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Ecological character displacement: glass half full or half empty?

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Ecological character displacement (ECD), the evolutionary divergence of competing species, has oscillated wildly in scientific opinion. Initially thought to play a central role in community assembly and adaptive radiation, ECD recovered from a 1980s nadir to present-day prominence on the strength of many case studies compiled in several influential reviews. However, we reviewed recent studies and found that only nine of 144 cases are strong examples that have ruled out alternative explanations for an ECD-like pattern. We suggest that the rise in esteem of ECD has outpaced available data and that more complete, rather than simply more, case studies are needed. Recent years have revealed that evolutionary change can be observed as it occurs, opening the door to experimental field studies as a new approach to studying ECD.

Ecological character displacement

ECD, the idea that sympatric species that compete for the same set of limited resources should be favored by natural selection to diverge in resource use and phenotype (Box 1) [1], is thought to be a key driver of evolutionary diversification and adaptive radiation [2]. In a comprehensive and thought-provoking recent monograph devoted entirely to the evolutionary significance of character displacement, Pfennig and Pfennig [3] conclude in their final paragraph: 'Character displacement...plays a key, and often decisive, role in generating and maintaining biodiversity.' Moreover, ECD exemplifies eco-evolutionary dynamics, the rapid feedback cycle between evolution and ecology [4,5]. During its 56-year history, ECD has experienced a roller-coaster ride of support in the scientific community, first being embraced enthusiastically, then suffering withering criticism and rejection of its general importance, and most recently climbing back to prominence. In this paper, we review the fall and rise of ECD and conclude that, just as many prematurely discarded it during the 1970s, ECD is now being excessively embraced. We show that the data, although mostly consistent with ECD, have not advanced at the same rate as positive opinion during ECD's revival. To fill this knowledge gap, we suggest a research approach

meant to complement existing data on ECD: the evolutionary experiment.

The rise, fall, and resurrection of ECD

The rise of ECD during the 1950s and 1960s coincided with the focus of community ecology on interspecific competition as a major player governing species interactions and community assembly. At that time, MacArthur [6] argued that if not for differences in feeding times, canopy heights occupied, and perches used, warbler species would have competitively excluded one another in northeast US conifer forests. Connell [7] showed that interspecific competition structured intertidal barnacle communities, and Hutchinson [8] proposed that the regular beak-size differences in sympatry among three species of Galápagos tree finch were differences 'necessary to permit two [or more] species to co-occur in different niches but at the same level of a food web.' These and other studies (reviewed in [9]) meshed with intuition gleaned from verbal and mathematical models of competitive exclusion [10,11], minimum size ratios [8], and limiting similarity (see Glossary) [12,13]. Steeped in this competition-dominated, MacArthurian worldview, evolutionary ecologists found it straightforward to predict ECD: natural selection should favor two species that compete for limited resources to evolve differences that allow coexistence. ECD quickly became 'nearly axiomatic in the ecological literature' [14] and was considered a major driver of evolutionary diversification, freely invoked in many cases solely on the basis of a difference in size or trophic traits between sympatric species (reviewed in [15]).

However, the importance of interspecific resource competition came under attack during the 1970s and early 1980s (discussed in [16,17]). Various authors argued that the 'ubiquitous role of competition' in nature [18] had little support from either observation or experiment [15,18–20].

