broad categories (Novoplansk, 2009): (1) avoiding competition by responses that minimize competitive interaction (e.g., using alternate resources); (2) enhancing resource acquisition through "inducible offense" or "competitive confrontation," which gain access to more of a limited resource and increases the negative influence on competitors; and (3) tolerating competition by maximizing fitness under current and future poor resource conditions. Negative frequency dependent avoidance of competition by shifting resources has received most attention in evolutionary studies of animals (Rueffler et al., 2006; Pfennig and Pfennig, 2012a), but resource replacement can take other forms, such as plasticity in habitat use (e.g., Mitchell et al., 1990), dispersal (e.g., Allen et al., 2008) and cannibalism (e.g., Andersson et al., 2007). Changes in behavior also influences competitiveness through size of territories and willingness to exclude intruders (e.g., Dill, 1983; Peiman and Robinson, 2010), and increased foraging effort (e.g., Mitchell et al., 1990). Long-term morphological responses can also enhance competitive ability particularly when resources are non-replaceable. For example, plants regularly express morphological responses in shoots, leaves and roots that enhance light, water and chemical capture (Callaway et al., 2003; Novoplansky, 2009), and colonial bryozoans express changes in colony structure that enhances competition for space (Harvell, 1999).

When populations face extreme and unavoidable competition, beneficial responses that tolerate reduced resource uptake include "making the best of a bad situation" by changing life history strategy or schedule, such as accelerated development and maturation in stunted populations of fish (e.g., Heath and Roff, 1996; Heibo et al., 2005), deferring development in plants awaiting canopy gaps and other organisms awaiting release from high competition (e.g., Canham, 1988; Blanckenhorn, 1998), and manipulating offspring competitiveness, tolerance or dispersal through maternal effects (Galloway and Etterson, 2007; Allen et al., 2008). Distinctions among the three types of possible responses to competition (avoid, compete, tolerate) are important because they can differentially affect competition and other species interactions (Callaway et al., 2003).

Finally, in order for adaptive phenotypic plasticity to evolve, heritable variation must be present in whether and/or how individuals respond to environmental signals. As noted above, most natural populations are thought to harbor such genetic variation (Schlichting and Pigliucci, 1998; Whitman and Agrawal, 2009), including cues associated with changes in resource and/or competitor abundance (Robinson and Parsons, 2002; Pfennig et al., 2007). Therefore, we do not explicitly review evidence of such heritable variation here. We do note, however, that variation in plasticity can have other important evolutionary effects. For example, variation in plastic responses that is functionally related to diversity in resource use can sharpen frequency-dependent selection (Svanbäck and Bolnick, 2007) and therefore drive rapid adaptive evolution (Lande, 2009). Additionally, variation in plasticity may significantly reduce the risk of extinction by competitive exclusion, and by so doing reduce the rate of diversity loss over evolutionary time scales (Baldwin, 1896; Morgan, 1896; Robinson and Dukas, 1999; Agrawal, 2001; Price et al., 2003; Fordyce, 2006; Richards et al., 2006; Ghalambor et al., 2007; Chevin and Lande, 2010; Pfennig and McGee, 2010; Davidson et al., 2011). Thus plasticity can have both a direct positive effect on diversification as discussed earlier, and an *indirect* effect on diversity by reducing its loss and thereby *preserving* biodiversity.

In sum, theory and empirical studies suggest that resource competition fosters conditions that favor the evolution and refinement of adaptive plasticity. Thus, competition should frequently promote conditions that favor adaptive plasticity in the form of "inducible competitors".

4 Evolution of Inducible Competitors

If competition does indeed promote the evolution of phenotypic plasticity, then there should be evidence that: (1) organisms respond to competition by facultatively altering their phenotype; and (2) such induced responses increase fitness.

