



Convergent Evolution

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Introduction

Convergent evolution is typically defined as the repeated evolution of similar traits in independent evolutionary lineages inhabiting similar environments. Convergence has played a key role in evolutionary biology in at least three ways. First, convergent evolution provides natural replicates that can be used to address general questions in the field that transcend the limitations of studying single evolutionary events. Second, convergent evolution has notoriously confounded studies that attempt to estimate phylogenetic relationships among species; only by identifying convergent traits can we hope to uncover the shared derived characters that denote historical relationships among species. Finally, the overall prevalence of convergence speaks to the long-term predictability of evolution. Studies of convergent evolution have a long history in both paleontology and phylogenetic systematics, and remarkable examples of the convergent evolution of traits, organisms, and even whole communities have been identified and described. However, the interpretation of convergent evolution is not without controversy. Some view convergent evolution as ubiquitous across the tree of life, thus marking the predictability of evolution even over long time scales. Others view convergent evolution as a rare fluke of evolution, and believe that evolution is dominated by chance events. Additionally, some evolutionary biologists view convergent evolution as the result of deterministic natural selection and adaptation, while others see the mark of genetic and/or developmental constraints. Recent advances in evolutionary developmental biology and genomics have given us a wealth of new information about the mechanisms of convergent evolution. This work has focused on the genetics of adaptation, and in separating cases of parallelism—a special case of convergent evolution where independent evolutionary lineages evolve the same trait using the same genes and/or developmental pathways—from convergence, where lineages evolve similar traits using unique developmental pathways.

General Overviews

Review papers and textbooks, such as Futuyma 2013 tend to focus on how one can identify convergent evolution and on presenting particularly compelling examples of convergence or lack thereof. A few authors have attempted to make broad generalizations based on these observations. Gould 1990 argues that evolution is dominated by historical contingency, while Conway Morris 2004 (see also papers in Conway Morris 2008) and McGee 2011 argue that convergence is ubiquitous. Conway Morris 2004 argues for both adaptive and constraint-based mechanisms for convergence, while McGee 2011 leans most heavily on constraints as a mechanism. Losos 2011 is a nice early-21st-century review paper that carefully describes what we can (and cannot) learn from studies of convergent evolution.

Conway Morris, Simon. 2004. *Life's solution: Inevitable humans in a lonely universe*. Cambridge, UK: Cambridge Univ. Press.

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This book catalogues convergent evolution across a wide range of taxa and time scales. Conway Morris argues that convergence is common and that the universe is predictable—even going so far as to argue for the inevitability of the evolution of our own species.

[Find this resource:](#)

Conway Morris, Simon, ed. 2008. *The deep structure of biology: Is convergence sufficiently ubiquitous to give a directional signal?* West Conshohocken, PA: Templeton Foundation.

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This edited volume includes chapters on a wide range of topics in convergent evolution, including both empirical results and philosophical considerations.

[Find this resource:](#)

Futuyma, Douglas J. 2013. *Evolution*. Sunderland, MA: Sinauer.

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This now-classic textbook discusses convergent evolution explicitly in Chapter 3 (Patterns of Evolution), but the topic also appears in several other contexts and chapters.

[Find this resource:](#)

Gould, Steven J. 1990. *Wonderful life: The Burgess Shale and the nature of history*. New York: W. W. Norton.

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Gould's classic book uses the Burgess Shale—a fossil field with exceptional preservation of the soft body parts of an astounding assortment of middle Cambrian fossils—as an argument in favor of the role of chance and contingency in evolution.

[Find this resource:](#)

Losos, Jonathan B. 2011. Convergence, adaptation, and constraint. *Evolution* 65:1827–1840.

DOI: 10.1111/j.1558-5646.2011.01289.x [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

An excellent review focusing on what we can (and cannot) conclude from examples of convergent evolution. Losos argues that other forms of evidence (beyond phenotypic similarity) are needed to distinguish adaptive convergence from convergence due to genetic or developmental constraint.

[Find this resource:](#)

McGee, George. 2011. *Convergent evolution: Limited forms most beautiful*. Cambridge, MA: MIT Press.

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McGee reviews a multitude of examples of convergent evolution, from genes to phenotypes to behavior, and argues that the ubiquity of convergent evolution is mainly due to functional and developmental constraints.

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Models and Statistics

Mathematical models and statistical analysis have played a key role in our understanding of convergent evolution. Both models and simulations have been applied to determine when we should expect to see convergent evolution. Orr 2005; Chevin, et al. 2010; and Szendro, et al. 2013 describe such tests at the genetic level, and Stayton 2008 at the level of species' phenotypes. A battery of statistical tests have also been created to detect and describe convergent evolution of genes, such as in Zhang and Kumar 1997, and in traits as described in Harmon, et al. 2005; Stayton 2006; and Ingram and Mahler 2013.

Chevin, Luis-Miguel, Guillaume Martin, and Thomas Lenormand. 2010. Fisher's model and the genomics of adaptation: Restricted pleiotropy, heterogeneous mutation, and parallel evolution. *Evolution* 64:3213–3231.

DOI: 10.1111/j.1558-5646.2010.01058.x [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Chevin, et al. present a multivariate model of adaptation where mutations in a set of genes have pleiotropic effects on a set of traits. They use this model to calculate the probability of parallel evolution of genes, and relate this to the amount and type of pleiotropy in the model.

[Find this resource:](#)

Harmon, Luke J., Jason J. Kolbe, James M. Cheverud, and Jonathan B. Losos. 2005. Convergence and the multidimensional niche. *Evolution* 59:409–421.

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This paper uses multivariate statistical approaches to analyze convergent evolution in *Anolis* lizards. The authors compare the extent and pattern of multivariate convergent evolution across a range of distinct sets of characters, and find that patterns of convergence differ between these character sets.