Glossary

Apparent competition: indirect interaction in which one species negatively affects the other species by increasing predation by a shared predator.
Competitive exclusion: principle stating that two species that compete for the same set of resources cannot coexist, all other ecological factors equal.
Guild: any group of species that exploits similar resources in similar ways.
Intraguild predation: at least one member of a guild of competing species preys upon one or more other members.
Limiting similarity: a corollary of competitive exclusion, the maximum level of resource use overlap between two given species for which coexistence is still possible.
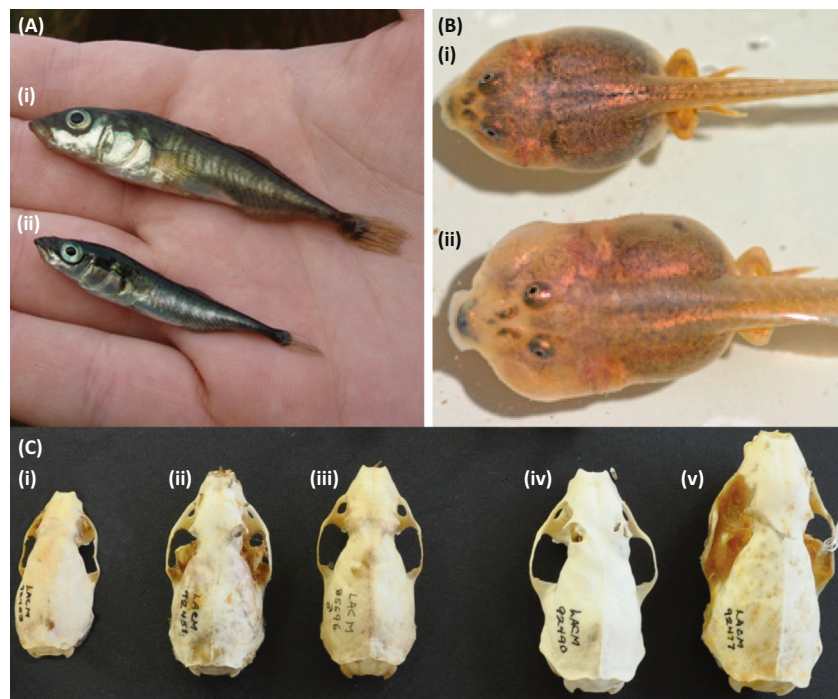

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Box 1. Process and pattern in ECD

The ECD process, as traditionally defined, has two steps: (i) interspecific competition for limited resources creates natural selection that favors those individuals most adept at partitioning resources, which (ii) drives populations to diverge adaptively, either by changing trait means or shrinking trait variance. Interspecific competition is the proximate cause of ECD, creating the resource-use partitioning that is the ultimate cause of phenotypic divergence. The process of ECD is thought to produce two different patterns of displacement: exaggerated divergence in sympatry and trait over-dispersion [2]. Exaggerated divergence in sympatry refers to the situation in which two species are similar in resource use and phenotype in allopatry, but diverge in sympatry. Trait overdispersion results when several sympatric species of the same ecological guild exhibit resource-use phenotypes that are more different from one another than expected by chance, also known as community-wide character displacement (Figure I) [19]. A third pattern, species-for-species matching, is occasionally cited: the replicated, independent evolution of guild structure [2].

Species interactions other than resource competition, however, could produce the same displacement patterns as ECD. One example is apparent competition [43,44]. In this scenario, species A brings its predator into sympatry with species B. To avoid this new predator, species B shifts its resource use and diverges in phenotype. This is an apparent response to competition that is only indirectly related to the presence of species A; the two species do not actually compete. Similarly, the outcomes of other species interactions can mimic ECD, including agonistic interactions [45], intraguild predation [46], and reinforcement [47,48]. Except for reinforcement, the importance of these other interactions to evolutionary divergence between closely related species is not known [2].

Independently of species interactions, however, nonevolutionary events or processes can also create a displacement pattern. Take, for example, the phenomenon of ecological sorting. Due to competitive exclusion, only those species that are different enough from one another may be able to coexist, so a pattern of trait overdispersion might result not from *in situ* coevolution (i.e., ECD), but from the inability of species that have not diverged sufficiently in allopatry to coexist. Similarly, local adaptation along an environmental gradient (e.g., [49]), phenotypic plasticity that mitigates a resource-use shift and precludes an evolutionary response [3], or even random associations [2], can create displacement patterns normally attributed to ECD.

