



## Character Displacement

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### Introduction

Character displacement is the phenomenon of species at the same trophic level evolving through natural selection in response to each other because of some costly interaction. It can result in a geographic pattern in which closely related species differ more from each other phenotypically (e.g., in morphology, coloration, or behavior) in areas where their ranges overlap than where their ranges do not overlap. The term “character displacement” was originally used to refer to this geographic pattern, and some biologists continue to use it that way. However, since the 1970s, most researchers have used the term to refer to specific evolutionary processes. Two forms of character displacement, ecological character displacement (ECD) and reproductive character displacement (RCD), are widely recognized. A third form, agonistic character displacement (ACD), was proposed more recently and is gaining recognition. ECD is caused by indirect (exploitative) competition between species for common resources (e.g., food, nesting sites) and usually results in reduced resource overlap (i.e., niche divergence), although, in theory, exploitative competition can also cause niche convergence. RCD is caused by reproductive interference between species (e.g., courtship, mating, hybridization) and invariably reduces the frequency or cost of the interaction. RCD is synonymous with “reinforcement” when it increases the level of reproductive isolation between hybridizing species. RCD can result in patterns of divergence in easily observable traits, such as courtship signals and activity schedules, but it can also involve more subtle changes, such as evolved shifts in sensitivity to heterospecific seminal products. ACD occurs in two modes, divergent and convergent. Convergent ACD is the expected mode when interspecific resource defense is adaptive, while divergent ACD is the expected mode when interspecific resource defense is not adaptive. Convergent ACD is caused by competition between species for mates or other resources and can result in convergence in traits involved in competitor recognition (e.g., agonistic signals, neural templates) and enhancements in interspecific fighting ability (e.g., tactics, weaponry). Divergent ACD is caused by aggressive interference between species and reduces the frequency or cost of the interaction, through divergence in traits involved in competitor recognition or that affect the rate of interspecific encounters. Character displacement processes are widely considered to have a major role in structuring ecological communities, in the generation of phenotypic diversity, and in the evolution of barriers to reproduction between populations, culminating in speciation.

### General Overviews

Pfennig and Pfennig 2012 is the most comprehensive and current book on character displacement and its myriad consequences. Schluter 2000 dispels the once common view that little or no evidence exists for ecological character displacement (ECD), while also identifying gaps in the evidence. Dhondt 2012 provides a succinct review of some well-supported cases of ECD. Grant and Grant 2014 chronicles a thoroughly documented case of ECD in action on a Galapagos island. Coyne and Orr 2004 reviews the tumultuous history of reinforcement theory and the empirical evidence that spurred theoreticians to figure out how to model it correctly. Nosil 2012 examines the roles of both reinforcement and ECD in speciation. Grether, et al. 2013 reviews agonistic character displacement (ACD) theory and the evidence available for this form of character displacement. See also [Ecological Character Displacement](#), [Reproductive Character Displacement](#), and [Agonistic Character Displacement](#).

**Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sunderland, MA: Sinauer.**

Summarizes the “extraordinarily tortuous history” of the theory of reinforcement, the state of empirical research, and alternative explanations for enhanced prezygotic isolation in sympatry (chapter 10).

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**Dhondt, A. A. 2012. *Interspecific competition in birds*. Oxford: Oxford Univ. Press.**

Summarizes key evidence for ECD in selected species, including, but not restricted to, birds (chapter 10).

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**Grant, P. R., and B. R. Grant. 2014. *40 years of evolution: Darwin’s finches on Daphne Major Island*. Princeton, NJ: Princeton Univ. Press.**

Most studies of character displacement are based on comparing populations to make inferences about evolution past. This book synthesizes the results of a different approach: studying evolution as it unfolds. One product of this long-term effort is a fully documented case of ECD in the beak of the finch *Geospiza fortis* after the Island of Daphne Major was colonized by a larger finch, *G. magnirostris* (chapter 7).

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**Grether, G. F., C. N. Anderson, J. P. Drury, et al. 2013. The evolutionary consequences of interspecific aggression. *Annals of the New York Academy of Sciences* 1289.1: 48–68.**

Compares ACD theory with alternative theoretical frameworks, discusses how to distinguish between character displacement processes empirically, and reviews the state of theory and empirical evidence for ACD, concluding that the evidence is substantial but further research is needed.

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**Nosil, P. 2012. *Ecological speciation*. Oxford: Oxford Univ. Press.**

Discusses various aspects of the hypothesis that reproductive isolation evolves in response to species interactions and emphasizes the difficulty of distinguishing reinforcement from ECD (chapters 3, 4, and 6).

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**Pfennig, D. W., and K. S. Pfennig. 2012. *Evolution’s wedge: Competition and the origins of diversity*. Berkeley: Univ. of California Press.**

The only book devoted entirely to character displacement and one of few advanced treatments to cover both reproductive character displacement and ECD. Character displacement is presented as a unifying principle that can be applied to many fundamental questions in biology.

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**Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford: Oxford Univ. Press.**

Places research on ECD into a historical context, reviews the underlying theory, and critically reviews the evidence from observational, predictive and experimental studies (chapter 6). Concludes that the evidence supports a role for ECD in evolutionary diversification, but further research is needed.

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## **Textbooks**

No single textbook covers character displacement adequately. Most ecology and evolution textbooks devote only a page or two to character displacement, and some present an antiquated view of the subject. Most ecology textbooks only mention ecological character displacement (ECD), and most evolution textbooks only mention reproductive character displacement (RCD) or reinforcement. The subject is absent from recent textbooks on animal behavior and behavioral ecology, even though character displacement processes are often driven by, and can involve shifts in, behavior. The best all-around textbook for both ECD and RCD is Futuyma and Kirkpatrick 2017. Additional RCD examples can be found in Barton, et al. 2007 and Bergstrom and Dugatkin 2016. Arguably, the best available ecology textbook for ECD is Cain, et al. 2014, but additional examples can be found in Smith and Smith 2015 and Molles 2016. No textbook yet covers agonistic character displacement. Pfennig and Pfennig 2012 (cited under General Overviews) could be used as an advanced textbook on ECD and RCD, perhaps for graduate courses.

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**Barton, N. H., D. E. G. Briggs, J. A. Eisen, D. B. Goldstein, and N. H. Patel. 2007. *Evolution*. Cold Springs Harbor, NY: Cold Springs Harbor Laboratory.**

Chapter 22 includes a section on reinforcement, with putative examples in broadly sympatric species (*Ficedula* flycatchers, *Drosophila* fruit flies), and a brief discussion of why this evolutionary process is less likely to occur in narrow zones of sympatry. No other forms of character displacement are covered.

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**Bergstrom, C. T., and L. A. Dugatkin. 2016. *Evolution*. 2d ed. New York: Norton.**

Chapter 14 (Species and Speciation) includes a box on secondary contact that defines reinforcement as a process and RCD as a pattern that can result from reinforcement. One example of such a pattern in snails is described and illustrated in figures. No other examples, or theoretical or empirical issues related to character displacement, are covered.