[Find this resource:](#)

Ingram, Travis, and D. Luke Mahler. 2013. SURFACE: Detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion. *Methods in Ecology and Evolution* 4:416–425.

DOI: 10.1111/2041-210X.12034 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Describes an innovative statistical approach using continuous phenotypic characters to identify sets of convergently evolved species on a phylogenetic tree.

[Find this resource:](#)

Orr, H. Allen. 2005. The probability of parallel evolution. *Evolution* 59:216–220.

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In this paper, Orr derives the probability of parallel evolution (the substitution of the same beneficial mutation) for two populations living in identical environments. The probability of parallel evolution depends on the number of different beneficial mutations available to the population.

[Find this resource:](#)

Stayton, C. Tristan. 2006. Testing hypotheses of convergence with multivariate data: Morphological and functional convergence among herbivorous lizards. *Evolution* 60:824–841.

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Proposes methods for quantifying convergent evolution using multivariate comparative data.

Find this resource:

Stayton, C. Tristan. 2008. Is convergence surprising? An examination of the frequency of convergence in simulated datasets. *Journal of Theoretical Biology* 252:1–14.

DOI: 10.1016/j.jtbi.2008.01.008 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A simulation study that shows that convergent evolution can be surprisingly common even when characters are simulated using simple, nondeterministic random walk models.

Find this resource:

Szendro, Ivan G., Jasper Franke, J. Arjan, G. M. de Visser, and Joachim Krug. 2013. Predictability of evolution depends nonmonotonically on population size. *Proceedings of the National Academy of Sciences of the United States of America* 110:571–576.

DOI: 10.1073/pnas.1213613110 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

The authors use a model of evolution on an empirically derived fitness landscape from a fungus to investigate the repeatability of adaptive change in replicate populations. They find that the probability of convergent evolution depends in a complex way on population size.

Find this resource:

Zhang, Jianzhi, and Sudhir Kumar. 1997. Detection of convergent and parallel evolution at the amino acid sequence level. *Molecular Biology and Evolution* 14:527–536.

DOI: 10.1093/oxfordjournals.molbev.a025789 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

This paper introduced an approach for identifying convergent and parallel substitutions in amino acids in a phylogenetic context, and to determine whether the number of such changes is greater than expected by chance.

Find this resource:

Phylogenetics and Homoplasy

Convergent evolution leads to patterns of homoplasy—similarities among taxa that are not due to common descent. Homoplasy, in turn, is a major complicating factor in the process of reconstructing phylogenetic trees from character data as demonstrated in Moore and Willmer 1997. Wake, et al. 2011 reviews how identifying convergent evolution has long been a concern for those interested in reconstructing phylogenetic trees. Phylogenetics is now dominated by molecular data and statistical inference, which has two main consequences. First, as molecular trees become better resolved, we can identify putative cases of character convergence with more certainty. Mueller, et al. 2004 offers a particularly good example of this. Second, the conflict between molecular and morphological phylogenetics has, in some cases, become more and more pronounced. In the case of squamates, for example, Gauthier, et al. 2012 shows that a well-supported molecular phylogenetic tree requires that we hypothesize extensive (and previously unsuspected) convergent evolution of phenotypic characters across a wide range of clades of snakes and lizards.

Gauthier, Jacques A., Maureen Kearney, Jessica A. Maisano, Olivier Rieppel, and Adam D. B. Behlke. 2012. Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History* 53:3–308.

DOI: 10.3374/014.053.0101 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

There is a long history of conflict between molecular and morphological phylogenetic hypotheses for squamates (snakes and lizards). Gauthier, et al. discuss the extreme amounts of homoplasy (convergence) that are required to model the morphological character data on the molecular tree.

[Find this resource:](#)

Moore, Janet, and Pat Willmer. 1997. Convergent evolution in invertebrates. *Biological Reviews of the Cambridge Philosophical Society* 72:1–60.

DOI: 10.1017/S0006323196004926 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

This paper discusses issues and examples of convergent evolution causing homoplasy in invertebrate systematics. Includes a nice general discussion of issues of convergent evolution in systematics.

[Find this resource:](#)

Mueller, Rachel L., J. Robert Macey, Martin Jaekel, David B. Wake, and Jeffrey L. Boore. 2004. Morphological homoplasy, life history evolution, and historical biogeography of plethodontid salamanders inferred from complete mitochondrial genomes. *Proceedings of the National Academy of Sciences of the United States of America* 101:13820–13825.

DOI: 10.1073/pnas.0405785101 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Mueller, et al. use twenty-seven complete mitochondrial genome sequences to reconstruct a phylogenetic tree of plethodontid salamanders. They suggest convergent evolution in a number of key traits across species, including a larval life stage, the evolution of projectile tongues, and the ability to lose the tail as a defense mechanism.

[Find this resource:](#)

Wake, David B., Marvalee H. Wake, and Chelsea D. Specht. 2011. Homoplasy: From detecting pattern to determining process and mechanism of evolution. *Science* 331:1032–1035.

DOI: 10.1126/science.1188545 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A review of homology and homoplasy in systematics. This paper includes a comprehensive discussion of the fading distinction between convergence and parallelism as we learn more about the genetic and developmental basis of convergent traits.

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Developmental Constraints and Parallelism

When discussing the independent evolution of similar traits, the distinction between “parallel” and “convergent” evolution is frequently made (with parallelism described as either an alternative to or a subset of convergent evolution). Arendt and Reznick 2007 discusses how definitions of these terms vary through the literature. Although few authors emphasize the parallel or convergent direction of evolution in morphospace as Stayton 2006 notes (cited under Models and Statistics), most definitions focus either on the developmental mechanisms by which the traits are produced, as in Alberch and Gale 1985 and Jaekel and Wake 2007, or on the phylogenetic distance between the species in question. In fact, these two definitions may be related, as argued in Hall 2003, since reuse of the same developmental pathways seems most likely among closely repeated species.

