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Is convergence surprising? An examination of the frequency of convergence in simulated datasets

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Abstract

Although convergence is recognized as a central concept in evolutionary biology, very few tools are available for the quantitative study of this phenomenon. Moreover, although many evolutionary assertions assume that convergence should be rare in the absence of influences on organismal phenotypes such as natural selection or constraint, no studies have tested whether this is the case. I simulate random evolution (Brownian motion model) of quantitative characters along phylogenies with varying numbers of terminal taxa, numbers of traits, variance structure, and tree balance, and quantify the amount of convergence observed in these datasets using four metrics. The amount of convergence observed in a dataset increases with increasing number of taxa and decreasing number of traits, approaching the maximum possible amount of convergence under certain circumstances. Some convergence is expected in almost all datasets. Comparison of empirical datasets to those produced by random evolution provides a test of whether empirical datasets actually show elevated levels of convergence. Out of three test datasets, two show more convergence than expected. Given that high levels of convergence can be produced simply by random evolution, no explanation may be necessary for instances of convergence discovered in an evolutionary investigation.
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1. Introduction

Convergence seems to be ubiquitous throughout the tree of life. The "evolution of similar features independently in different evolutionary lineages" (Futuyma, 1998) has been found in many organismal phenotypes, from ecology, behavior, and morphology (Blackledge and Gillespie, 2004; Grenier and Greenberg, 2005; Langerhans et al., 2006; Melville et al., 2006; Moore and Willmer, 1997; Nevo, 1979; Wiens et al., 2006; Wittkopp et al., 2003) to genes, proteins, enzymes or enzyme active sites (Charnock et al., 2002; Chen et al., 1997; Govindarajan and Goldstein, 1996; Kornegay et al., 1994; Lawn et al., 1997; Mattevi et al., 1996). Virtually all current biology texts address this phenomenon (e.g., Campbell et al., 2003, p. 307; Freeman, 2005, p. 501; Starr and Taggart, 2004, p. 313). Although studies that have found evidence of convergence are probably published more often than studies that have searched for convergence and not found it, this phenomenon has certainly been documented many times in many different groups.

In fact, convergence seems so common throughout the tree of life that this predominance serves as the foundation for many evolutionary theories and has been the subject of inquiry itself. For example, convergence discovered in an investigation is often used as evidence of adaptation (Blackledge and Gillespie, 2004; Endler, 1982; Futuyma, 1998, p. 123; Grenier and Greenberg, 2005; Harmon et al., 2004; Langerhans et al., 2006; Rosenblum, 2006; Stebbins, 1951) and to demonstrate the power of natural selection. Many modern evolutionary biology textbooks will present a figure of marsupials and their placental "counterparts" to illustrate the power of natural selection to shape organismal form (Futuyma, 1998, p. 221). In contrast, some biologists have used the prevalence of convergence as evidence that natural selection is not all-powerful; these researchers argue that the prevalence of convergence is

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evidence of constraints that channel the evolutionary process into a limited number of possible outcomes (Conway Morris, 1998; Henry et al., 1999; Lakes-Harlan et al., 1999; Mardulyn et al., 1997; Mooney and Dunn, 1970; see also Wake, 1991). Both kinds of arguments, and many more (Moore and Willmer, 1997), are predicated on the impression that convergence is very common throughout the tree of life. Implicit in such arguments is the notion that the amount of convergence observed is much higher than would be expected at random—i.e., without the action of natural selection or constraints on organismal phenotypes. However, this assumption has been neither quantified nor tested, probably because most researchers assume that, lacking any strong influences on the evolutionary process, convergence would be extremely rare in any given phylogeny (this is reflected in the fact that most cladistic methods attempt to minimize homoplasy, including convergence, when reconstructing trees).

In this paper I investigate whether convergence is really as unlikely as biological intuition suggests. I simulate random, undirected evolution (Brownian motion model) of quantitative traits along a variety of phylogenies. Then I calculate the amount of convergence in the resulting data using four methods, and summarize patterns of expected convergence for a variety of trees and tree parameters. Finally, I compare observed levels of convergence in real datasets to that expected under a null model of random evolution.