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**Cain, M. L., W. D. Bowman, and S. D. Hacker. 2014. *Ecology*. 3d ed. Sunderland, MA: Sinauer.**

Chapter 12 (Competition) defines character displacement as the evolutionary process of divergent ECD, discusses the challenge of inferring process from pattern, with examples, including an illustration of beak divergence in Darwin's finches. Describes an experimental test for ECD in stickleback fish and cites other field and laboratory experiments, the results of which suggest that ECD occurred. No other character displacement processes are mentioned.

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**Futuyma, D. J., and M. Kirkpatrick. 2017. *Evolution*. 4th ed. Sunderland, MA: Sinauer.**

Introduces ECD in chapter 3 (Natural Selection and Adaptation), with an example of the process in action in Darwin's finches, and discusses the mechanics of ECD in greater detail, with additional examples, in chapter 13 (Interactions among Species). Explains character release, with a sunfish example. Describes community-wide character displacement in weasels. Defines interference competition and describes a case of enhanced interspecific competitive ability in plants. Covers reinforcement in chapter 9 (Species and Speciation), with plant and *Drosophila* examples.

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**Molles, M. C., Jr. 2016. *Ecology: Concepts and applications*. 7th ed. New York: McGraw Hill.**

Chapter 13 (Competition) defines character displacement as a pattern, one example is described briefly (Darwin's finches), and others are mentioned. The rest of the brief section focuses on the problem of inferring evolutionary process from pattern and appears not to have been updated since 1992. The final sentence cites a 2005 paper and notes that the number of demonstrations of character displacement is increasing, but none are described.

**Smith, T. M., and R. L. Smith. 2015. *Elements of ecology*. 9th ed. Boston: Pearson.**

Chapter 13 (Interspecific Competition), in a section on coexistence and resource partitioning, defines character displacement as divergent ECD and details one well-documented case of the process in action: divergence in beak size between two species of Darwin's finches on the island of Daphne Major in the Galapagos. No other character displacement processes are mentioned.

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**Zimmer, C., and D. J. Emlen. 2016. *Evolution: Making sense of life*. 2d ed. Greenwood Village, CO: Roberts.**

Chapter 8 includes a box on ECD with two examples: divergence in beak size in Darwin's finches and divergence in toe pads of *Anolis* lizards after an experimental introduction. The lizard example is not a clear case of ECD, however, because the shift in morphology is not hypothesized to be caused by exploitative resource competition. Chapter 13 devotes one sentence to reinforcement.

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## Journals

Research articles on character displacement are usually published in journals that specialize on ecology, evolutionary biology, or both, although some are published in taxon-specific journals and general science journals. Ecology and evolutionary biology journals include *American Naturalist*, *Ecology*, *Ecology Letters*, *Evolution*, *Journal of Evolutionary Biology*, *Journal of Animal Ecology* and *Proceedings of the Royal Society B*. Reviews on character displacement are often published in *Annals of the New York Academy of Sciences*, *Annual Review of Ecology, Evolution, and Systematics*, and *Trends in Ecology and Evolution*.

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***American Naturalist*. 1867–.**

Known for publishing high-impact research articles, both empirical and theoretical, as well as concept papers and short reviews, in both ecology and evolutionary biology.

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***Annals of the New York Academy of Sciences*. 1824–.**

Annually publishes, *The Year in Evolutionary Biology*, which features invited reviews on topics in evolutionary biology.

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***Annual Review of Ecology, Evolution, and Systematics*. 1970–.**

Publishes broad review articles in ecology, evolutionary biology, and systematics.

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## *Ecology*

A leading journal best known for publishing substantial research articles in ecology. Also publishes several other types of contributions, including notes, concept papers, and book reviews.

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***Ecology Letters*. 1998–.**

A very highly ranked and selective journal that aims to publish the most novel research in "ecology," broadly defined. Publishes primary research articles, short reviews and perspectives.

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### ***Evolution.* 1947–.**

The top journal specializing on evolutionary biology. Publishes research articles, brief communications, commentaries, and book reviews. Has probably published more papers on character displacement than any other journal.

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### ***Journal of Animal Ecology.* 1932–.**

Publishes research articles, reviews, and commentaries on a wide range of topics in animal ecology.

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### ***Journal of Evolutionary Biology.* 1988–.**

A general evolution journal that publishes research articles, brief communications, and reviews.

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### ***Proceedings of the Royal Society B.* 1905–.**

A general biology journal that specializes on publishing novel articles on organismal topics, including ecology, behavior, and evolution. Also publishes reviews and invited perspectives.

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### ***Trends in Ecology and Evolution.* 1986–.**

Publishes invited reviews, letters, and opinion articles in all areas of ecology and evolutionary biology, including behavioral ecology and phylogenetics.

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## **Terminology**

The character displacement literature is a terminological thicket. Even today, the terminology is used in almost as many ways as there are researchers studying character displacement, and some authors use different definitions in different papers. No doubt, much of the terminological variation can be understood in terms of the questions of greatest interest to the writers, but for newcomers to the field, it can be daunting. One disciplinary difference is that most recent papers on ecological character displacement (ECD) define it as an evolutionary process, while many papers on reproductive character displacement (RCD) still define it as a pattern. The geographic patterns produced by the two types of interspecific interactions can be indistinguishable, which makes defining ECD as a process and RCD as a pattern problematic (e.g., see Konuma and Chiba 2007). The term “reinforcement” is used in at least four distinct ways in evolutionary biology, not counting the definition used in psychology, which means that defining RCD as a pattern produced by reinforcement is ambiguous. Attempts to revise the terminology, or certain aspects of it, can be found in many places, including Abrams 1986; Abrams and Cortez 2015; Butlin 1987; Gerhardt 2013; Goldberg and Lande 2006 (cited under Testing for Character Displacement); Grant 1972 (cited under Ecological Character Displacement); Grether, et al. 2013 (cited under General Overviews); Pfennig and Pfennig 2009; Pfennig and Pfennig 2012 (cited under General Overviews); Stuart, et al. 2017; and Taper and Case 1985.

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### **Abrams, P. A. 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theoretical Population Biology* 29:107–160.**

Defines ECD as any genetically based change in resource utilization that is caused by interspecific competition, in agreement with Grant 1972 (cited under Ecological Character Displacement). Explores two-resource species, two-consumer species models and shows that the competing species can diverge, evolve in parallel, or converge in resource use in response to the interaction.

**Abrams, P. A., and M. H. Cortez. 2015. Is competition needed for ecological character displacement? Does displacement decrease competition? *Evolution* 69.12: 3039–3053.**

Presents results from a two-resource species, two-consumer species model based on the Lotka-Volterra interspecific competition equations. Argues, based on the results, that ECD should not be thought of as an adaptive response to reduce interspecific competition but instead as an evolutionary response to the shift in the relative abundances of different resources that results from another species' utilization of the resources.

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**Butlin, R. 1987. Speciation by reinforcement. *Trends in Ecology and Evolution* 2:8–13.**

Considers both reinforcement and RCD to be evolutionary processes caused by interspecific mating, the difference between them being that, under reinforcement, hybrids have non-zero fitness, while under RCD, if hybrids are produced, their fitness is zero. Presents RCD and ECD as comparable processes that occur between species, while reinforcement occurs between populations that have yet to become separate, genetically isolated species.