These ideas relate parallelism to long-standing discussions of the role of developmental constraints in evolution (Alberch and Gale 1985). New genetic and developmental data challenge simplistic paradigms of “same” or “different” mechanisms, which has led scientists, as presented in Schwenk and Wagner 2004 and Arendt and Reznick 2007, to adopt an explicitly hierarchical view of convergent evolution.

Alberch, Pere, and Emily A. Gale. 1985. A developmental analysis of an evolutionary trend: Digital reduction in amphibians. *Evolution* 39:8–23.

DOI: 10.2307/2408513 Save Citation » Export Citation » E-mail Citation »

A classic study that integrates phylogenetics, development, and experimental manipulation of developing embryos to argue that developmental constraints have shaped digit evolution in amphibians. This paper also represents a very early example of evolutionary work that integrates information from developmental biology (“evo-devo”).

Find this resource:

Arendt, Jeff, and David Reznick. 2007. Convergence and parallelism reconsidered: What have we learned about the genetics of adaptation? *Trends in Ecology and Evolution* 23:26–32.

DOI: 10.1016/j.tree.2007.09.011 Save Citation » Export Citation » E-mail Citation »

Reviewing the genetic basis of adaptation, the authors argue that closely related species that evolve convergent traits can show distinct genes or developmental pathways of adaptation, and distant relatives can share genetic mechanisms. They argue that the term parallel evolution is overly ambiguous and should not be used.

Find this resource:

Hall, Brian K. 2003. Descent with modification: The unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biological Reviews of the Cambridge Philosophical Society* 78:409–433.

DOI: 10.1017/S1464793102006097 Save Citation » Export Citation » E-mail Citation »

An insightful historical overview of homology, homoplasy, convergence, and parallelism.

Find this resource:

Jaekel, Martin, and David B. Wake. 2007. Developmental processes underlying the evolution of a derived foot morphology in salamanders. *Proceedings of the National Academy of Sciences of the United States of America* 104:20437–20442.

DOI: 10.1073/pnas.0710216105 Save Citation » Export Citation » E-mail Citation »

This study represents a nice example of a developmental perspective on parallelism. The authors examine the evolution of webbed feet in bolitoglossine salamanders, and argue that this trait is most likely generated repeatedly through the similar developmental mechanism of paedomorphosis across this clade.

Find this resource:

Schwenk, Kurt, and Gunter P. Wagner. 2004. The relativism of constraints on phenotypic evolution. In *Phenotypic integration: Studying the ecology and evolution of complex phenotypes*. Edited by Massimo Pigliucci and Katherine Preston, 390–408. Oxford: Oxford Univ. Press.

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A nice discussion of various forms of evolutionary constraints and how they relate to the origins of complex phenotypes.

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Convergent Evolution Is Not Always Expected

As noted in Donoghue 2005, it is easy to get caught up in the numerous examples of convergent evolution, and lose sight of the fact that there are also a tremendous number of examples of a lack of convergent evolution—for example, species with unique characteristics, or species on one continent with no analogue on another. A number of fundamental hypotheses have been discussed to explain the absence of convergent evolution. Gould 2002 argued that many of these reflect various forms of evolutionary constraint. Schluter 1996 and Maynard Smith, et al. 1985 explain how these constraints can involve genetics and/or development. Many-to-one relationships between form and function can also result in species that converge in function but not in morphology. Wainwright 2007 reviews many examples of this, and Young, et al. 2010 presents one compelling example.

Donoghue, Michael J. 2005. Key innovations, convergence, and success: Macroevolutionary lessons from plant phylogeny. *Paleobiology* 31:77–93.

DOI: 10.1666/0094-8373(2005)031[0077:KICASM]2.0.CO;2 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

A broad synthetic view of plant evolution, highlighting both examples of convergent evolution and also examples of architectural limitations that prevent the evolution of certain types of traits in certain plant lineages.

[Find this resource:](#)

Gould, Stephen J. 2002. *The structure of evolutionary theory*. Cambridge, MA: Belknap.

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Gould's lengthy overview of his perspective on macroevolution consistently highlights the role of historical contingency in influencing long-term patterns of diversity.

[Find this resource:](#)

Maynard Smith, John, Richard M. Burian, Stuart Kaufman, et al. 1985. Developmental constraints and evolution: A perspective from the Mountain Lake Conference on developmental evolution. *Quarterly Review of Biology* 60:265–287.

DOI: 10.1086/414425 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

A general overview of constraints on evolution and how they can influence evolution. Sections of predictability relate closely to ideas about the occurrence of convergent evolution.

[Find this resource:](#)

Schluter, Dolph. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–1774.

DOI: 10.2307/2410734 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Paper that introduced the concept of genetic lines of least resistance, which describe the effects of quantitative genetic constraints on adaptive evolution.

[Find this resource:](#)

Wainwright, Peter C. 2007. Functional versus morphological diversity in macroevolution. *Annual Review of Ecology, Evolution, and Systematics* 38:381–401.

DOI: 10.1146/annurev.ecolsys.38.091206.095706 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A review of the evolution of diversity in form and function. Wainwright emphasizes many-to-one mapping of form to function, which can result in convergence in function but a lack of convergence in form.

[Find this resource:](#)

Young, Rebecca L., Michael J. Sweeney, and Alexander V. Badyaev. 2010. Morphological diversity and ecological similarity: Versatility of muscular and skeletal morphologies enables ecological convergence in shrews. *Functional Ecology* 24:556–565.