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Figure I. Classic examples of ECD. **(A)** Benthic (i) and limnetic (ii) morphs of the threespine stickleback (*Gasterosteus aculeatus*) have diverged in body shape and body size in sympatry [30]. **(B)** In sympatric ponds, tadpoles of the Mexican spadefoot toad (*Spea multiplicata*) develop into omnivore morphs (i) more frequently and tadpoles of the Plains spadefoot toad (*Spea bombifrons*) develop into carnivore morphs (ii) more frequently than either species does in allopatry [42]. **(C)** Arranged by sex and size, and with sexes treated as separate 'morphospecies', adjacent pairs of morphospecies of the North American weasel guild exhibit approximately equal size ratios in skull and canine size (community-wide character displacement) ([50], but see [49]). Pennsylvanian specimens of (i) a female least weasel (*Mustela nivela*), (ii) a female ermine (*Mustela erminea*), (iii) a male ermine, (iv) a female long-tailed weasel (*Mustela frenata*), and (v) a male long-tailed weasel. Reproduced, with permission, from L. Southcott (A), D. Pfennig (B), and S. Meiri (C).

Wiens [18] noted that the arguments for resource competition were often based on faulty logic, namely that: (i) competition theory predicts differences in resource use; (ii) empirical studies invariably find some difference in resource use; and (iii) these differences are cited as evidence of competition, but without conducting the experiments necessary to establish that competition was responsible. Indeed, to many, the ECD hypothesis had become unfalsifiable [20]: if species differing in resource use were shown to compete, then competition was considered to have caused the divergence, but if they were found not to compete, then the 'Ghost of Competition Past' must have already caused them to diverge to such an extent that they no longer compete [21].

Concomitant with resource competition's perceived decline in importance researchers re-examined the theoretical and evidentiary basis for ECD and found it wanting [15,18–20]. An influential theoretical model showed that

ECD could evolve only under a restricted set of ecological conditions [22], whereas re-analysis of previously published data against statistical null models found that size differences among potential competitors were often no greater than that expected by chance [19,20]. Moreover, a slew of alternative processes were proposed that could create a pattern similar to ECD (Box 1) [2,15]. By the end of the 1970s, few examples of ECD had survived the gauntlet [18–20] and, according to some, 'the notion of coevolutionary shaping of competitor's niches [had] little support' [21].

However, these critiques did not go uncontested, and some researchers quickly came to the defense of interspecific competition and ECD (e.g., [9,23–25]); the resulting spirited debates spawned a wealth of research over the following decade that helped turn the tide of scientific opinion back in favor of ECD. Specifically, experimental studies garnered stronger evidence for the prevalence of interspecific resource competition in nature (reviewed in [23,26,27]), whereas theoretical models with more realistic assumptions about resource use functions and trait variances suggested that the conditions under which ECD could evolve were less restrictive than previously thought (e.g., [28,29]; reviewed in [2]). Moreover, Schluter and McPhail [30] standardized a rigorous approach to the study of ECD by proposing a set of six testable criteria that a strong case of ECD should be able to pass (Box 2), thus addressing the criticisms of the 1970s and early 1980s that workers accepted case studies too readily as evidence of ECD before adequately addressing alternative explanations (Box 1).

However, perhaps most important for the revival of ECD were two reviews by Schluter [2] and Dayan and Simberloff [17] that synthesized an enormous number of studies from the final two decades of the 20th century. These reviews revealed a long list of case studies, some more comprehensive than others, but nearly all providing at least some support for an ECD hypothesis [2,17]; almost every subsequent discussion of ECD has cited one or both of these reviews.

Thus, today, ECD is again widely considered an important agent of diversification in evolution, a view now regularly expressed without reservation or qualification. A quote from a recent paper by Rando *et al.* [31] exemplifies the common sentiment: '[ECD] provides a unifying framework for understanding the evolutionary mechanisms of species coexistence and how diversity is maintained.' Similarly, Goldberg *et al.* [32] write: 'Ecological character displacement is considered to be widespread in nature and an important determinant of morphological and ecological differences between widespread species.'

In contrast to this widespread consensus, however, we argue that the current near-paradigmatic status of ECD is not consistent with the available data. Although the critiques of the 1970s and early 1980s might have been overly dismissive of ECD, we feel that current opinion is overly accepting. As we show in the next section, case studies of ECD put forth since the contentious debates of the 1970s and early 1980s have increased in quantity, but still few ironclad examples exist. For most cases, interspecific competition has not been documented and confounding mechanisms have not been ruled out.