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**Gerhardt, H. C. 2013. Geographic variation in acoustic communication: Reproductive character displacement and speciation. *Evolutionary Ecology Research* 15:605–632.**

Considers RCD to be a geographic pattern with multiple possible causes, including reinforcement. Reviews putative cases of RCD involving acoustic communication and finds a few robust examples.

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**Konuma, J., and S. Chiba. 2007. Ecological character displacement caused by reproductive interference. *Journal of Theoretical Biology* 247:354–364.**

Shows, with a mathematical model, that selection against reproductive interference can cause divergence in a resource use trait if the trait is also used for mate recognition. Infers that the process of RCD can inadvertently cause sympatric divergence in resource use, which could be interpreted (erroneously) to be a product of ECD.

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**Pfennig, K. S., and D. W. Pfennig. 2009. Character displacement: Ecological and reproductive responses to a common evolutionary problem. *Quarterly Review of Biology* 84:253–276.**

Advocates using process-based definitions. Defines ECD as trait evolution stemming from selection to lessen resource competition and RCD as trait evolution stemming from selection to lessen sexual interactions between species. Considers reinforcement to be a special case of RCD that occurs between hybridizing species.

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**Stuart, Y. E., S. A. Inkpen, R. Hopkins, and D. I. Bolnick. 2017. Character displacement is a pattern: So, what causes it? *Biological Journal of the Linnean Society* 121:711–715.**

Defines character displacement as the geographic pattern of divergence in sympatry, regardless of the cause. Considers ECD, RCD, and agonistic character displacement (ACD) to be among the processes that could produce this geographic pattern. Appears to overlook that character displacement processes are not always expected to cause divergence in sympatry (see Testing for Character Displacement).

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**Taper, M. L., and T. J. Case. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66.2: 355–371.**

Develops and explores quantitative genetic models of ECD. Briefly considers the process-based definition of character displacement of Grant 1972 (cited under Ecological Character Displacement), concluding that it is too difficult to use. Defines character displacement as greater character dissimilarity in sympatry compared to allopatry, regardless of the cause.

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## **Ecological Character Displacement**

The term “character displacement” was coined by Brown and Wilson 1956, but Darwin 1859 deserves credit for the original idea that species that compete for common resources diverge from each other through natural selection. Stuart and Losos 2013 summarizes the rise, fall and resurgence of empirical support for this idea in the late 20th and early 21st century. The evolutionary process of ecological character displacement (ECD) became a central concept in community ecology in the 1960’s but began to lose support in the 1970’s. Reviews such as Grant 1972 and Connell 1980 pointed out flaws in the empirical evidence for ECD, and newly developed statistical approaches failed to distinguish putative character displacement patterns from random patterns (e.g., see Strong, et al. 1979, cited under Community-Wide Character Displacement). An influential theory paper, Slatkin 1980, was widely interpreted to indicate that ECD was only likely to occur under special circumstances. Although subsequent theoretical papers, such as Milligan 1985, were more favorable to ECD, and new empirical examples continued to appear, the perception that the theory lacked empirical support was widespread through the 1990s. Stuart and Losos 2013 credit two papers, Schluter 2000 and Dayan and Simberloff 2005, with moving the pendulum of scientific opinion on ECD in the other direction. Schluter 2000 reviews the empirical literature and finds that while only a few studies meet all established criteria for ECD, many studies meet some criteria and cannot be rejected based on the data available. Dayan and Simberloff 2005 reevaluates the empirical evidence, concludes that the evidence for species pairwise ECD is substantial, and encourages more research on the phenomenon of community-wide (i.e., multispecies) character displacement. Using the same criteria as Schluter 2000, Stuart and Losos 2013 reviews the evidence for ECD, acknowledges that some compelling examples of ECD exist, such as Grant and Grant 2006 (also see Lamichhaney, et al. 2016), but argues that, despite decades of research effort, there are few conclusive studies and that more research is needed before it will be clear whether ECD deserves to be considered, again, to have a major role in structuring ecological communities.

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### **Brown, W. L. Jr., and E. O. Wilson. 1956. Character displacement. *Systematic Zoology* 5:49–64.**

The seminal review of character displacement and still well worth reading. Defines character displacement as a pattern of enhanced divergence in sympatry compared to allopatry. Describes two forms of natural selection that could produce the pattern “ecological displacement” and “reinforcement,” ecological displacement being caused by selection against exploitative resource competition and reinforcement being caused by selection against cross-species mating. Discusses several empirical examples and issues.

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### **Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35.2: 131.**

Argues that species are less likely to coevolve through competition than through interspecific interactions in which one species is dependent on the presence of the other, such as predation and parasitism. Finds little direct evidence that species have evolved in response to each other due to competition and famously refuses to accept the argument that present-day species differences reflect the “ghost of competition past.”

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### **Darwin, C. 1859. *On the origin of species by means of natural selection, or, the preservation of favored races in the struggle for life*. London: John Murray.**

Chapter 4, on natural selection, includes a section on “divergence of character.” Starts by describing divergence between breeds of domesticated animals and then explains how natural selection, combined with differential extinction of lineages of intermediate forms, would result in divergence between species over many generations.

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**Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: The next generation. *Ecology Letters* 8:875–894.**

Reviews the rollercoaster history of ECD, how it came to be a central theory in community ecology through the mid-1970s, the sudden dive in theoretical and empirical support in the late 1970s and early 1980s, and followed by the steady accumulation of rigorous empirical evidence and improved theoretical support, through 2004. Standing issues and priorities for future research on ECD are discussed.

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**Grant, P. R. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society* 4:39–68.**

Often cited for being critical of the evidence for ECD, this review makes at least three other important contributions that are often overlooked: (i) redefining character displacement as a process; (ii) clarifying that character displacement is a different process than character release; and (iii) pointing out that character displacement can generate multiple geographic patterns, including character convergence or no geographic pattern at all.

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**Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. *Science* 313.5784: 224–226.**

Documents, for the first time, the process of ECD occurring in nature, from the initial encounter between competing species to the evolutionary change resulting from directional natural selection caused by food competition. Based on a thirty-three-year study of a species of Darwin's finch on an undisturbed island in the Galapagos.

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**Lamichhaney, S., F. Han, J. Berglund, et al. 2016. A beak size locus in Darwin's finches facilitated character displacement during a drought. *Science* 352.6284: 470–474.**

Shows that a gene correlated with species differences beak size was under strong selection in the character displacement event documented in Grant and Grant 2006, thus providing further evidence that the character shift has a genetic basis.

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**Milligan, B. G. 1985. Evolutionary divergence and character displacement in two phenotypically-variable, competing species. *Evolution* 39.6: 1207–1222.**

Extends the modeling approach of Slatkin 1980 and finds, with more realistic assumptions, evolutionary divergence to be a likely outcome of interspecific competition.

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**Schluter, D. 2000. Ecological character displacement in adaptive radiation. *American Naturalist* 156:S4–S16.**

A concise version of the book chapter on character displacement in Schluter 2000 (cited under General Overviews) and an influential review that helped revive interest in ECD.

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**Slatkin, M. 1980. Ecological character displacement. *Ecology* 61.1: 163–177.**

Clarifies that the process of ECD can be understood in terms of two opposing “pressures”: selection caused by the resource spectrum, which favors convergence between species in resource exploitation traits, and selection caused by the presence of the other species, which favors divergence. Models this process and finds that divergence occurs under some conditions, but under other conditions, the species converge or one goes extinct.

