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Different evolutionary dynamics led to the convergence of clinging performance in lizard toepads[†]

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Does convergent evolution always result from different lineages experiencing similar evolutionary dynamics? Hagey et al. (2017) report the dynamics of adhesive performance evolution to be distinct in two lizard clades (anoles and geckos) despite independent convergence in adhesive toe pad structures, suggesting convergence can occur with dissimilar macroevolutionary dynamics.

Convergent evolution, the evolution of similar features in distantly related species or groups, has long fascinated evolutionary biologists. For example, the striking similarity in the wings of bats and birds and the convergence of streamlined body shape among fish, dolphins, and ichthyosaurs have been avenues of great intrigue and captivation (Losos 2017). Due to their similarity, examples of phenotypic convergence are often hypothesized to have arisen through similar evolutionary dynamics or processes. However, there are many factors that can either constrain or enable phenotypic trait evolution, and the degree to which that is idiosyncratic among convergent lineages remains unclear. For example, if a lineage encounters an ecological opportunity, it may be provided with evolutionary access to a wide variety of ecological niches in which to diversify (Stroud and Losos 2016). Conversely, trait diversification may be constrained if that group is limited by its developmental, genetic, or biomechanical capabilities (Arnold 1992). The proliferation of well-sampled, time-calibrated phylogenies has enabled robust analyses of how phenotypic traits evolve and diversify through time and among lineages. Investigating how these opposing forces lead to remarkable convergence on the macroevolutionary landscape is important to understanding the nature and predictability of evolution.

In this issue, Hagey et al. (2017) explore the evolutionary tempo (rate) and mode (pattern) of the performance of subdigital adhesive toepads, which have evolved convergently in two distantly related clades of lizards. Adhesive toepads are specialized morphological modifications that substantially increase the ability of a lizard to cling to surfaces. To measure clinging ability performance among species, the authors measured the angle at which lizards detached from a rotating glass slide. This performance trait, known as the toe detachment angle (TDA), was measured in 250 individual lizards (13 species of *Anolis* lizards (anoles) and 46 species of geckos). Ancestral state reconstruction revealed that toepads most likely evolved three times in lizards: once each in anoles, geckos, and skinks (although the authors note that other studies suggest multiple origins in geckos). Hagey et al. hypothesized that the diversification of adhesive performance in anoles and geckos differed as a result of unique evolutionary dynamics.

To test this, the authors fitted several models of trait diversification to the adhesive performance data. Their models included variations of two common models, the Brownian motion (BM) model and the Ornstein–Uhlenbeck (OU) model, which included the ancestral state of no toepads. (See Fig. 1 for an explanation of these models of trait diversification.) The analysis revealed that the diversification of adhesive toepad performance in geckos was

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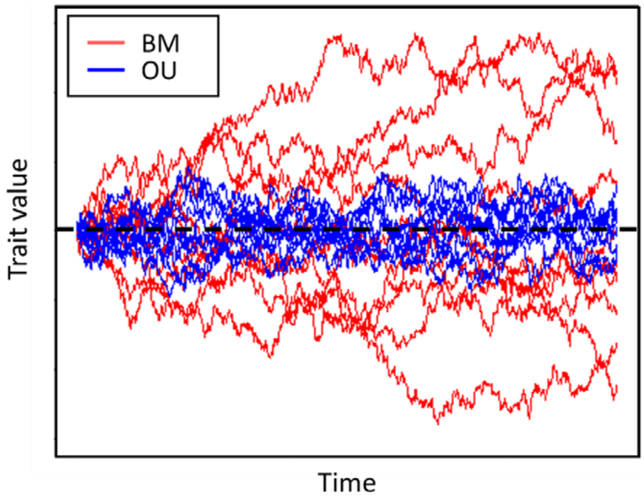

Figure 1. Conceptual figure showing the nature of trait diversification under Brownian motion (BM; red) and Ornstein–Uhlenbeck (OU; blue) evolutionary models. In both models, evolution of a trait over time is defined by two parameters that define the rate of spread (σ^2) and root trait value (shown by a black dotted line). The OU model has an additional parameter (α) that defines the strength of pull toward the trait optimum (θ); therefore, evolution of a trait following the OU model is restricted within a region of trait space (i.e., constrained/bounded over time). The BM model is unbounded and has no such restrictions. Hagey et al. (2017) found clinging performance, measured by toe detachment angle, to better fit a BM model for geckos and an OU model for anoles, after accounting for independent origins of toe pads. Note that this is a conceptual model demonstrating the diversification of a single trait; Hagey et al. (2017) tested complex evolutionary scenarios (e.g., multiple trait optima) using additional parameters. This figure uses simulated data for 10 lineages per model using R package *phytools* (Revell 2012).

unconstrained—their data were best fitted by a BM model. This suggests that gecko toepads diversified under few selective constraints and a wealth of evolutionary opportunities. In contrast, the evolution of adhesive performance in anoles appeared heavily constrained—it was best fitted by an OU model, specifically with a root state of 0 and a single optimum. The authors suggest that this could have been due to consistent selective constraints such as limited access to ecological opportunities. In contrast to geckos, anoles are less diverse in both ecology and toepad morphology, and are geographically limited, only being found naturally in the Neotropics.

Stephen J. Gould (2002) proposed that "replaying the tape of life" would not result in a repeat of the same phenotypes we observe today due to the stochastic nature of evolution. However, Hagey et al. and a suite of recent studies (e.g., Grundler and Rabosky 2014; Smith and Goldberg 2015) have found compelling evidence that trait convergence among clades can arise from different evolutionary dynamics. Investigating the convergence of phenotypic traits using well-resolved time-calibrated phylogenies will continue to be important in our quest to understand the nature of evolution. Hagey et al. take us a step further by analyzing the evolutionary mode and tempo of a performance trait upon which natural selection has led to a convergence in morphology. Other studies that adopt this approach will also benefit from a more complete understanding of the evolutionary dynamics of trait diversification compared to studies that only consider morphological trait data.

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