Box 2. Testing ECD

The following six criteria are meant to rule out alternative processes that might lead to an ECD pattern [30]. Falsification of any of the six criteria indicates that observed differences did not result from ECD.

Criterion 1: phenotypic differences between species result from evolved genetic differences among populations in sympatry versus allopatry

Character displacement is an evolutionary hypothesis, yet the number of examples of adaptive phenotypic plasticity continues to increase [51,52]. Thus, the potential for plastic responses to produce a pattern of ECD must be ruled out. Adaptive reaction norms evolved in response to competition (e.g., spadefoot toads [53]), however, are consistent with ECD.

Criterion 2: the character displacement pattern could not arise by chance

Sympatric species might differ in phenotype solely as a result of random processes; thus, appropriate statistical tests must be used to demonstrate that the differences observed are greater than expected by chance.

Criterion 3: the character displacement pattern results from an evolutionary shift rather than from species sorting

Interspecific competition may allow only species that are phenotypically divergent to coexist, but such divergence among sympatric species need not have resulted from *in situ* displacement. Instead, species might have diverged in allopatry for other reasons, only then becoming capable of successfully colonizing and coexisting in regions of sympatry. Such allopatric divergence scenarios must be ruled out as a cause of an ECD pattern.

Criterion 4: changes in phenotype (i.e., character displacement) match ecological shifts in resource use

The theory of ECD suggests that two species diverge in phenotype in response to competitively mediated shifts in resource use. Thus, there should be a clear functional link between the displaced trait and the partitioned resource.

Criterion 5: sites of allopatry and sympatry do not differ appreciably in environment

Species adapt to many biotic and abiotic components of their environment. Adaptation to undetected differences in resource availability between sympatry and allopatry may create an ECD pattern (e.g., [49]). Thus, the possibility that an ECD pattern could be driven by variation in environmental factors other than the presence of competitors should be ruled out.

Criterion 6: evidence shows that similar phenotypes compete for limited resources

The process of ECD is predicated on the occurrence of interspecific resource competition driving phenotypic divergence. However, several other interspecific interactions could cause the evolution of phenotypic differences (Box 1, main text). Demonstration of ECD thus requires ruling out other interactions by demonstrating competition for resources.

Revisiting the evidence for character displacement
A dearth of strong cases

To survey the current state of evidence concerning ECD and determine whether stronger evidence has accumulated over time, we re-examined the reviews of Schluter [2] and Dayan and Simberloff [17], and complemented them with our own survey of ECD studies published since 2005. We measured each putative case of ECD against Schluter and McPhail's criteria [30], which provide a rigorous, standardized, and quantitative way to evaluate the strength of evidence for ECD.

The first observation from these reviews is that there is no shortage of cases documenting a pattern consistent with ECD and satisfying at least one ECD criterion. Schluter [2] identified 64 such cases spanning the years 1964–2000 (Table S1 and Text S1 in the supplementary material

online). Dayan and Simberloff [17] simply reported putative cases of ECD, so we went back and scored each study for the ECD criteria. To do this, we trained our scoring against Schluter's [2] for those studies that were shared by both reviews and then scored the studies unique to Dayan and Simberloff [17] published after 1992. This revealed another 40 cases of ECD, approximately two-thirds of which were published after 2000 (Table S1 in the supplementary material online). Our survey of papers published since 2005 yielded another 40 cases that met at least one criterion (Table S2 and Text S2 in the supplementary material online). Clearly, there are plenty of putative cases of ECD in the literature, but how well supported are they?