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**Stuart, Y. E., and J. B. Losos. 2013. Ecological character displacement: Glass half full or half empty? *Trends in Ecology & Evolution* 28.7: 402–408.**

Summarizes the rise, fall and resurrection of ECD, examines the empirical studies reviewed in Schluter 2000, Dayan and Simberloff 2005, and forty additional studies and concludes that there are very few conclusive studies. Argues that the pendulum of scientific opinion regarding the importance of ECD has swung too far in the positive direction. Suggests that planned evolutionary experiments are the most promising approach for further testing the theory.

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## **Reproductive Character Displacement**

Reproductive character displacement (RCD) between “good” species has never been very controversial, and there are many undisputed examples, but RCD between species that hybridize (also known as reinforcement) poses some theoretical challenges, as summarized in Coyne and Orr 2004 (cited under General Overviews) and more briefly in Liou and Price 1994. Early mathematical models of reinforcement appeared to show that the process is unlikely to occur, and yet there was good empirical evidence that it does occur in some taxa, most notably Coyne and Orr 1989, which compares pre- and post-zygotic isolation between sympatric and allopatric species pairs of *Drosophila*. Liou and Price 1994 provides a resolution of this predicament, with a genetic model that is more realistic than previous models and simulation results indicating that reinforcement can occur under a wide range of genetic and ecological conditions. For general reviews of reinforcement and its role speciation, see Servedio and Noor 2003 and Coyne and Orr 2004 (cited under General Overviews). Gerhardt 2013 (cited under Terminology) reviews examples of RCD involving acoustic communication. Bacquet, et al. 2015 and Weber, et al. 2016 document macroevolutionary patterns strongly suggestive of RCD in chemical communication in insects. Gac and Giraud 2008 reports a macroevolutionary pattern consistent with RCD in one of two fungal genera studied. Hopkins, et al. 2012 presents genetic evidence for divergent selection in a classic example of RCD in plants. Hudson and Price 2014 argues that RCD more commonly involves narrowing of female mate recognition functions than divergence in the male traits upon which mate recognition is based and provides some evidence for this in birds. For an update on one such example, see Wheatcroft and Qvarnström 2017. Hoskin and Higgie 2010 presents the idea that many species interactions can generate a pattern of RCD, which, in turn, can increase reproductive isolation, not only between species interacting in sympatry but also between displaced and non-displaced conspecific populations.

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**Bacquet, P. M. B., O. Brattström, H. -L. Wang, et al. 2015. Selection on male sex pheromone composition contributes to butterfly reproductive isolation. *Proceedings of the Royal Society B* 282.1804: 2014–2734.**

Surveys wing coloration and pheromone chemical composition in sympatric butterflies of the genus *Bicyclus* in relation to geographic overlap. Finds a repeated pattern of greater divergence in male sex pheromone composition, but not in wing coloration, between sympatric, compared to allopatric species. Further shows that allopatric species in this genus are not younger than sympatric species, which favors RCD over two other processes that could explain the same geographic pattern, namely, species sorting and differential fusion.

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**Coyne, J. A., and H. A. Orr. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43.2: 362–381.**

Analyzes data on over one hundred pairs of closely related *Drosophila* species with known genetic distances and finds a clear pattern strongly suggestive of reinforcement: mating discrimination and post-zygotic isolation evolve in similar rates in allopatric species, but mating discrimination evolves sooner than post-zygotic isolation in sympatric species. A 1997 paper by the same authors analyzes a larger dataset and yields similar findings.

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**Gac, M. L., and T. Giraud. 2008. Existence of a pattern of reproductive character displacement in Homobasidiomycota but not in Ascomycota. *Journal of Evolutionary Biology* 21.3: 761–772.**

Reports a pattern of enhanced premating isolation among sympatric species of one fungus genus (*Homobasidiomycota*) but not in another (*Ascomycota*) and suggests that the difference might be related to a phylogeny-dependent life-history trait. Infers that the geographic pattern in *Homobasidiomycota* is consistent with RCD but also with species sorting and differential fusion.

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**Hopkins, R., D. A. Levin, and M. D. Rausher. 2012. Molecular signatures of selection on reproductive character displacement of flower color in *Phlox drummondii*. *Evolution* 66.2: 469–485.**

Shows, with population genetic analyses, that gene flow and genetic drift cannot account for a classic RCD pattern of flower color variation, thereby strengthening the case for divergent selection. Also provides evidence for a selective sweep in one of two flower color genes studied.

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**Hoskin, C. J., and M. Higgie. 2010. Speciation via species interactions: The divergence of mating traits within species. *Ecology Letters* 13.4: 409–420.**

Argues that a diverse array of species interactions, including reinforcement but also including mimicry, predation, parasitism, and so on can generate a pattern of RCD (i.e., greater divergence of mating traits in sympatry compared to allopatry) and that this can cause populations exposed to the species interaction to diverge from other populations of the same species in mating traits, thereby driving rapid speciation.

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**Hudson, E. J., and T. D. Price. 2014. Pervasive reinforcement and the role of sexual selection in biological speciation. *Journal of Heredity* 105.S1: 821–833.**

Reports that, in birds, divergence in song and plumage traits is a poor predictor of whether species mate assortatively in hybrid zones. Argues that RCD more often occurs through refinements in female mate preferences than by further divergence in the male traits on which mate preferences are based.

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**Liou, L. W., and T. D. Price. 1994. Speciation by reinforcement of premating isolation. *Evolution* 48:1451–1459.**

Develops a multi-locus genetic model of RCD that differs from previous models in that it allows for sexual selection, that is, the evolution of female preference and male trait loci. Uses computer simulations to explore the properties of the model and finds that reinforcement occurs under a wide range of realistic genetic and ecological conditions.

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**Servedio, M. R., and M. A. F. Noor. 2003. The role of reinforcement in speciation: Theory and data. *Annual Review of Ecology and Systematics* 34:339–364.**

Reviews the theory and evidence for reinforcement and concludes that whether reinforcement can or does happen is no longer in question but that its prevalence and importance for speciation remains unclear. Offers suggestions for guiding empirical research.

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**Weber, M. G., L. Mitko, T. Eltz, and S. R. Ramírez. 2016. Macroevolution of perfume signalling in orchid bees. *Ecology Letters* 19.11: 1314–1323.**

Uses phylogenetic models to test for macroevolutionary patterns in orchid bee perfume complexity and species-specificity. Finds a correlation between perfume complexity and the number of congeners in a species' range and evidence that perfume chemistry evolves very rapidly compared to other traits. Interprets these and other results as consistent with RCD, while acknowledging that species sorting could explain the same pattern.

**Wheatcroft, D., and A. Qvarnström. 2017. Reproductive character displacement of female, but not male song discrimination in an avian hybrid zone. *Evolution* 71.7: 1776–1786.**

The latest in a series of papers on RCD in hybridizing *Ficedula* flycatchers. Shows that while male song has converged in sympatry, the ability of females to discriminate between the songs of two species is enhanced in sympatry compared to allopatry.

