

A lizard with two tales: what diversification within *Sceloporus occidentalis* teaches us about species formation

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Abstract

In 1859, Charles Darwin proposed that species are not fundamentally different from subspecies or the varieties from which they evolve. A century later, Dobzhansky (1958) suggested that many such lineages are ephemeral and are likely to revert differentiation through introgression (Fig. 1A); only a few evolve complete reproductive isolation and persist in sympatry. In this issue of *Molecular Ecology*, Bouzid et al. (2021) show how new analytical methods, when applied to genome data, allow us to more precisely determine whether or not species formation follows the paths outlined by Darwin and Dobzhansky (Fig. 1B). The authors study the diversification of the lizard *Sceloporus occidentalis*, finding a continuum of genetic interactions between the preservation of genetic identity to genetic merger, analogous to what is exemplified by ring species. In doing so, they teach us two tales on species formation: that lineages are fractal byproducts of evolutionary processes such as genetic drift and selection, and that lineages are often ephemeral and do not always progress into species. Studying ephemeral lineages like those in *S. occidentalis* allows us to capture divergence at its earliest stages, and potentially to determine the factors that allow lineages to remain distinct despite pervasive gene flow. These lineages thus serve as a natural laboratory to address long standing hypotheses on species formation.

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A lizard with two tales: what diversification within *Sceloporus occidentalis* teaches us about species formation

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species. In doing so, they teach us two tales on species formation: that lineages are fractal byproducts of evolutionary processes such as genetic drift and selection, and that lineages are often ephemeral and do not always progress into species. Studying ephemeral lineages like those in *S. occidentalis* allows us to capture divergence at its earliest stages, and potentially to determine the factors that allow lineages to remain distinct despite pervasive gene flow. These lineages thus serve as a natural laboratory to address long standing hypotheses on species formation.

Keywords:

Speciation, hybridization, ring species, gene flow

Tale 1: The fractal nature of species

The first tale told by *S. occidentalis* is the fractal nature of lineage divergence. As populations spread across the landscape, they diverge due to adaptation to local conditions and due to genetic drift across distance, geographic barriers, and low-density areas. These two processes reinforce and facilitate each other, resulting in discontinuities in genetic variation perceived as evolutionary lineages. To understand how such evolutionary lineages form, species like *Sceloporus occidentalis* are ideal, because they are abundant throughout a large range that transverses a wide range of elevations, habitats, and climatic regimes. In this study, Bouzid et al. sample comprehensively throughout the *S. occidentalis* range. In doing so, they identify two major lineages within the species: one ranges along the coast up to the Sierra Nevada Mountains and the second extends east of the Sierra Nevada mountains into the arid Great Basin region (Fig. 1B). Within these lineages, they further identify genetic discontinuities that are coincident with previously glaciated mountain ranges and with steep ecological gradients in temperature and aridity. Concordance of genetic breaks with climatic and topographic transitions likely results from two, non-mutually exclusive processes. First, as inferred through modelling of historical demography, *S. occidentalis* occurs in a dynamic landscape that has been reshaped through repeated glacial cycles. As Bouzid et al. hypothesize, populations in the species persisted in isolated patches of habitat, which reflect current ecological boundaries. Second, gene flow across ecological transitions is often reduced (Endler 1977), both in cases of primary and secondary contact. This can lead to population breaks falling across ecological breaks. As recognized by Darwin and Dobzhansky, this tale of *Sceloporus occidentalis* shows that even cohesive species contain population substructure at multiple hierarchical levels, and that the formation of the genetic discontinuities observed today are a byproduct of drift and selection. Whether that divergence presages the formation of new species remains an open question addressed in Tale 2.

Tale 2: The ephemeral nature of species

The second tale told by *S. occidentalis* is the ephemerality of evolutionary lineages. As told by Tale 1, divergence is iterative and continuous, and populations evolve into lineages that may then evolve into species (Fig. 1A). This process can take a long time, and populations must persist throughout. But, many populations – perhaps most populations – go locally extinct before divergence is complete (Rosenblum *et al.* 2012). A well understood process that can trigger local extinctions is demographic stochasticity, but a probably equally important process is population expansion. When a population comes into secondary contact with previously isolated neighbors, it can go extinct either because they cannot compete or because they lost to hybridization (Kuhlwilm *et al.* 2019). In *S. occidentalis*, we see early evidence for the erosion of populations through hybridization and introgression. Two populations – the Pacific Northwest population and the East Sierra Nevada population – meet at the northern end of the range in northwestern United States (Fig. 1B). In and around this area of geographic overlap, several individuals show evidence for both hybridization and subsequent introgression, suggesting the populations have not yet evolved strong reproductive barriers. Additional sampling in this region would clarify if introgression is bounded and the likely evolutionary trajectory of these lineages. This pattern of hybridization is pervasive throughout the *S. occidentalis* range; there is evidence for admixture at all geographic boundaries between populations. Further, during their repeated glacial cycles, *S. occidentalis* likely experienced recurrent bouts of secondary contact, during which

introgression might have eroded previous population structure. Thus, some of the population structure observed in today’s snapshot is likely only a fraction of what has existed historically and is likely to be lost into the future.