There is abundant evidence that organisms can respond to competition or changed resource availability by facultatively altering their phenotype. Our brief review of the literature suggests many examples of inducible competitors in both plants and animals (supplementary Table 1), even when we exclude examples of plastic responses to researcher manipulation of resource type or availability (rather than to competitors per se). We have undoubtedly missed other examples of inducible competitors. Nonetheless, three important observations emerge. First, inducible competitors are widespread, occurring in diverse taxa and at all trophic levels. This suggests that competition can favor the evolution of inducible-competitors. Second, inducible competitors respond to both conspecific and heterospecific competition. This suggests that plasticity-mediated character displacement among heterospecifics may co-opt previously evolved conspecific competitively mediated responses as described above. Third, plastic responses to competitors are not limited to avoiding competition, but also include enhanced competitive ability and the capacity to tolerate unavoidable competition. Thus, competitively induced plasticity can reduce the costs of competition in different ways. More generally, when character displacement is broadly defined as "trait evolution that arises as an adaptive response to resource competition", then all three types of responses (potentially) constitute character displacement.

Is there any evidence that competitively-induced responses enhance fitness? Although adaptive plasticity can be challenging to test (Whitman and Agrawal, 2009), we highlight two cases indicting that plasticity is a likely target of selection. The first involves female reproductive behavior and success that has been monitored for over 30 years in a natural population of red deer *Cervus elaphus* on the Isle of Rum, Scotland.

Nussey et al. (2005) report on selection favoring plasticity in the spring calving date of females that is related to variation in resource competition during the prior fall. Competition fluctuates at two different temporal scales: decadal scale changes in deer population numbers, and annual scale changes in autumn weather - where wet conditions reflect reduced food availability in the fall prior to spring calving. At low deer density, dams calve earlier in springs that follow dry compared to wet autumns, demonstrating phenological plasticity to variation in resources in the prior fall and also variation in plastic responses.

Such a resource induced plastic response is advantageous, because in good years dams can nutritionally invest more heavily in offspring which also have longer summer growing seasons, both of which influence offspring overwinter survival. However, decadal scale fluctuations in deer numbers also vary between low numbers and carrying capacity. High deer population density (and so strong competition) reveals hidden variation among females in calving date responses to autumn resource conditions because only a small fraction of females can maintain the beneficial plastic response to fluctuating autumnal conditions. At high competition, selection also strongly favors these plastic females. Thus, females vary in their responsiveness to fall competitive conditions and selection strongly favors those females with beneficial plastic responses in calving date.

In the second case, competitively-induced responses to conspecific density has also been shown to enhance fitness in plants. Jewel weed *Impatiens capensis* from open canopy forest habitats experience more spatial variation in conspecific competitive conditions and have stronger plastic shade-avoidance responses to conspecific density than individuals from shaded woodland habitats where competition is more uniformly low. In a manipulative field experiment, Donohue et al (2000) demonstrated that selection on internode length and flowering date were more strongly density-dependent at open canopy compared to woodland sites, consistent with the adaptive divergence of plastic responses between populations experiencing low versus high variation in competition. These examples demonstrate the different ways available to test adaptive hypotheses about inducible competitors that could be applied to other cases reviewed in supplementary Table 1.

Our understanding of inducible competitors would be enhanced by addressing three sets of questions. In order to understand how competition drives of the evolution of plasticity we must clarify the scales at which competition varies in natural populations. What is the frequency and amplitude of competitive variation? Is variation in competition more likely in space or in time? Does variability typically differ between intraspecific versus interspecific competition, or between exploitative and interference interactions? Does the frequency occur at a scale that would favor adaptive plastic responses?

The second set of questions involves the reliability of competitive cues and how these evolve. What cues reliably indicate the intensity of competition? How reliable are direct competitor-competitor (interference competition) cues versus indirect consumer-resource cues (exploitative competition)? Do competitive cues provide sufficient time to respond? The apparent ubiquity of inducible competitors suggests that such cues are available or readily evolve. The benefits of plasticity are determined also by an interaction between cues and response times, but we know little of how the interaction between cues and response time evolve.