Of Schluter's 64 cases, only 20 cases met at least four criteria, and only five cases satisfied all six criteria (Figure 1; *Anolis* lizards once, three-spine sticklebacks twice, and Darwin's finches twice. The sticklebacks and finches are counted twice because they each meet two distinct patterns of ECD; Box 1). Schluter [2,33] concluded that the evidence overall was fairly supportive of an important role for ECD in evolutionary diversification, especially compared with earlier and less rigorous times. He did note, however, that the study of character displacement nevertheless has a long way to go. Key evidence is still lacking in most of the cases that have been described, particularly about the mechanisms' [33].
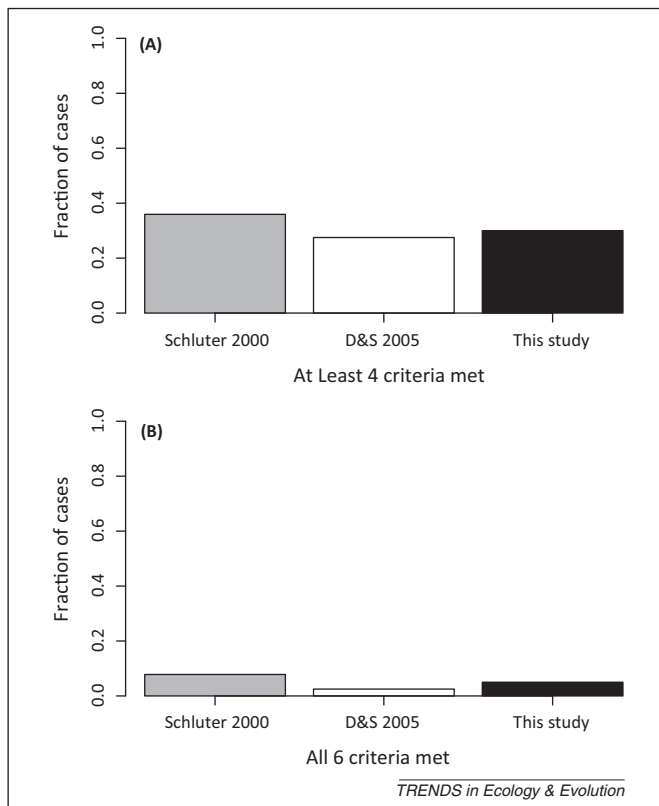

Figure 1. The fraction of cases in Schluter [2], Dayan and Simberloff (D&S) [17], and this study for which at least **(A)** four or **(B)** all six criteria were met. We considered only those cases that met at least one criterion and thus excluded ten additional cases discussed by D&S [17]. In some instances, the same case is considered in more than one review (e.g., stickleback; compare [2], Tables S1 and S2 in the supplementary material online). However, nearly every case was evaluated using only studies from within a given review; only one case was strengthened by combining data across reviews (*Canis* spp.; Table S1 in the supplementary material online). Thus, cases can be considered independent of one another across reviews.

Our scoring of the additional cases reviewed by Dayan and Simberloff [17] provides a similar story, suggesting that the strength of the evidence changed little relative to Schluter [2]. Of their 40 cases that met at least one criterion, only ten met at least four criteria, and only one, the three-spine stickleback, met all six (Figure 1; Table S1 in the supplementary material online).

To determine whether the quality of the evidence has increased in recent years, we reviewed papers published from 2005 to 2012 (Table S2 in the supplementary material online). From those papers, 40 cases emerged that satisfied at least one ECD criterion. Twelve of these cases met at least four criteria and two cases satisfied all six (*Escherichia coli* in a lab study and three-spine stickleback yet again; Figure 1).

In sum, the evidence for ECD has not improved greatly over the two decades since Schluter and McPhail's paper [30], even as the number of purported examples continues to increase. For the 144 cases examined in the three reviews, the average number of criteria met per case is only 3.3, whereas just over 5% of cases meet all six criteria. Moreover, those cases that provide strong support for ECD are restricted to only a few groups (i.e., anoles, sticklebacks, Darwin's finches, spadefoot toads, and carnivore and rodent guilds [2], Tables S1 and S2 in the supplementary material online). Although the number of cases consistent with ECD has grown over the past 20 years, the depth of the data underlying those cases has not.

Assessing individual criteria
How do the individual criteria fare and what can they tell us about the ecological and evolutionary processes generating patterns of ECD (Box 1; Figure 2)? Across all three reviews, for cases in which at least one criterion was met, criterion 2 (chance disproved) and criterion 4 (trait change matching resource use) were met most often (70% and 63% of cases, respectively), suggesting that the observed pattern of phenotypic divergence is often greater than expected if species evolved independently of one another, and that such divergence is usually consistent with changes in resource use.