DOI: 10.1111/j.1365-2435.2009.01664.x [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

An informative case study of how many-to-one mapping of form to function can result in convergence in function along with diversity in underlying morphological characteristics.

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Experimental Studies of Convergent Evolution

Experimental evolution has dramatically improved our understanding of convergent evolution. Kassen 2009 provides a nice review of this research area. By exposing independent evolutionary replicates to the same new environment, replicated experiments can test for the frequency of convergence in a controlled way. Many important experiments involve *E. coli* adapting and diversifying in the lab, including Weinreich, et al. 2006; Tenaillon, et al. 2012; and Herron and Doebeli 2013. Richard Lenski's famous long-term evolution experiment is a key example of this research, as in Woods, et al. 2006. A variety of other organisms have also been used in experimental evolution to understand convergence, including *Pseudomonas* in Rainey and Travisano 1998, guppies in Reznick and Bryga 1987, and viruses in Wichman and Brown 2010. Interestingly, the two most well-developed systems for experimental evolution show contradictory results in terms of the level of parallelism in replicated evolution: Wichman and Brown 2010 shows that the bacteriophage Φ X174 shows extensive parallelism at the level of individual mutations, while Lenski's long-term studies of *E. coli* show parallelism at the level of genes but not individual mutations. More work is needed to generalize these results.

Herron, Matthew D., and Michael Doebeli. 2013. Parallel evolutionary dynamics of adaptive diversification in *Escherichia coli*. *PLoS Biology* 11:e1001490.

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Doebeli's group studies the repeatable diversification of *E. coli* into two forms that differ predictably in their ability to metabolize glucose and acetate. Here, Herron and Doebeli show that this diversification is often associated with mutations in the same gene (and sometimes even at the same nucleotide position).

[Find this resource:](#)

Kassen, Rees. 2009. Toward a general theory of adaptive radiation: Insights from microbial experimental evolution. *Annals of the New York Academy of Sciences* 1168:3–22.

DOI: 10.1111/j.1749-6632.2009.04574.x [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A comprehensive review of the insights into adaptive radiation gained from experimental evolution. Includes a discussion of

convergent evolution in the section on experimental evolution and repeated radiation.

Find this resource:

Rainey, Paul B., and Michael Travisano. 1998. Adaptive radiation in a heterogeneous environment. *Nature* 394:69–72.

DOI: 10.1038/27900 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

The bacterium *Pseudomonas fluorescens* evolves into three evolved morphs (smooth, wrinkly spreader, and fuzzy spreader) in response to ecological opportunity. These morphs show distinct niche preferences and frequency-dependent dynamics that allow stable coexistence. This original study describes the system, and many subsequent follow-ups have demonstrated this phenomenon in more detail.

Find this resource:

Reznick, David N., and Heather Bryga. 1987. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* 41:1370–1385.

DOI: 10.2307/2409101 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Observational studies had suggested that guppies evolved predictable differences in life histories in response to predators. This paper describes the first of a series of introduction experiments (still ongoing, more than twenty-five years later) that demonstrate that guppies do evolve convergent life history phenotypes in response to their predators.

Find this resource:

Tenaillon, Olivier, Alejandra Rodríguez-Verdugo, Rebecca L. Gaut, et al. 2012. The molecular diversity of adaptive convergence. *Science* 335:457–461.

DOI: 10.1126/science.1212986 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

The authors adapted 115 populations of *E. coli* to high temperature, then sequenced one genome from each population. They uncovered a pervasive signal of convergent evolution of genes, operons, and functional groups (but only rarely convergence of individual point mutations). They also show a strong signature of epistatic interactions.

Find this resource:

Weinreich, Daniel M., Nigel F. Delaney, Mark A. DePristo, and Daniel L. Hartl. 2006. Darwinian evolution can follow only very few mutational paths to fitter proteins. *Science* 312:111–114.

DOI: 10.1126/science.1123539 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

E. coli can evolve resistance to the antibiotic β-lactamase via five mutations in a particular gene. Weinreich, et al. characterize the mutational landscape for antibiotic resistance in this gene. Of the 120 mutational pathways that link ancestral to resistant bacteria, only a few are accessible to selection, making evolutionary trajectories predictable.

Find this resource:

Wichman, Holly A., and Celeste J. Brown. 2010. Experimental evolution of viruses: Microviridae as a model system. *Philosophical Transactions of the Royal Society B* 365:2495–2501.

DOI: 10.1098/rstb.2010.0053 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

The bacteriophage ΦX174 is a model system for experimental evolution. This paper reviews and synthesizes previous work on ΦX174. The authors show that parallel evolution (defined here as the same substitution in two or more independent replicates) is rampant, involving nearly half of all mutations quantified thus far.

Find this resource:

Woods, Robert, Dominique Schneider, Cynthia L. Winkworth, Margaret A. Riley, and Richard E. Lenski. 2006. Tests of parallel molecular evolution in a long-term experiment with *Escherichia coli*. *Proceedings of the National Academy of Sciences of the United States of America* 103:9107–9112.

DOI: 10.1073/pnas.0602917103 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Woods, et al. used twelve populations of *E. coli* that have evolved in the laboratory since 1988 to compare four candidate loci to evolution in thirty-six randomly chosen “control” genes after ~20,000 generations of evolution. The authors found extensive parallelism at the level of candidate genes, but little at the level of individual mutations.

Find this resource:

Molecular Convergence

There have been a large number of studies of convergence at the molecular level, including studies of individual genes, gene networks, and whole genomes.