The third set involves the causes and consequences of different beneficial responses (e.g., avoid, compete, tolerate). Does the evolution of response type depend on replaceable vs. non-replaceable resources or on the scale of variation in competition? How do the different types of responses, in turn, feedback on the strength or variability of competition, and what are the subsequent evolutionary consequences of these different response types? Evolutionary biologists have primarily focused on competitive avoidance because of its potential to generate diversity. However, enhanced competitive ability may either impede diversification (e.g., if it increases the chances of competitive exclusion) or enhance diversification (e.g., if it triggers a co-evolutionary arms race of escalating competitive ability; see Pfennig and Pfennig 2012a, pp. 22–23). By contrast, the diversity consequences of tolerance responses are largely unexplored.

5 General Conclusions and Future Directions

Our goals were to highlight the centrality of competition in a variety of evolutionary responses that generate phenotypic diversity, and to outline a role for competitively mediated plasticity in the evolution of diversity (Fig. 1). Our attention to the latter goal was motivated by the widespread ecological observation of many different plastic responses to competition, which have received relatively little attention from evolutionary biologists despite widespread interest by ecologists (e.g., Morris, 2003). It is increasingly understood how competition plays a central role in the diversification of species by promoting ecological character displacement and in diversification within populations by driving the expansion of niche breadth (Fig. 1). Character displacement also potentially triggers ecological speciation and even adaptive radiation when competitively driven divergence results in reproductive isolation (reviewed in Schluter, 2000; Nosil, 2012; Pfennig and Pfennig, 2012a). Here, we have focused first on the less explored roles of competitively-induced plasticity in mediating subsequent evolutionary responses, such as ecological character displacement, and second on the evolution of inducible competitors that may prime (or constrain) subsequent evolutionary responses.

Competition—particularly when it is variable—contributes to many of the key conditions that favors adaptive plastic responses. Competition has also been shown to generate selection that favors the evolution of inducible competitors in plants and animals. We also review a growing body of research (organized around the theory of "genetic accommodation"; *sensu* West-Eberhard, 2003) that focuses on how plasticity can contribute to rapid adaptive diversification (Fig. 1), but argue that the role of inducible competitors in this process may be under-appreciated.

As with the uncertainties specifically related to inducible competitors above, there are a number of unresolved issues about how competitively-mediated plastic responses influence evolution that also promise to be fruitful areas for future research.

First is to identify the proximate mechanisms of competitively mediated phenotypic divergence, whether this divergence occurs within or between species. Traditionally, competitively mediated phenotypic divergence (e.g., character displacement) was assumed to come about strictly through allelic or gene frequency change that is relatively insensitive to the environment. However, competitively-induced plastic responses appear to be widespread. Moreover, under certain circumstances, such plastic shifts can promote trait evolution, such as when variation in reaction norms become a target of competitively mediated selection or when an environmentally induced trait is transmitted reliably across generations even in the absence of genetic specification of that trait (see above). Given that plastic responses may be especially important in mediating interactions with novel competitors, special attention should be given to studying the proximate mechanisms of competitively mediated phenotypic divergence in populations that have only recently encountered novel or exotic heterospecific competitors (e.g., see Pfennig and Martin 2009). This situation also allows tests of whether plastic responses to novel heterospecific competition are biased by or co-opt responses to conspecific competition.

Second, greater effort should go into developing either theory or novel empirical approaches that test if genetically canalized change and induced responses differ in their ease and likelihood of mediating phenotypic divergence under competition. For example, phenotypic plasticity may play an important role in facilitating character displacement because plasticity tends to produce especially rapid and population-wide phenotypic responses. The speed of any competitively mediated response is likely to be important if slower responses generally increase the likelihood of competitive exclusion (instead of character displacement) occurring (Rice and Pfennig, 2007). Theoretical efforts can immediately evaluate the validity of this idea.

Third, greater effort should go into designing empirical studies aimed at determining whether populations (or species) consisting of more plastic genotypes confronted with a novel competitor, diversify more rapidly (and more readily) than those consisting of less plastic genotypes. Rapidly evolving organisms, such as microbes are ideal for such studies because of their short generation time and our ability to manipulate competition (e.g., see Rainey and Travisano, 1998; Tyerman et al., 2008; Bono et al., 2013). Moreover, at least some microbes display striking plasticity that may mediate competitive interactions (e.g., see Ptashne, 2004). Microorganisms that vary in plastic responses to competition could also be used to determine if competition favors the evolutionary refinement and enhancement of plasticity (i.e., if competition favors plasticity in the first place). More importantly, such organisms would lend themselves well for studying the role of phenotypic plasticity in mediating competitive interactions among conspecifics, and whether these responses once evolved mediate heterospecific competition, and possibly promote speciation and adaptive radiation.