The mechanism underlying the pattern of divergence, however, is often unclear. Resource competition (criterion 6) is the biotic interaction thought to drive ECD; yet, it is documented in only 17% of cases (Figure 2). Thus, it is possible that displacement patterns might instead have evolved from other interspecific interactions, such as intraguild predation or apparent competition (Box 1). It is also possible, however, that in many cases the existence of an ECD-like displacement pattern may have nothing to do with an evolved response to interspecific interactions. For example, only 41% of cases showed that environmental conditions were similar among sites (criterion 5; Figure 2), so many putative patterns of ECD could be the result of local adaptation to environmental heterogeneity, irrespective of the presence of an interacting competitor. Similarly, *in situ* diversification (criterion 3) was documented in just over half of the cases (Figure 2), so many patterns of ECD might not be an evolutionary outcome of interspecific interactions, but instead an ecological outcome of processes such as dispersal, environmental filtering, and competitive
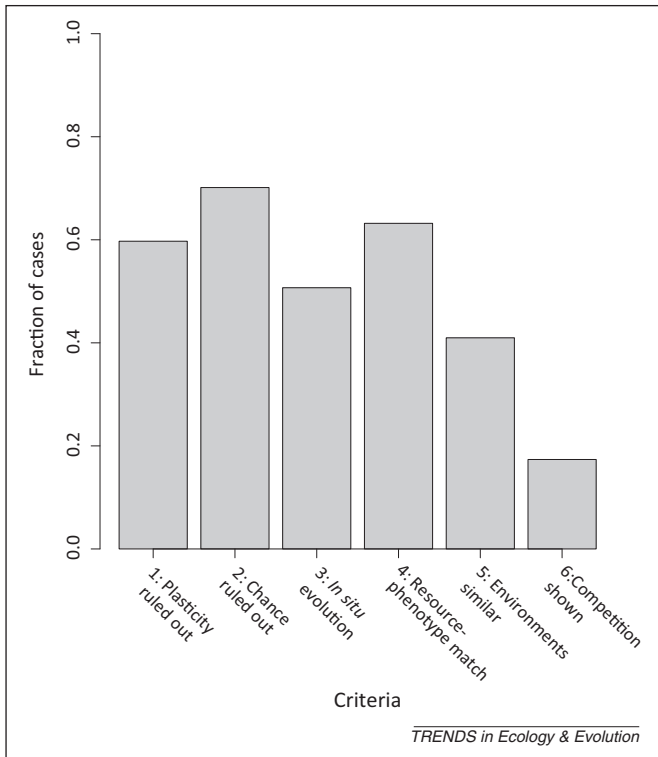
Figure 2. The fraction of cases for which each criterion was met. We pooled the cases from all reviews ([2,17], and this study) for which at least one criterion was met. We note that, following Schluter [2], we assumed a genetic basis for any case of trait overdispersion (Box 1, main text) because these patterns are based on species in sympatry whose differences likely have a genetic component.

exclusion (Box 1). In sum, most putative cases of ECD published during the past 20 years are also consistent with a host of evolutionary and ecological mechanisms other than interspecific resource competition (Box 1).

Glass half full or half empty?
Taken together, the state of the evidence for ECD can be viewed in one of two ways. Under the glass half-full view, Schluter [2,33] was certainly justified in noting that there are many reasonably well supported cases, especially in the context of the backlash of the 1970s–1980s. Most criteria are individually satisfied many times across all cases (Figure 2), and the most recent treatment of character displacement [3] does not place undue emphasis on meeting all the ECD criteria in each case: 'an overly rigorous application of [the six] criteria can be as problematic as not applying the criteria in the first place' (p. 16). Thus, perhaps it is sufficient to have many reasonably supported examples of ECD.