My objectives in this paper are: (1) to develop multiple methods for measuring convergence among quantitative datasets, (2) to test these methods in simulations in which the true evolutionary history of a group is known, and (3) to use these methods to assess the amount of convergence that is expected in datasets developed using varying phylogenies under a model of undirected evolution.

2. Defining and measuring convergence

I have chosen to investigate this phenomenon using quantitative data for three reasons. First, many classic, yet untested, examples of convergence (such as convergence between ecological equivalents among marsupials and placentals) involve traits such as size and shape, which are better approached with quantitative data rather that discrete characters. Second, null models are available to assess the expected amount of homoplasy in datasets of discrete characters (Archie, 1996). Third, quantitative methods are becoming available for the analysis of phenotypic evolutionary patterns (Pie and Weitz, 2005).

Convergence has been classically documented with qualitative descriptions (Gregory, 1951; Shapiro, 1978) but is increasingly recognized, described, and tested with quantitative data (Cody and Mooney, 1978; Croder, 1980; Eldredge, 1968; Fuentes, 1976; Harmon et al., 2004; Hertel, 1994; Langerhans et al., 2006; Losos et al., 1998; Mares, 1975, 1976; Melville et al., 2006; Metzger and Herrel, 2005; Niemi, 1985; Pianka, 1986, p. 141; Rosenblum, 2006;

Schluter, 1986; Stayton, 2005, 2006; Westneat et al., 2005). However, the assessment of convergence is usually accomplished with metrics designed to measure homoplasy, not just convergence, such as the consistency index (CI), retention index (RI), and Blomberg's MSE_0/MSE (Blomberg et al., 2003). Even the quantitative convergence index (1-RI; Ackerly and Donoghue, 1998), which was developed to measure quantitative convergence, really measures the total amount of homoplasy in a dataset (Ackerly, personal communication) and thus counts parallelisms and reversals as well as convergence. Other measures can only be used when a subset of taxa have already been designated as putatively convergent (Fuentes, 1976; Harmon et al., 2004; Losos et al., 1998; Stayton, 2006) or to discover convergent taxa among two trees (Melville et al., 2006), not when an overall measure of the amount of convergence in a single tree is desired. The development of null models of measures of convergence for quantitative data is clearly necessary.

For quantitative data, there seems to be no consensus regarding a definition for convergence. All definitions include some notion of similarity among distantly related taxa. In addition to this pattern, many definitions also include some idea of a process or mechanism for convergence, including: adaptation to common selective regimens (Cody and Mooney, 1978), common developmental pathways (Tucker, 1997), common constraint (Wake, 1991), or other criteria (Saether, 1983; see also Cody and Mooney, 1978).

I have chosen to quantify convergence according to a purely pattern-based, geometrical definition (first suggested by Osborn, 1905, see also Haas and Simpson, 1946): *convergence occurs when two taxa evolve to be more similar to one another than their ancestors were to each other*. This can be visually illustrated in the context of a two-dimensional trait space; the convergent taxon is closer in this space than to its sister taxon, and indeed, the branches leading to the two taxa "converge"—they point towards one another (Fig. 1A). Convergence here is only defined based on phenetic similarity, not on the relative relationships among taxa, the processes that produced the similarity, or any other criterion. Thus, an assessment of convergence in this paper does not require any knowledge of selective regimen or any adaptive processes.

Some reviewers have criticized the lack of an adaptive component to a definition of convergence; I have chosen a pattern-based definition of convergence for four reasons. First, not all definitions of convergence require adaptation (even if this is understood to be the process that most often produces convergence). Second, if convergence can be produced by many different processes (adaptation, common developmental pathways, or undirected evolution, for example), then only a purely pattern-based definition of convergence will allow future study of the relative importance of each of these processes in producing convergent phenotypes. Lacking such a simple,