Fourth, we should not neglect evaluating conditions under which phenotypic plasticity may impede diversification. There are two primary ways whereby phenotypic plasticity may constrain diversification (reviewed in Schlichting, 2004). First, if plasticity provides a genotype a cheap and reliable mechanism to produce multiple phenotypes each optimal for a different environmental (and hence, selective) regime, then genetic alternatives (e.g., alternative alleles or genotypes) may not have a selective advantage (Price et al., 2003). Second, because phenotypic plasticity provides a mechanism whereby *different* genotypes can produce the *same* phenotype, it can hide genetic differences between such phenotypes from selection (Wright, 1931). How common these conditions are met in natural populations is an important empirical question.

Finally, although we have focused on plasticity and competition, the ideas presented here may apply more generally to other agents of selection, such as predation (e.g., see Scoville and Pfrender, 2010). Variation in predation risk has driven the evolution of inducible defenses in many organisms (Tollrian and Harvell, 1999). Future studies could investigate to what extant having anti-predator responses may also influence adaptive diversification (e.g., see Langerhans et al., 2004; Losos et al., 2004). Such studies are necessary before we can evaluate whether resource competition is as (or more) important than other biotic and abiotic agents of selection in promoting diversification and whether some such agents are more likely than others to favor the evolution of adaptive phenotypic plasticity in the first place.

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Supplementary Table 1 Representative examples of competitively-induced responses (categorized by trophic type)

Induced taxon	Competitor	Resource	Response	Benefit	Reference
Primary producers					
Impatiens capensis (Jewel weed)	Conspecific	Light	Morphology, Life history	Compete	Dudley and Schmitt, 1995, 1996; Donohue et al., 2000
Trifolium repens (Clover)	Conspecifics, Heterospecific	Light	Morphology	Compete	Bittebierre et al., 2012
Pseudanabaena (Cyanobacterium)	Heterospecific	Light	Molecular	Compete	Stomp et al., 2008
Scleropogon brevifolius (Burrograss)	Heterospecific	Water	Morphology	Compete	Novoplansky and Goldberg, 2001
Quercus douglasii (Blue Oak)	Heterospecific	Water	Morphology, Life history	Tolerate	Rice et al., 1993
Glycine max (Soybean)	Conspecific	Water, chemicals	Morphology	Compete	Gersani et al., 2001
Abutilon theophrasti (Velvetleaf)	Heterospecific	Light	Morphology	Compete/ Tolerate	Weinig, 2000
Ranunculus reptans (Buttercup)	Heterospecific	?	Morphology	Compete/ Avoid?	Van Kleunen and Fischer, 2001
Campanulastrum americanum (American bellflower)	Undetermined	Light	Offspring life history	Tolerate	Galloway and Etterson, 2007
Pisum sativum (Pea)	Conspecific	Water, chemicals	Morphology	Compete	O’Brien et al., 2005