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## **Agonistic Character Displacement**

Agonistic character displacement (ACD) theory emerged as a synthesis of multiple hypotheses that previously were only partially connected in the literature. Lorenz 1962 describes a process of phenotypic divergence in sympatry caused by selection arising from the costs of interspecific territorial aggression in coral reef fishes and later extends the hypothesis to other taxa. Orians and Willson 1964 proposes that interspecific territoriality in birds is usually a transitory state but that it can be maintained by selection, under certain ecological circumstances. Murray 1971 assumes that interspecific territoriality is misdirected intraspecific territoriality and explores ecological consequences of this and other assumptions. Cody 1969 describes an evolutionary process in which species converge in territorial signals because of the benefits of interspecific territorial defense, and names the process “character convergence.” Cody 1973 develops the character convergence hypothesis further and provides additional examples. Murray 1976 raises multiple objections to the character convergence hypothesis, including that species need not converge in territorial signals to evolve the ability to recognize each other as competitors. Case and Gilpin 1974 and Gill 1974 describe how selection could favor increases in interspecific competitive ability through interference mechanisms, including aggression, and Gill 1974 calls the process “ $\alpha$  selection” (a reference to the parameter  $\alpha$  in early competition models). Grether, et al. 2009 weaves these and related ideas together into the common theoretical framework of ACD and shows, with a mathematical model, that divergence and convergence between species in territorial signals (and competitor recognition) are both plausible outcomes of geographic overlap between species, depending, in part, on the relative levels of interspecific and intraspecific resource competition. Grether, et al. 2009 and Grether, et al. 2013 (cited under General Overviews) review the empirical evidence for ACD. Tynkkynen, et al. 2004 (cited under Testing for Character Displacement) presents evidence for divergent ACD in the wing coloration of *Calopteryx* damselflies. Tobias and Seddon 2009 (cited under Testing for Character Displacement) presents a compelling case of convergent ACD in antbird song. Drury, et al. 2015 extends ACD theory to include evolved responses to reproductive interference and show that levels of reproductive interference predict levels of aggressive interference in *Hetaerina* damselflies.

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**Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences, USA* 71:3073–3077.**

Develops and explores the consequences of an interspecific competition model with separate parameters for exploitation and interference.

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**Cody, M. L. 1969. Convergent characteristics in sympatric species: A possible relation to interspecific competition and aggression. *Condor* 71:223–239.**

Describes striking similarities in coloration and song between sympatric species of birds. Introduces the hypothesis of character convergence and describes the ecological circumstances to which it is likely to apply. Gives detailed examples of character convergence related to interspecific territoriality in several groups of birds. Discusses alternative hypotheses for the same patterns.

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**Cody, M. L. 1973. Character convergence. *Annual Review of Ecology and Systematics* 4:189–211.**

Further explains the underpinnings of the character convergence hypothesis and its relationship to with ecological character displacement. Describes additional putative examples of character convergence in birds.

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**Drury, J. P., K. W. Okamoto, C. N. Anderson, and G. F. Grether. 2015. Reproductive interference explains persistence of aggression between species. *Proceedings of the Royal Society B* 282: 2014–2256.**

Presents simulation results showing that interspecific territoriality can evolve in response to, or be maintained by, selection arising from reproductive interference between species. Presents results from a comparative study showing that levels of reproductive interference predict levels of interspecific territoriality in damselflies.

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**Gill, D. E. 1974. Intrinsic rate of increase, saturation density, and competitive ability. 2. Evolution of competitive ability. *American Naturalist* 108:103–116.**

Shows how the evolution of enhancements in interspecific interference competition ability, termed  $\alpha$ -selection, differs from the concepts of r- and K-selection.

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**Grether, G. F., N. Losin, C. N. Anderson, and K. Okamoto. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews* 84:617–635.**

Synthesizes previous literature on aggression between species. Presents a model of ACD in which agonistic traits diverge or converge, depending on the level of interspecific resource competition. Discusses differences between ACD, RCD, and ECD. Develops criteria for testing whether geographic patterns are likely to have been caused by ACD. Surveys the literature and finds evidence for ACD comparable to the observational evidence for ECD in Schluter 2000 (cited under General Overviews).

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**Lorenz, K. 1962. The function of colour in coral reef fishes. *Proceedings of the Royal Institute of Great Britain* 39:282–296.**

Proposes that much of the diversity of coral reef coloration has arisen as a product of selection against interspecific territorial aggression.

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**Murray, B. G. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52:414–423.**

Develops the misdirected intraspecific aggression hypothesis to explain cases of interspecific territoriality, and patterns of interspecific dominance interactions, in birds.

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**Murray, B. G. 1976. Critique of interspecific territoriality and character convergence. *Condor* 78:518–525.**

Criticizes the convergence hypothesis and disputes the proposed examples in Cody 1969 and Cody 1973.

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**Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. *Ecology* 45:736–745.**

Considers interspecific territoriality to be a costly byproduct of incomplete divergence between species in territorial signals that would usually be selected against but which can be adaptive, and maintained by selection, under certain ecological circumstances, such as structurally simple habitats and highly specialized niches. Interprets known cases of interspecific territoriality in birds as consistent with this hypothesis.

## Testing for Character Displacement

The traditional approach is to start with an observation of geographic pattern consistent with character displacement and then attempt to rule out alternative explanations for the pattern, such as chance, genetic drift, hybridization and species sorting, while also testing for evidence of the hypothesized species interaction. Schluter 2000 (cited under General Overviews) summarizes this approach and lists criteria for carrying out the process of elimination to test for ecological character displacement (ECD). Grether, et al. 2009 (cited under Agonistic Character Displacement) uses a modified version of Schluter's criteria to test for both divergent and convergent agonistic character displacement (ACD). There are two widely recognized problems with this approach, however. First, eliminating all alternative explanations for a geographic pattern can be extremely difficult, as explained in Dayan and Simberloff 2005 (cited under Ecological Character Displacement). Second, character displacement processes need not produce the classic geographic pattern of divergence in sympatry, or any geographic pattern, as pointed out in Grant 1972 (cited under Ecological Character Displacement) and later demonstrated with model simulations in Lemmon, et al. 2004 and Goldberg and Lande 2006. Goldberg and Lande 2006 encourages researchers to test for other geographic patterns indicative of character displacement processes, such as clinal variation along gradients in species relative abundance (e.g., see Tynkkynen, et al. 2004). Another observational approach is to reverse the usual order of investigation; that is, start with evidence for a species interaction (e.g., interspecific aggression), and then test for the predicted geographic pattern, as in Tobias and Seddon 2009. Grether, et al. 2013 (cited under General Overviews) provides additional examples and suggests that this approach is more likely to be successful than starting with a geographic pattern, if the goal is to understand the evolutionary consequences of species interactions. Tobias, et al. 2014 illustrates how multivariate phylogenetic analyses can be used to distinguish between alternative character displacement scenarios in large comparative datasets. Grant and Grant 2006 (cited under Ecological Character Displacement) and Sidorovich, et al. 1999 provide examples of using "natural experiments" to test for character displacement. Planned experiments have been used to test for selection and responses to selection caused by species interactions. For example, Schluter 1994 presents an experimental study of ECD, and Matute 2010 presents an experimental study of reinforcement. Stuart and Losos 2013 (cited under Ecological Character Displacement) advocate the use of replicated, multigenerational field experiments to test for ECD and outline how such experiments could be carried out. For an example, see Stuart, et al. 2014.