REVIEW PAPERS

There are a large number of studies investigating the genetic basis of convergent phenotypes—too many to list here. Even when limiting the discussion to molecular convergence, one can still identify a hierarchy of similarity, from sequence to function (Doolittle 1994). Work on molecular convergence has been reviewed in Wood, et al. 2005; Gompel and Prud'homme 2009; Stern and Orgogozo 2009; Christin, et al. 2010; and Elmer and Meyer 2011 and synthesized in Conte, et al. 2012, to give some general insights into the genetics of convergent evolution.

Christin, Pascal-Antoine, Daniel M. Weinreich, and Guillaume Besnard. 2010. Causes and evolutionary significance of genetic convergence. *Trends in Genetics* 26:400–405.

DOI: 10.1016/j.tig.2010.06.005 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A review of what is known about the genetic basis of convergent phenotypes across a wide range of taxa. Includes a discussion of convergent recruitment, where homologous genes are repeatedly recruited to independently evolve a novel function across lineages.

Find this resource:

Conte, Gina L., Matthew E. Arnegard, Catherine L. Peichel, and Dolph Schlüter. 2012. The probability of genetic parallelism and convergence in natural populations. *Proceedings of the Royal Society B* 279:5039–5047.

DOI: 10.1098/rspb.2012.2146 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A meta-analysis of studies of the genetic basis of convergent evolution with two main findings. First, the probability of gene reuse in natural examples of convergent evolution is high, from 32 percent (mapping studies) to 55 percent (candidate gene studies) of the time. Second, the probability of gene reuse declines as taxa become more distantly related.

Find this resource:

Doolittle, Russell F. 1994. Convergent evolution: The need to be explicit. *Trends in Biochemical Sciences* 19:15–18.

DOI: 10.1016/0968-0004(94)90167-8 Save Citation » Export Citation » E-mail Citation »

Focusing on molecular evolution, Doolittle argues that convergence should be divided into four categories: sequence, structural, mechanistic, and functional convergence. This article predates much of the recent work on the genetic basis of convergent evolution, so Doolittle's categorizations are even more relevant now than when the paper was originally published.

Find this resource:

Elmer, Kathryn R., and Axel Meyer. 2011. Adaptation in the age of ecological genomics: Insights from parallelism and convergence. *Trends in Ecology and Evolution* 26:298–306.

DOI: 10.1016/j.tree.2011.02.008 Save Citation » Export Citation » E-mail Citation »

A general overview of genetic parallelism and convergence, this paper includes a discussion of methods for studying parallel evolution in genomes, as well as a set of well-developed case studies.

Find this resource:

Gompel, Nicolas, and Benjamin Prud'homme. 2009. The causes of repeated genetic evolution. *Developmental Biology* 332:36–47.

DOI: 10.1016/j.ydbio.2009.04.040 Save Citation » Export Citation » E-mail Citation »

This review of the genetic basis of the repeated evolution of similar phenotypes focuses on the genetic and developmental pathways that underlie variation in species' traits. The authors emphasize several specific hypotheses about parallel evolution.

Find this resource:

Stern, David L., and Virginie Orgogozo. 2009. Is genetic evolution predictable? *Science* 323:746–751.

DOI: 10.1126/science.1158997 Save Citation » Export Citation » E-mail Citation »

A review of the predictability of evolution at the genetic level, focusing on predictions based on gene function, genetic networks, developmental biology, and population biology.

Find this resource:

Wood, Troy E., John M. Burke, and Loren H. Rieseberg. 2005. Parallel genotypic adaptation: When evolution repeats itself. *Genetica* 123:157–170.

DOI: 10.1007/s10709-003-2738-9 Save Citation » Export Citation » E-mail Citation »

A review of parallel genetic adaptation in both experimental evolution and natural systems.

Find this resource:

CONVERGENCE IN GENOMES AND GENOMIC NETWORKS

As genomic analysis becomes increasingly common, studies of Molecular Convergence can be applied over broader genomic scales. A few such studies have already been published. Some analyses focus on sets of paralogous genes, which are the result

of duplication events or genomic networks associated with particular phenotypes as in Conant and Wagner 2003; Fraser, et al. 2004; and Jost, et al. 2008, while others focus on broad comparisons of whole genomes or epigenetic systems as presented in Feil and Berger 2007; McCutcheon, et al. 2009; and Merhej, et al. 2009. As one might expect, the increased information available at genomic scales blurs the line between “parallel” and “convergent” molecular evolution, as repeated cases of adaptation frequently show a mix of similar and unique genetic signatures. Hohenlohe, et al. 2010 provides one compelling example in sticklebacks.

Conant, Gavin C., and Andreas Wagner. 2003. Convergent evolution of gene circuits. *Nature Genetics* 34:264–266.

DOI: 10.1038/ng1181 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Conant and Wagner looked at patterns of common ancestry in genetic networks. Comparing *E. coli* and *S. cerevisiae*, they argue that transcriptional regulatory networks represent convergent evolution of entire gene circuits.

Find this resource:

Feil, Robert, and Frederic Berger. 2007. Convergent evolution of genomic imprinting in plants and mammals. *Trends in Genetics* 23:192–199.

DOI: 10.1016/j.tig.2007.02.004 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

This review argues that imprinting in flowering plants and mammals, though strikingly similar, represents convergent evolution, and that similar epigenetic systems have arisen at least twice independently.

Find this resource:

Fraser, James A., Stephanie Diezmann, Ryan L. Subaran, et al. 2004. Convergent evolution of chromosomal sex-determining regions in the animal and fungal kingdoms. *PLoS Biology* 2:2243–2255.

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The authors use comparative genomics to reconstruct the evolution of the mating type loci in fungi. They argue that the events leading to the evolution of sex determination in fungi were similar to those that led to the evolution of sex chromosomes in mammals.