Continued Supplementary Table 1

Induced taxon	Competitor	Resource	Response	Benefit	Reference
Herbivores					
Cnidaria Gorgonacea	Heterospecific	Space	Morphology	Compete	Harvell, 1999
Scleractinia	Heterospecific	Space	Morphology	Compete	Harvell, 1999
Antipatharia	Heterospecific	Space	Morphology	Compete	Harvell, 1999
Hydozoa	Conspecific, Heterospecific	Space	Morphology	Compete	Harvell, 1999
Membranipora membranacea (Bryozoan)	Conspecific	Space	Morphology	Compete	Padilla et al., 1996; Harvell, 1999
Bugula neritina (Bryozoan)	Conspecific	Space, food	Offspring size, Life history, Behavior, Morphology	Compete, Avoid	Allen et al., 2008; Gooley et al., 2010
Keratella (Rotifer)	Heterospecific	Food	Morphology	Tolerate	Gilbert, 1999
Oreina spp. (Leaf beetles)	Heterospecific	Food	Life history	Tolerate	Roder et al., 2008
Epirrita autumnata (Moth) larvae	Conspecific	Food	Life history	Tolerate	Tammaru et al., 2000
Strongylocentrotus purpuratus (Sea urchin)	Undetermined	Food	Morphology	Compete	Edwards and Ebert,1991
Cervus elaphus (Red deer)	Conspecific	Browse	Phenology	Compete	Nussey et al., 2005
Amazilia tobaci (Coppery-rumpled hummingbird)	Heterospecific	Floral nectar	Behavior, Morphology	Compete/ Avoid	Feinsinger and Swarm, 1982
Carnivores					
Oncorhynchus kisutch (Coho salmon) juveniles	Conspecific	Territory, Food	Behavior	Compete	Dill, 1983
Perca flavescens (Yellow perch)	Heterospecific	Food	Behavior	Avoid	Hanson and Leggett, 1986
Perca fluviatilus (Eurasian Perch)	Conspecific	Food	Behavior, Morphology	Avoid	Svanbäck and Persson, 2004, 2009
Gasterosteus aculeatus (Threespine stickleback)	Conspecific	Food	Behavior	Avoid	Svanbäck and Bolnick, 2007
Lepomis spp. (Centrarchid sunfishes)	Heterospecific	Food, Habitat	Behavior	Avoid	Werner and Hall, 1976, 1977, 1979
Lepomis macrochirus (Bluegill sunfish)	Conspecific, Undetermined	Food, Habitat	Behavior	Avoid	Werner et al., 1981; Werner et al., 1983
Salvelinus fontinalis (Brook charr)	Heterospecific	Food, Habitat	Behavior, Morphology	Avoid	Magnan, 1988; Magnan and Fitzgerald, 1984
Salmo gairdneri (Rainbow trout)	Heterospecific	Stream Habitat	Behavior	Avoid	Gatz et al., 1987
Eupomacentrus spp. (Damselfish)	Heterospecific	Territory, Food	Behavior	Compete	Thresher, 1976; Ebersole, 1977
Coryphopterus glaucofraneum (Bridled goby), *Gnatholepis thompsoni* (Goldspot goby)	Conspecific, Heterospecific	Food	Behavior	Compete	Forrester et al., 2006
Embiotoca jacksoni (Black surfperch)	Heterospecific	Food	Behvior	Avoid	Schmitt and Coyer, 1983
Ambystoma tigrinum (Tiger salamander) larvae	Conspecific	Food	Morphology, Behavior	Avoid	Maret and Collins, 1997
Sturnus unicolor (Spotless starling) juveniles	Conspecific	Food	Morphology, Development	Compete	Gil et al., 2008
Falco tinnunculus (Kestrels), *Asio otus* (Long-eared owls)	Heterospecific	Food	Behavior	Avoid	Korpimaki, 1987
Antechinus stuartii (Dasyurid marsupial)	Heterospecific	Food	Behavior	Avoid	Dickman, 1986
Omnivores					
Formica integroides (Wood ant)	Heterospecific	Habitat	Behavior (colony)	Compete	Tanner, 2008
Rana sylvatica (Wood frogs) larval	Conspecific Heterospecific	Periphyton	Morphology, Behavior	Compete	Relyea, 2000, 2004; Relyea and Auld, 2005
Semibalanus balanoides (Acorn barnacle)	Conspecific	Food, Space	Morphology	Compete	Bertness et al., 1998
Scathophaga stercoraria (Yellow dungfly)	Conspecific	Food	Life history	Tolerate	Blanckenhorn, 1998
Spea spp. (Spadefoot toads) larvae	Conspecific Heterospecific	Food	Morphology, Behavior	Avoid	Pfennig, 1992; Pfennig and Murphy, 2000

Shown are the taxa responding (induced taxon) to a competitor (conspecific, heterospecific, both or undetermined), the shared resource, the type of response (behavior, morphology, life history, etc.), and the type of benefit expected to reduce the negative effect of competition (avoiding, enhancing or, tolerating competition).

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