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**Goldberg, E. E., and R. Lande. 2006. Ecological and reproductive character displacement on an environmental gradient. *Evolution* 60:1344–1357.**

Uses spatial models to explore geographic patterns produced by character displacement processes. Reports that ECD is less likely than RCD to generate the classic pattern of divergence in sympatry. Surveys the empirical literature and concludes that character displacement studies often lack sufficient sampling to discern the geographic patterns produced by character displacement processes and provides advice on collecting data suitable for testing for such patterns.

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**Lemmon, A. R., C. Smadja, and M. Kirkpatrick. 2004. Reproductive character displacement is not the only possible outcome of reinforcement. *Journal of Evolutionary Biology* 17:177–183.**

Using a stepping-stone model, shows that the process of reinforcement does not necessarily result in the classic character displacement pattern of divergence in sympatry. Cautions that absence of the geographic pattern should not be taken as evidence against the evolutionary process. Also shows that female mate preferences and male display traits need not exhibit the same geographic patterns under reinforcement.

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**Matute, D. R. 2010. Reinforcement of gametic isolation in *Drosophila*. *PLoS Biology* 8.3.**

Documents a putative example of reinforcement in fruit flies, *Drosophila* spp., on an island where the two species hybridize. Also presents results of an experiment in which flies from an allopatric site are maintained in the presence of the other species in the laboratory. Finds that reproductive isolation increased in the experimental laboratory colonies after just four generations, supporting the reinforcement hypothesis.

**Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* 266:798–801.**

Pioneers the use of controlled experiments to test character displacement theory. Uses hybridization to create a population of fish with high levels of morphological variation and measures growth and survival in relation to the presence and absence of one of the parental species. Finds that in the presence of the parental species, individuals most similar to the parental species in morphology had depressed growth rates, as predicted by ECD theory.

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**Sidorovich, V., H. Kruuk, and D. Macdonald. 1999. Body size, and interactions between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe. *Journal of Zoology* 248.4: 521–527.**

Documents body size changes in European mink, polecat, and American mink before and after the study area, in Belarus, was invaded by American mink. Body size divergence was predicted, but instead the species converged in body size over a ten-year period, perhaps because of aggressive interference and resource competition. Whether the changes in body size were genetic or environmental was not determined.

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**Stuart, Y. E., T. S. Campbell, P. A. Hohenlohe, R. G. Reynolds, L. J. Revell, and J. B. Losos. 2014. Rapid evolution of a native species following invasion by a congener. *Science* 346.6208: 463–466.**

Reports that introducing *Anolis sagrei* to islands caused a native lizard species, *Anolis carolinensis*, to shift to using higher perches, probably because of aggressive interactions between the species. Over a twenty-year period, *A. carolinensis* evolved larger toe pads, perhaps in response to the behavioral shift. No such shifts occurred on control islands, where *A. sagrei* was absent.

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**Tobias, J. A., C. K. Cornwallis, E. P. Derryberry, S. Claramunt, R. T. Brumfield, and N. Seddon. 2014. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature* 506:359–363.**

Examines patterns of trait divergence in relation to sympatry in a large clade of territorial birds and finds, after controlling for evolutionary divergence times, an overall pattern of convergence between species in song.

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**Tobias, J. A., and N. Seddon. 2009. Signal design and perception in *Hypocnemis* antbirds: Evidence for convergent evolution via social selection. *Evolution* 63:3168–3189.**

Presents a compelling case of song convergence between interspecifically territorial antbirds.

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**Tynkkynen, K., M. J. Rantala, and J. Suhonen. 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *Journal of Evolutionary Biology* 17:759–767.**

Reports a pattern of clinal variation in the wing spot size of male *Calopteryx splendens* along a gradient of variation the relative abundance of *Calopteryx virgo*. Also shows that *C. virgo* males are more aggressive to *C. splendens* males with larger wing spots. Hypothesizes that the geographic pattern is a consequence of selection to reduce interspecific aggression (i.e., divergent ACD).

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## Community-Wide Character Displacement

The term “community-wide character displacement,” which first appeared in Strong, et al. 1979, refers to a pattern of morphological divergence between sympatric species, caused by interspecific competition, in an entire community, assemblage, or feeding guild. The

classic evidence for community-wide character displacement is a pattern of equal body size ratios between adjacent species in a community, an idea that can be traced back to Hutchinson 1959 and is known as Hutchinson's rule. Ecological character displacement (ECD) is one process that could produce such a pattern, but differential colonization and extinction (collectively referred to as "species sorting") and geographic clines can produce similar patterns. Most published studies analyze patterns of morphological variation in relation to range overlap and focus on the question of whether a pattern consistent with community-wide character displacement exists. Strong, et al. 1979 introduces the approach of comparing trait dispersion patterns to null model simulations, bringing a new level of quantitative rigor to the field. However, Hendrickson 1981 analyzes the same data as Strong, et al. 1979 and obtains different results. For a more recent application of the null model approach, see Marchinko, et al. 2004. Dayan and Simberloff 2005 (cited under Ecological Character Displacement) observes that the literature on community-wide character displacement is dominated by a small number of taxonomic groups. Studies on mammalian carnivores are particularly common; representative examples include Dayan, et al. 1990; Werdelin 1996; Davies, et al. 2007; and Meiri, et al. 2011. Werdelin 1996 and Huntley, et al. 2008 illustrate the use of paleontological (i.e., fossil) data to test for community-wide character displacement. Many papers reporting community-wide character displacement end with a discussion of how the patterns could have been produced by multiple processes and that ecological data are needed to verify that competition occurs. Such follow-up studies remain rare, but there are a few examples. McDonald 2002 compiles data on the diets of weasels and other mustelids, a group previously shown to exhibit patterns of community-wide character displacement in tooth and body size, and finds no evidence for the predicted dietary niche divergence. Meiri, et al. 2011 shows that patterns of community-wide character displacement in weasels disappear after taking geographic clines into account, which suggests that dietary niche divergence was not predicted, after all.

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**Davies, J. T., S. Meiri, T. G. Barraclough, and J. L. Gittleman. 2007. Species co-existence and character divergence across carnivores. *Ecology Letters* 10.2: 146–152.**

Carries out a phylogenetic sister-taxa analysis of terrestrial mammalian carnivores and finds that tooth size is the strongest predictor of range overlap, that sister species that differ most in tooth size have the greatest range overlap, and that the pattern persists after controlling for time since divergence. Concludes that the overall results are consistent with both ECD and species sorting but that specific aspects of the results are indicative of ECD.

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**Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1990. Feline canines: Community-wide character displacement among the small cats of Israel. *American Naturalist* 136.1: 39–60.**

Frequently cited as evidence for community-wide character displacement. Reports regular spacing of canine diameters, but no such pattern in skull lengths, between morphospecies in the small-felid guild of Israel. Treats the sexes as separate morphospecies, due to pronounced sexual dimorphism. Cautions that the ecology of the species is poorly known and that direct evidence for interspecific food competition is lacking.

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**Hendrickson, J. A., Jr. 1981. Community-wide character displacement reexamined. *Evolution* 35.4: 794–809.**

Reanalyzes two island bird data sets in Strong, et al. 1979 using improved statistical tests and obtains different results. Rejects the null hypothesis of no community-wide character displacement for one morphological trait in one group of bird communities and for two morphological traits in the other but does not interpret the results as strong evidence for character displacement.