However, we take the glass half-empty view. Despite more than 20 years of emphasis on rigorous examination of ECD hypotheses, we still have only nine cases that meet the gold standard by satisfying all six criteria and, as noted above, these nine cases come from a taxonomically limited portion of the biological world. Moreover, it is difficult to determine the frequency and importance of ECD, because positive cases are likely to be published more often than are negative ones. ECD might indeed be a pervasive process driving evolutionary diversification, and more and more potential examples are being put forward, but the

evidence in support of this proposition is still not overwhelming. At this point, the community needs not more cases of ECD, but better documented ones.

Rapid evolution and the experimental study of evolution in nature
One of the major developments in evolutionary biology over the past 25 years is the recognition that, when directional selection is strong, evolution proceeds rapidly enough to be measurable over ecological time, a realization that spawned the new field of eco-evolutionary dynamics [4,5,34–36]. Neither Schluter [2] nor Dayan and Simberloff [17] noted any studies documenting the evolution of ECD in real time, perhaps not surprising given how recently it was realized that evolution can act rapidly. Nonetheless, since 2005, one such study has appeared: a long-term observational study of Darwin's finches by Grant and Grant [37] documented a shift in beak size by *Geospiza fortis* in response to competition with a recent colonist, *Geospiza magnirostris*, for drought-limited seed resources (Box 3). Observing the evolution of ECD in action provides the benefit of immediately confirming that divergence has occurred *in situ* (criterion 3). If such evolution is repeated in multiple localities, then chance can also be ruled out (criterion 2). Thus, we expect that additional long-term studies similar to that of Grant and Grant [37] will provide stronger evidence for ECD in a variety of organisms. This might be especially true as climate change and species introductions continue to bring together novel sets of potentially interacting species in quasi-experimental settings.

Perhaps even more importantly, however, the reality of rapid evolutionary change suggests the possibility of conducting experiments in nature to test evolutionary hypotheses directly, which the work of Endler, Reznick, and colleagues has done for guppy life-history traits responding to different predator conditions (e.g., [38]). Direct experimental studies of ECD in the field would present the opportunity to observe ECD as it happens, while simultaneously controlling for many factors that have confounded observational studies of ECD (Box 3).

Laboratory biologists, of course, have known for some time that ECD can be observed in real time; indeed, some of the best examples of ECD have come from laboratory experiments with microbes (e.g., [39,40]) and bean weevils [41]. Several groups have used elegant field experimental approaches to estimate the strength of past natural selection that could have led to present-day patterns of ECD, but those studies focused on populations that had already diverged [33,42]. The next step, then, is to pair two or more undiverged competitor species to determine experimentally if and how ECD evolves. We envision a series of experiments carried out in settings that mimic nature as closely as possible (i.e., ponds, small islands, or large enclosures), involving transplants of local native species or taking advantage of recent species invasions that have brought together putative competitors with no recent history of competition.

Although no field experiment will perfectly control for all factors that affect evolution in nature, carefully designed experiments would address the factors that tend

Box 3. Observing ECD in Darwin's finches

In a study of Darwin's finches, Grant and Grant [33] documented the evolution of ECD across one generational boundary. In 2004, depletion of seed resources during a major drought on Daphne Major island brought the medium ground finch, *Geospiza fortis*, into competition with the large ground finch, *Geospiza magnirostris*, for large seeds. *G. fortis* altered its resource use towards smaller seeds available in the seed bank and natural selection drove evolution towards smaller beaks that were more adept at using such seeds (Figure I).

The change in phenotype matched the change in resource use (criterion 4) because the shift to smaller seeds was matched by a shift to a functionally more efficient smaller beak size. This was an evolved response (criterion 1; beak size has high heritability in this population and should respond to strong directional selection) that occurred *in situ* (criterion 3). Three decades of data from the years prior to the 2004 drought served as a control, suggesting that there were no other environmental factors that could have driven the beak size shift (criterion 5). Three lines of evidence directly implicate resource competition for seeds (criterion 6): (i) during a 1977 drought, prior to the colonization of *G. magnirostris*, *G. fortis* relied on large seeds when small seeds were depleted, indicating that the two species can overlap in resource use; (ii) behavioral observations in 2004 suggested that *G. magnirostris* fed on a much higher fraction of large seeds than did *G. fortis*; and (iii) during the 2004 drought, the *G. fortis* population declined to a level lower than during any past drought. Of course, because this was a singular event, Grant and Grant [33] could not rule out the possibility that the decrease in beak size by *G. fortis* during the drought in the presence of *G. magnirostris* was a coincidence (criterion 2) [54], although the wealth of long-term data in this study suggests that that possibility is unlikely.