Find this resource:

Hohenlohe, Paul A., Susan Bassam, Paul D. Etter, Nicholas Stiffler, Eric A. Johnson, and William A. Cresko. 2010. Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genetics* 6:e10000862.

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A study of patterns of genomic divergence in threespine stickleback that have convergently adapted to freshwater environments. Independent freshwater populations of stickleback that have convergent phenotypes show both parallel and nonparallel patterns of genomic evolution.

Find this resource:

Jost, Manda C., David M. Hillis, Ying Lu, John W. Kyle, Harry A. Fozard, and Harold H. Zakon. 2008. Toxin-resistant sodium channels: Parallel adaptive evolution across a complete gene family. *Molecular Biology and Evolution* 25:1016–1024.

DOI: 10.1093/molbev/msn025 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Rather than looking at individual genes, Jost, et al. investigate patterns of parallel evolution across a gene family related to resistance to tetrodotoxin (TTX) and saxitoxin (STX).

[Find this resource:](#)

McCutcheon, John P., Bradon R. McDonald, and Nancy A. Moran. 2009. Convergent evolution of metabolic roles in bacterial co-symbionts of insects. *Proceedings of the National Academy of Sciences of the United States of America* 106:15394–15399.

DOI: 10.1073/pnas.0906424106 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A spectacular example of convergent evolution involving interactions between symbionts. Symbiotic bacteria in the genus *Sulcia* occur in both sharpshooters and cicadas, and can produce only eight of ten essential amino acids. In the two hosts, two distantly related bacterial species have evolved to supply the missing amino acids.

[Find this resource:](#)

Merhej, Vicky, Manuela Royer-Carenzi, Pierre Pontarotti, and Didier Raoult. 2009. Massive comparative genomic analysis reveals convergent evolution of specialized bacteria. *Biology Direct* 4:13.

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Obligate intracellular bacteria, including both mutualists and parasites, have reduced genomes. This study shows that these host-dependent bacteria show a suite of convergent changes in their genomes compared to their free-living ancestors, including the repeated loss of a predictable set of genes.

[Find this resource:](#)

Phenotypic Convergence

Convergent evolution of phenotypes has fascinated evolutionary biologists for decades, and so there are a large number of interesting examples that one can find for a wide range of traits and species. A large number of studies have discussed convergent evolution of morphological characteristics. Interesting examples span a wide range of traits and taxa, including plants in Knudsen and Tollsten 2008; arthropods in Oakley and Cunningham 2002; sharks and fishes in Donley, et al. 2004; amphibians in Clark, et al. 2005; and reptiles in Rosenblum 2006. Examples of convergent evolution are not restricted to morphological characters; in fact, there are a large number of examples of convergent evolution of behaviors: Blackledge and Gillespie 2004 illustrates this with web structure in spiders; Emery and Clayton 2004 with cognitive ability in mammals and birds; and Gleiss, et al. 2011 in gait and flight patterns.

Blackledge, Todd A., and Rosemary G. Gillespie. 2004. Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences of the United States of America* 101:16228–16233.

DOI: 10.1073/pnas.0407395101 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Studying repeated radiations of Hawaiian web-building spiders, Blackledge and Gillespie identify convergent web structures among repeatedly evolved ecotypes on different islands in Hawaii. These web structures are a physical manifestation of convergence in web-building behavior.

[Find this resource:](#)

Clark, Valerie C., Christopher J. Raxworthy, Valerie Rakotomalala, Petra Sierwald, and Brian L. Fisher. 2005. Convergent evolution of chemical defense in poison frogs and arthropod prey between Madagascar and the Neotropics. *Proceedings of the National Academy of Sciences of the United States of America* 102:11617–11622.

DOI: 10.1073/pnas.0503502102 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Clark, et al. show that poison frogs in Madagascar sequester toxic compounds from their arthropod prey, a strategy that is strikingly similar—but independently derived—from that of poison frogs in the Neotropics.

Find this resource:

Donley, Jeanine M., Chugay A. Sepulveda, Peter Konstantinidis, Sven Gemballa, and Robert E. Shadwick. 2004.

Convergent evolution in mechanical design of lamnid sharks and tunas. *Nature* 429:61–65.

DOI: 10.1038/nature02435 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A detailed look at body shape and biomechanics of lamnid sharks shows a deep and surprising level of convergence with tunas, another large pelagic cruising clade. This similarity extends to the biomechanics of movement and their arrangement of muscles and tendons.

Find this resource:

Emery, Nathan J., and Nicola S. Clayton. 2004. The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science* 306:1903–1907.

DOI: 10.1126/science.1098410 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

This study argues that cognitive studies of crows show that these birds rival nonhuman primates in tool use, social intelligence, and other aspects of intelligence. This would represent convergent evolution of complex cognitive abilities in two quite distantly related clades of vertebrates.

Find this resource:

Gleiss, Adrian C., Salvador J. Jorgensen, Nikolai Liebsch, et al. 2011. Convergent evolution in locomotory patterns of flying and swimming animals. *Nature Communications* 2:352.

[Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

In this paper, Gleiss, et al. show that gait patterns of marine vertebrates are strikingly similar to patterns shown in species with undulating flight.

Find this resource:

Knudsen, Jette T., and Lars Tollsten. 2008. Floral scent in bat-pollinated plants: A case of convergent evolution. *Botanical Journal of the Linnean Society* 119:45–57.

DOI: 10.1111/j.1095-8339.1995.tb00728.x [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

Knudsen and Tollsten show that distantly related plant species that are pollinated by bats show striking convergence in their floral scents, including the presence of sulfur-containing compounds, some of which are unique to bat-pollinated flowers.