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**Huntley, J. W., Y. Yanes, M. Kowalewski, et al. 2008. Testing limiting similarity in Quaternary terrestrial gastropods. *Paleobiology* 34.3: 378–388.**

Tests for patterns suggestive of ECD and community-wide character displacement in longitudinal and cross-sectional samples of fossil gastropods over a 42,500-year period. Finds only a transient pattern of community-wide character displacement in body size. Cautions that standard cross-sectional studies of character displacement only provide evolutionary "snapshots" and can be misleading.

**Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93.870: 145–159.**

A wide-ranging essay that, among other topics, considers how different the niche of species needs to be for them to coexist in the same community. Reports finding consistent ratios (1.1–1.4) of metric characters (e.g., skull length, bill length) between pairs of species within guilds. Discusses this finding in relation to ECD and species sorting.

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**Marchinko, K. B., M. T. Nishizaki, and K. C. Burns. 2004. Community-wide character displacement in barnacles: A new perspective for past observations. *Ecology Letters* 7.2: 114–120.**

Tests for community-wide character displacement in two communities of barnacles using null models. Finds a pattern of interspecific spacing consistent with ECD in feeding leg lengths but not in shell morphology. Cautions that the competitive mechanism is unknown and that the pattern could have been caused by species sorting as opposed to selection.

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**McDonald, R. A. 2002. Resource partitioning among British and Irish mustelids. *Journal of Animal Ecology* 71.2: 185–200.**

Synthesizes results of diet studies of mustelids in the British Isles and finds no evidence to support the hypothesis that previously reported character displacement patterns are associated with dietary niche divergence. Suggests that interspecific aggression might account for character displacement in canine diameters but does not clarify the hypothesized selective mechanism.

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**Meiri, S., D. Simberloff, and T. Dayan. 2011. Community-wide character displacement in the presence of clines: A test of Holarctic weasel guilds. *Journal of Animal Ecology* 80.4: 824–834.**

Explains how geographic clines can obscure character displacement patterns or generate patterns that can be confused with character displacement. Corrects for clinal variation while testing for character displacement in two three-species weasel guilds and finds that a previously reported pattern of character divergence is replaced by a pattern of character convergence in sympatry. Discusses possible reasons for the absence of divergent character displacement in weasels.

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**Strong, D. R., L. A. Szyska, D. S. Simberloff, and A. Szyska. 1979. Test of community-wide character displacement against null hypotheses. *Evolution* 33.333: 897–913.**

Pioneers the use of computer algorithms to compare null communities to actual communities. Analyzes morphological dispersion in three insular avifauna communities and finds little evidence that the actual communities have greater morphological dispersion than randomly assembled communities. Finds a pattern of morphological convergence, not divergence, in Galapagos island finch communities.

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**Werdelin, L. 1996. Community-wide character displacement in Miocene hyaenas. *Lethaia* 29.1: 97–106.**

Documents patterns of dental parameters in fossil hyenas and finds statistical evidence for roughly equal ratios of lower carnassial lengths and blade lengths between sympatric species in the late Miocene. Compares the results to a similar pattern in modern canids.

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## **Character Displacement and Speciation**

All character displacement processes can, in principle, contribute to speciation in two basic ways: (i) by increasing the level of pre- or

post-zygotic reproductive isolation between the interacting populations themselves and (ii) by increasing the level of pre- or post-zygotic reproductive isolation between one or both interacting populations and allopatric populations of the same species. Most papers on character displacement and speciation focus on the first of these possibilities and, more specifically, on how selection against hybrids can increase the level of pre-zygotic reproductive isolation between the interacting populations (i.e., reinforcement). The idea that character displacement can lead to reproductive isolation between allopatric conspecific populations is not new but recently has received renewed attention and empirical support. Ortiz-Barrientos, et al. 2009 names the phenomenon of reinforcement incidentally resulting in reproductive isolation between allopatric populations “cascade reinforcement.” Studies reporting evidence for cascade reinforcement include Hoskin, et al. 2005; Kozak, et al. 2015; Lemmon 2009; and Rice and Pfennig 2010. For other examples, see reviews in Kozak, et al. 2015; Nosil 2012 (cited under General Overviews); and Ortiz-Barrientos, et al. 2009. Seehausen and Schluter 2004 proposes that a type of divergent agonistic character displacement (ACD) arising from color-based aggression biases is an important driver of speciation in African lake cichlids. Qvarnström, et al. 2012 describes several different mechanisms through which ACD could increase the level of reproductive isolation between populations. For example, population divergence in male phenotypes through ACD could cause in divergence in female mate recognition through sexual imprinting. When ecological character displacement (ECD) causes allopatric conspecific populations to diverge in resource-use traits, interpopulation hybrids can be poorly adapted to either environment. For a demonstration of this kind of post-mating isolation, see Pfennig and Rice 2007. For an example of ECD contributing to reproductive isolation between sympatric populations, see Boughman, et al. 2005. Chapter 8 in Pfennig and Pfennig 2012 (cited under General Overviews) is a highly accessible review of speciation and ways in which RCD and ECD might contribute to speciation.

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**Boughman, J. W., H. D. Rundle, and D. Schluter. 2005. Parallel evolution of sexual isolation in sticklebacks. *Evolution* 59:361–373.**

Presents evidence that body size and male coloration diverge in predictable directions between replicate pairs of sympatric stickleback populations, and that this reduces the rate of interpopulation mating. Body size divergence was previously shown to arise from ECD in this system.

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**Hoskin, C. J., M. Higgie, K. R. McDonald, and C. Moritz. 2005. Reinforcement drives rapid allopatric speciation. *Nature* 437.7063: 1353–1356.**

Presents evidence that reinforcement has increased the level of reproductive isolation not only between sympatric populations of frogs of different lineages but also between allopatric populations of frogs of the same lineage (i.e., cascade reinforcement).

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**Kozak, G. M., G. Roland, C. Rankhorn, A. Falater, E. L. Berdan, and R. C. Fuller. 2015. Behavioral Isolation due to Cascade Reinforcement in *Lucania Killifish*. *American Naturalist* 185.4: 491–506.**

Tests for reinforcement and cascade reinforcement of both male and female mate preferences in killifish. Finds evidence for reinforcement of both male and female mate preferences in both species and evidence for cascade reinforcement within one of the species.

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**Lemmon, E. M. 2009. Diversification of conspecific signals in sympatry: Geographic overlap drives multidimensional reproductive character displacement in frogs. *Evolution* 63.5: 1155–1170.**

Reports patterns consistent with reinforcement in male calls in two species of frog. Presents evidence that the shifts in calls reduce the probability of the species hybridizing in sympatry and has resulted in incipient reproductive isolation between conspecific populations of one of the species (i.e., cascade reinforcement).

**Ortiz-Barrientos, D., A. Grealy, and P. Nosil. 2009. The genetics and ecology of reinforcement: Implications for the evolution of prezygotic isolation in sympatry and beyond. *Annals of the New York Academy of Sciences* 1168:156–182.**

Reviews the theory and evidence for reinforcement. Names and formalizes the “cascade reinforcement” hypothesis. Concludes that progress has been made but important gaps in the evidence for reinforcement remain.