What advantages did the evolution-in-action approach provide? First, the population was observed evolving in real time, leaving no question of *in situ* phenotypic change (criterion 3). Second, the change was observed to occur during the peak of resource limitation, thus ruling out alternative environmental factors that could drive such a pattern (criterion 5) and directly implicating interspecific competition (criterion 6). These three criteria are the most difficult to meet

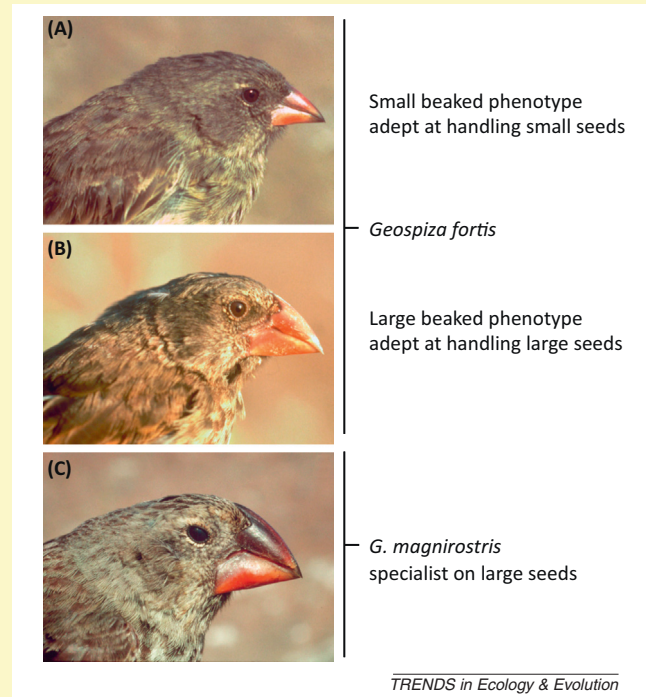with observational data alone (see Figure 2 in main text).

Figure I. Large-beaked *Geospiza fortis* **(B)** were inferior competitors to *Geospiza magnirostris* **(C)** for large seeds during the 2004 drought. As large seeds became depleted in the seed bank, natural selection favored smaller-beaked *G. fortis* **(A)** that were better able to exploit small seeds [37]. Reproduced, with permission, from P. Grant and R. Grant.

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to confound observational studies by controlling variables such as environmental heterogeneity (criterion 5) and pre-existing divergence (criterion 3), by providing replication (criterion 2), and by further clarifying any causal link between the presence of resource competition (criterion 6) and morphological divergence in resource-related traits (criterion 4). Such experiments address these criteria directly and simultaneously. The evolutionary experiment, combined with studies that address phenotypic plasticity (criterion 1) and further explore the mechanistic nature of the species interactions (i.e., confirming or rejecting resource competition as the driving interspecific interaction), will help provide more conclusive evidence concerning whether ECD truly is a major driver of evolutionary diversification and adaptive radiation.

Concluding remarks

Our findings suggest that most cases of ECD are also consistent with other evolutionary and ecological processes. Perhaps not coincidentally, then, in the few cases where support for ECD is unequivocal, we have a good understanding of the underlying eco-evolutionary dynamics: how does resource depletion lead to competition, and then natural selection, then evolutionary divergence (e.g., Darwin's finches; Box 3)? Understanding such dynamics provides a clearer understanding of the ECD and such research can reveal new ECD patterns not currently

predicted by theory (e.g., repeated bouts of competition and divergence [39]). In sum, despite nearly two decades of rigorous study, the jury is still out on the evolutionary importance of character displacement; however, with the advent of eco-evolutionary thinking and the application of evolutionary experiments in the field, the next two decades should lead to a decisive verdict.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2013.02.014.

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