Find this resource:

Oakley, Todd H., and Clifford W. Cunningham. 2002. Molecular phylogenetic evidence for the independent evolutionary origin of an arthropod compound eye. *Proceedings of the National Academy of Sciences of the United States of America* 99:1426–1430.

DOI: 10.1073/pnas.032483599 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Oakley and Cunningham show that myodocopids—a clade of ostracods that have compound eyes—are nested within a clade of species without compound eyes. They present analyses that this phylogenetic pattern most likely reflects convergent evolution of compound eyes in arthropods.

[Find this resource:](#)

Rosenblum, Erica B. 2006. Convergent evolution and divergent selection: Lizards at the White Sands ecotone. *American Naturalist* 167:1–15.

DOI: 10.1086/498397 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Rosenblum shows that three distinct lizard species have independently evolved pale white coloration to adapt to a novel habitat type in White Sands, New Mexico.

[Find this resource:](#)

Integrative Multilevel Approaches to Understanding Convergence

Convergence is an inherently hierarchical phenomenon, spanning multiple levels of biological organization (see General Overviews). In a few cases, detailed studies have shown the mechanisms of convergence, and in turn highlighted the interrelationships between genetics, development, and phenotypes in evolution: see examples such as pigment patterns in *Drosophila* in Wittkopp, et al. 2003 and mice in Manceau, et al. 2010; morphology in sticklebacks in Colosimo, et al. 2005; electrical communication in fishes in Arnegard, et al. 2010; flower shape in Cooley, et al. 2011; and lizard morphology in Kolbe, et al. 2011. The natural replication of convergent evolution means that such studies can give exceptionally broad insights into the predictability of evolution.

Arnegard, Matthew E., Derrick J. Zwickl, Ying Lu, and Harold H. Zakon. 2010. Old gene duplication facilitates origin and diversification of an innovative communication system twice. *Proceedings of the National Academy of Sciences of the United States of America* 107:22172–22177.

DOI: 10.1073/pnas.1011803107 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Two groups of teleost fishes have evolved forms of electrical communication. Arnegard, et al. use an approach that integrates phylogenetics and genetics to show that in both of these groups the same voltage-gated sodium channel gene was co-opted to spur innovation in both clades.

[Find this resource:](#)

Colosimo, Pamela F., Kim E. Hosemann, Sarita Balabhadra, et al. 2005. Widespread parallel evolution in sticklebacks by repeated fixation of Ectodysplasin alleles. *Science* 307:1928–1933.

DOI: 10.1126/science.1107239 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

The authors connect the convergent evolution of freshwater stickleback around the world to variation at the Ectodysplasin locus, finding that repeated evolution of the same trait was likely due to evolution from standing genetic variation rather than postulating new mutations in each independent population.

Find this resource:

Cooley, Arielle M., Jennifer L. Modliszewski, Megan L. Rommel, and John H. Willis. 2011. Gene duplication in *Mimulus* underlies parallel floral evolution via independent trans-regulatory changes. *Current Biology* 21:700–704.

DOI: 10.1016/j.cub.2011.03.028 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A study of the genetic basis of convergent coloration in *Mimulus* highlights the role of the duplication of regulatory genes in independent lineages.

Find this resource:

Kolbe, Jason J., Liam J. Revell, Brian Szekely, Edmund D. Brodie III, and Jonathan B. Losos. 2011. Convergent evolution of phenotypic integration and its alignment with morphological diversification in Caribbean *Anolis* ecomorphs. *Evolution* 12:3608–3624.

DOI: 10.1111/j.1558-5646.2011.01416.x [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

A comparison of trait variation within and among a set of anole species shows the effects of genetic constraints (in the form of quantitative genetic variances and covariances, the G matrix) influencing patterns of convergent evolution.

Find this resource:

Manceau, Marie, Vera S. Domingues, Catherine R. Linnen, Erica B. Rosenblum, and Hopi E. Hoekstra. 2010. Convergence in pigmentation at multiple levels: Mutations, genes and function. *Philosophical Transactions of the Royal Society Series B* 365:2439–2450.

DOI: 10.1098/rstb.2010.0104 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

This paper compares the convergent evolution of cryptic coloration across vertebrates, and show examples of convergent evolution caused by the same mutations, by different mutations in the same gene, and by entirely different genes. Different mutations in the same gene need not be functionally equivalent to result in convergence.

Find this resource:

Wittkopp, Patricia J., Barry L. Williams, Jayne E. Selegue, and Sean B. Carroll. 2003. *Drosophila* pigmentation evolution: Divergent genotypes underlying convergent phenotypes. *Proceedings of the National Academy of Sciences of the United States of America* 100:1808–1813.

DOI: 10.1073/pnas.0336368100 [Save Citation »](#) [Export Citation »](#) [E-mail Citation »](#)

This comparison of the genetic basis of convergent evolution in coloration in *Drosophila* shows clearly that similar phenotypes can have entirely distinct genetic bases in different species.

Find this resource:

Parallel and Convergent Speciation

Ecological speciation, where the process of speciation is driven by natural selection against intermediate forms, is an important mechanism for generating biodiversity. Some of the most convincing examples of ecological speciation are when that speciation is repeated, for example *Drosophila* in Rundle, et al. 2000; walking stick insects in Nosil, et al. 2002; mosquitofish in Langerhans,

et al. 2007; and lizards in Rosenblum and Harmon 2011. This repeated, “parallel” speciation, reviewed in Johannesson 2001, forms a link between convergent and/or parallel evolution and the origin of new species.

Johannesson, Kersten. 2001. Parallel speciation: A key to sympatric divergence. *Trends in Ecology and Evolution* 16:148–153.