Why have *S. occidentalis* populations met this fate, when populations in other species in the same biogeographic region remain distinct upon secondary contact? Bouzid et al. present evidence that gene flow between populations of *S. occidentalis* is reduced across climatic transitions, consistent with adaptation leading to ecological barriers. Data from mate choice experiments and interpopulation crosses could reveal if other barriers to gene flow exist between these populations. Regardless of the extent of reproductive barriers, they appear insufficient to limit introgression completely. More generally, in many taxa, reproductive barriers evolve as a function of divergence time (Pereira & Wake 2009; Singhal & Moritz 2013). Given the recent divergence time estimated in *S. occidentalis* (~700,000), the ecological instability of the dispersal barriers (currently arid habitats), and the high dispersal rate of this species, these conditions simply might be insufficient for reproductive barriers to evolve.

What can we learn from such fractal and ephemeral lineages?

In *S. occidentalis*, geographic isolation of two arms of expansion maintains genetic differentiation, whereas secondary contact between lineages leads to genetic merger and the gradual reversion of divergence. This process is a clear example of Darwinian species formation, where subspecies evolve into species and back. While ephemeral lineages (i.e. varieties, subspecies, or races) challenge binary notions of taxonomy (De Queiroz 2020), such systems have been prized as examples of clarity for evolutionary biologists (Dobzhansky 1958). The most emblematic examples are perhaps ring species, because, in a single system, they present the full spectrum of outcomes expected to occur when incipient lineages come into secondary contact, from unrestricted gene flow to full reproductive isolation (Pereira & Wake 2009). Yet, systems that have not evolved strong reproductive isolation, such as *S. occidentalis*, provide important insights into the processes that drive species divergence early in lineages’ histories. These processes are otherwise difficult to observe. Further, the finding that leaky genetic borders are coincident with environmental transitions, suggests that natural selection has played a role in population divergence, but that it is not strong enough to reduce genome flow genome wide. Studying such permeable boundaries between taxa remains an important task in evolutionary biology because they allow us to identify the phenotypes and the associated genomic regions that remain differentiated in the face of introgression, informing us about the nature of species boundaries (Harrison & Larson 2014).

For centuries, systematists have been archiving endless forms of ephemeral lineages in natural history museums through bird skins in drawers, insects dried on pins, and plants on herbarium sheets. Now is the time to revisit these classical systems to better understand speciation. Ephemeral lineages provide an opportunity to ally information from natural history (e.g. information on species distribution, their environment, mating traits) to gene-level analyses to understand both which adaptations persist despite recombination and their underlying genetic basis. Moreover, these ephemeral lineages also might explain why intermediate stages of species formation seem absent in species radiations (Roux *et al.* 2016), a pattern that has often been interpreted as resulting from rapid divergence when lineages approach a “tipping point”. As exemplified by *S. occidentalis*, such pattern could also arise from introgressive hybridization and swamping between ephemeral lineages, which is consistent with identification of introgression from ghost populations in extant species (Kuhlwilm *et al.* 2019). These dynamics suggests that much of the population structure we see within species is likely to be ephemeral (Rosenblum *et al.* 2012) and that many of the recent radiations we see on Earth will perhaps be lost to the vagaries of time. As envisioned by Dobzhansky (Fig. 1A), Bouzid et al. (2021) are demonstrating that subspecies, varieties and races are not less valuable than “good species” and that in fact they are key for understanding the formation of well delineated species.

Figure 1. Ephemeral ring diversification in *Sceloporus occidentalis*. A. As envisioned by Dobzhansky, evolutionary lineages can either merge through gene flow or acquire reproductive isolation (adapted from Dobzhansky, 1958). B. The genetic patterns of genetic diversification of *S. occidentalis* through space recapitulate patterns expected through time, as lineages establishing secondary contact become genetically

homogeneous and geographically isolated lineages remain distinct (adapted from Bouzid et al., 2021).

References:

Bouzid NM, Archie JW, Anderson RA, Grummer JA, Leaché AD (2021) Evidence for ephemeral ring species formation during the diversification history of western fence lizards (*Sceloporus occidentalis*). *Mol Ecol.* , **30** : XXX-XXX

Darwin C (2011). The origin of species. William Collins.

De Queiroz K (2020) An updated concept of subspecies resolves a dispute about the taxonomy of incompletely separated lineages. *Herpetological Review* , **51** , 459–461.

Dobzhansky T (1958) Species after Darwin. In: *A century of Darwin*(ed Barnett SA). A century of Darwin. Heinemann, London.

Endler JA (1977) Geographic variation, speciation, and clines. *Monogr Popul Biol* , **10** , 1–246.

Harrison RG, Larson EL (2014) Hybridization, introgression, and the nature of species boundaries. *Journal of Heredity* , **105** , 795–809.

Kuhlwilm M, Han S, Sousa VC, Excoffier L, Marqués-Bonet T (2019) Ancient admixture from an extinct ape lineage into bonobos. *Nature Publishing Group* , 1–11.

Pereira RJ, Wake DB (2009) Genetic leakage after adaptive and nonadaptive divergence in the *Ensatina eschscholtzii* ring species. *Evolution* , **63** , 2288–2301.

Rosenblum EB, Sarver BAJ, Brown JW *et al.* (2012) Goldilocks Meets Santa Rosalia: An Ephemeral Speciation Model Explains Patterns of Diversification Across Time Scales. *Evol. Biol.* , **39** , 255–261.

Roux C, Fraisse C, Romiguier J *et al.* (2016) Shedding Light on the Grey Zone of Speciation along a Continuum of Genomic Divergence. *PLoS Biol* , **14** , e2000234.

Singhal S, Moritz C (2013) Reproductive isolation between phylogeographic lineages scales with divergence. *Proc R Soc B* , **280** , 20132246–20132246.