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**Pfennig, D. W., and A. M. Rice. 2007. An experimental test of character displacement’s role in promoting postmating isolation between conspecific populations in contrasting competitive environments. *Evolution* 61.10: 2433–2443.**

Tests for incipient post-zygotic reproductive isolation between populations of toads from two different competitive environments, namely, the presence or absence of a competing species. Reports that tadpoles resulting from between-environment population crosses had lower growth rates than tadpoles from within-environment population crosses and that the growth rate differences were greatest in the presence of competitors.

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**Qvarnström, A., N. Vallin, and A. Rudh. 2012. The role of male contest competition over mates in speciation. *Current Zoology* 58.3: 493–509.**

Examines the role of male mate competition in speciation. Treats ACD as a type of RCD caused by interspecific competition for mates. Identifies several ways in which ACD could reduce gene flow between populations, most of which have substantial indirect support but remain to be tested directly.

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**Rice, A. M., and D. W. Pfennig. 2010. Does character displacement initiate speciation? Evidence of reduced gene flow between populations experiencing divergent selection. *Journal of Evolutionary Biology* 23.4: 854–865.**

Tests for and finds a reduction in gene flow between populations of toads in two different selection regimes, namely the presence or absence of a congener. Reviews previous research providing evidence for both ECD and RCD in this species pair. Interprets the results as consistent with the hypothesis that character displacement can initiate speciation.

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**Rundle, H. D., and P. Nosil. 2005. Ecological speciation. *Ecology Letters* 8:336–352.**

Reviews the theory and evidence for ecological speciation. Considers ECD and RCD to be processes that could drive speciation but finds no direct evidence that ECD has contributed to reproductive isolation.

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**Seehausen, O., and D. Schluter. 2004. Male-male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proceedings of the Royal Society B* 271:1345–1353.**

Proposes that negatively frequency-dependent selection on male coloration arising from aggression biases drives color divergence within and between species and promotes speciation in African lake cichlids. Presents data consistent with this hypothesis.

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## **Character Displacement, Phenotypic Plasticity, and Learning**

Many organisms exhibit phenotypically plastic responses to the presence of other species. In cases where species compete for resources or interfere with each other reproductively or aggressively, such plastic responses can be in the same direction that character displacement theory predicts. For example, Pfennig and Martin 2010 describes how two species of spadefoot toads differ from each

other in sympatry in a way that reduces resource competition. In one of the species, the character shift involves genetic differences between allopatric and sympatric populations, but in the other species, the character shift is entirely a plastic response, mediated through maternal effects. Pfennig and Martin 2009 discusses how maternal effects might contribute to ecological character displacement (ECD), particularly in the early stages. Learning is another, large category of phenotypically plastic responses that can mediate interspecific interactions. For example, Laiolo 2012 shows that song learning mediates interspecific territorial interactions in larks; and Svensson, et al. 2010 shows that female damselflies learn to avoid mating with heterospecific males. Grant and Grant 2010 documents a shift in the song of two finch species, mediated by learning, after a new species enters the community. Plants also exhibit phenotypically plastic responses to the presence of competitors (e.g., see Table 2.1 in Pfennig and Pfennig 2012, cited under General Overviews). Based on the standard criteria for demonstrating character displacement, population differences in the shifted character must be shown to have a genetic basis (e.g., see Schluter 2000, cited under General Overviews). Robinson and Wilson 1994 points out that this criterion, or the way it is traditionally applied, is too restrictive, because the ability to exhibit a phenotypically plastic response could itself be an evolved response to past interspecific interactions. Grether, et al. 2013 (cited under General Overviews) argues that it is still necessary to provide evidence that the plastic response has evolved in response to the species interaction (e.g., that populations differ genetically in the norm of reaction). Losos, et al. 2000; Pfennig and Pfennig 2012; and Robinson and Pfennig 2013 discuss the hypothesis, and evidence, that plastic responses to heterospecific competitors can lead to the evolution of genetic differences between populations. Stuart, et al. 2014 (cited under Testing for Character Displacement) report evidence from an introduction experiment of a plastic behavioral response to heterospecifics leading to the evolution of a genetically based morphological shift in *Anolis* lizards.

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**Grant, B. R., and P. R. Grant. 2010. Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences* 107.47: 20156–20163.**

Documents changes in the songs of Darwin's finches over a thirty-two-year period, showing that the songs of two species shifted after a dominant third species with a similar song frequency colonized the island. Alternative explanations for the song shifts are considered and the hypothesis that best accounts for the results is based on the "peak shift" phenomenon in which learning is biased in a direction away from a negative stimulus.

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**Laiolo, P. 2012. Interspecific interactions drive cultural co-evolution and acoustic convergence in syntopic species. *Journal of Animal Ecology* 81.3: 594–604.**

Documents song convergence via learning in sympatry and the effects of this on interspecific territorial interactions between two species of *Galerida* larks.

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**Losos, J. B., D. A. Creer, D. Glossip, et al. 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* 54.1: 301–305.**

Shows that raising *Anolis* lizards on perches of different diameters affects hindlimb development. Hypothesizes that this phenotypically plastic response facilitated adaptive divergence between *Anolis* species in leg length (i.e., ECD).

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**Pfennig, D. W., and R. A. Martin. 2009. A maternal effect mediates rapid population divergence and character displacement in spadefoot toads. *Evolution* 63:898–909.**

Shows that the shift in the ratio of two trophic morphs of spadefoot toad tadpoles between allopatric and sympatric sites is caused by a maternal condition effect. Discusses the role of maternal effects in ECD.

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**Pfennig, D. W., and R. A. Martin. 2010. Evolution of character displacement in spadefoot toads: Different proximate mechanisms in different species. *Evolution* 64.8: 2331–2341.**

Shows that the proximate basis of a character shift differs between two species of spadefoot toads.

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**Pfennig, D. W., and K. S. Pfennig. 2012. Development and evolution of character displacement. *Annals of the New York Academy of Sciences* 1256:89–107.**

Develops the plasticity-first hypothesis for character displacement and suggests ways that the hypothesis could be tested.

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**Robinson, B. W., and D. W. Pfennig. 2013. Inducible competitors and adaptive diversification. *Current Zoology* 59.4: 537–552.**

Reviews theory and evidence that resource competition leads to the evolution of phenotypically plastic responses to competitors, which, in turn, expose the populations to new selection regimes that further promote adaptive diversification.

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**Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: A neglected literature. *American Naturalist* 144.4: 596–627.**

Reviews the literature, searching for previously unreported cases of ECD and character release in fishes, and finds several new examples. Discusses the traditional criterion that differences between sympatric and allopatric populations must be genetic to consider the character shift to be due to character displacement and concludes that this criterion is too restrictive.

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**Svensson, E. I., F. Eroukhmanoff, K. Karlsson, A. Runemark, and A. Brodin. 2010. A role for learning in population divergence of mate preferences. *Evolution* 64.11: 3101–3113.**

Shows that in sympatry, female *Calopteryx splendens* damselflies learn, through mating experience, to avoid mating with heterospecific males, whereas in allopatry experimentally introduced heterospecific males are preferred.

[back to top](#)