DOI: 10.1016/S0169-5347(00)02078-4 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

This review paper presents models and examples from nature of the process of parallel speciation.

[Find this resource:](#)

Langerhans, R. Brian, Matthew E. Gifford, and Everton O. Joseph. 2007. Ecological speciation in *Gambusia* fishes. *Evolution* 61:2056–2074.

DOI: 10.1111/j.1558-5646.2007.00171.x [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Langerhans, et al. show that *Gambusia* fishes from blue holes in the Bahamas are undergoing parallel speciation driven by divergent predator regimes.

[Find this resource:](#)

Nosil, Patrik, Bernard J. Crespi, and Cristina P. Sandoval. 2002. Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* 417:440–443.

DOI: 10.1038/417440a [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Nosil, et al. show that populations of walking sticks have undergone parallel speciation adapting to two distinct host plants.

[Find this resource:](#)

Rosenblum, Erica B., and Luke J. Harmon. 2011. “Same same but different”: Replicated ecological speciation at White Sands. *Evolution* 65.4: 946–960.

DOI: 10.1111/j.1558-5646.2010.01190.x [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

The authors investigate convergent speciation across three lineages of lizards at White Sands, New Mexico, using an analysis of genetics, morphology, and color. This study is unique compared to others in this section in that the lineages undergoing parallel or convergent speciation are quite distantly related to one another.

[Find this resource:](#)

Rundle, Howard D., Laura Nagel, Janette W. Boughman, and Dolph Schlüter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. *Science* 287:306–308.

DOI: 10.1126/science.287.5451.306 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Threespine stickleback have repeatedly and convergently diverged into benthic (bottom-dwelling) and limnetic (top-dwelling) forms. The authors measure reproductive isolation between various populations of these fish, showing that isolation is strongest when associated with divergent natural selection.

[Find this resource:](#)

Community Convergence and Repeated Radiations

It is natural to extend ideas of convergence up to entire communities or ecosystems, as in Samuels and Drake 1997. Community convergence can be hindered by historical contingencies, so that even in similar habitats communities can differ: see studies of bird assemblages in Schlüter 1986 and Price, et al. 2000. Still, in some cases, researchers have found convergence between communities on different islands or island-like habitats—Hawaiian spiders in Gillespie 2004; Caribbean lizards in Losos 2009; cichlid fishes in Lake Tanganyika in Muschick, et al. 2012—or on continents, as in the Mediterranean plant assemblages in Mooney and Dunn 1970 and lizards in Melville, et al. 2006. The most spectacular examples of community convergence involve repeated radiations, where independent adaptive radiations result in a similar set of habitat specialists in different locations—as seen in Hawaiian spiders in Gillespie 2004 and lizards in Melville, et al. 2006 and Losos 2009.

Gillespie, Rosemary G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303:356–359.

DOI: 10.1126/science.1091875 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

Gillespie shows that similar sets of spider species have independently evolved on islands in the Hawaiian archipelago.

[Find this resource:](#)

Losos, Jonathan B. 2009. *Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles*. Berkeley: Univ. of California Press.

[Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

This comprehensive book reviews the adaptive radiation of anoles. Losos reviews the evidence that anoles have undergone repeated radiations into convergent communities on the four islands of the Greater Antilles.

[Find this resource:](#)

Melville, Jane, Luke Harmon, and Jonathan B. Losos. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society of London* 273:557–563.

DOI: 10.1098/rspb.2005.3328 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

This paper looks at convergence in desert lizard communities between North America and Australia, comparing both pairs of species and the structure of the entire lizard community.

[Find this resource:](#)

Mooney, Howard A., and E. Lloyd Dunn. 1970. Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. *Evolution* 24:292–303.

DOI: 10.2307/2406805 [Save Citation](#) » [Export Citation](#) » [E-mail Citation](#) »

This broad comparison of plant communities in Mediterranean climates around the world argues that communities are convergent in structure and function.

[Find this resource:](#)

Muschick, Moritz, Adrian Indermauer, and Walter Salzburger. 2012. Convergent evolution within an adaptive radiation of cichlid fishes. *Current Biology* 22:2362–2368.

DOI: 10.1016/j.cub.2012.10.048 Save Citation » Export Citation » E-mail Citation »

Muschick, et al. present a quantitative assessment of convergent evolution of cichlid communities in Lake Tanganyika. These fishes show multiple instances of convergence in both morphology and feeding, but—contrary to other examples of convergent evolution in communities—convergent forms often occur sympatrically with one another.

Find this resource:

Price, Trevor, Irby J. Lovette, Eldredge Bermingham, H. Lisle Gibbs, and Adam D. Richman. 2000. The imprint of history on communities of North American and Asian warblers. *American Naturalist* 156:354–367.

DOI: 10.1086/303397 Save Citation » Export Citation » E-mail Citation »

This paper compares warbler communities in two continents. Although Price, et al. find some similarities between the two communities, they also find substantial differences, which they attribute to historical effects of ancestry and biogeography.

Find this resource:

Samuels, Corey L., and James A. Drake. 1997. Divergent perspectives on community convergence. *Trends in Ecology and Evolution* 12:427–432.

DOI: 10.1016/S0169-5347(97)01182-8 Save Citation » Export Citation » E-mail Citation »

A review of community convergence that focuses on the ecological processes that can lead to predictable communities—or that can cause communities to diverge dramatically over time.

Find this resource:

Schlüter, Dolph. 1986. Tests for similarity and convergence of finch communities. *Ecology* 67:1073–1085.

DOI: 10.2307/1939830 Save Citation » Export Citation » E-mail Citation »

Schlüter develops a method to test for community convergence and applies it to finch communities from around the world, finding significant community convergence that also seems to be influenced by historical contingency.

Find this resource:

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