Received: 25 October 2021 | Accepted: 3 December 2021

DOI: 10.1111/mec.16321

MOLECULAR ECOLOGY WILEY

NEWS AND VIEWS

Perspective

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

Ricardo J. Pereira[1] | Sonal Singhal[2]

[1]Division of Evolutionary Biology, Faculty of Biology II, Ludwig-Maximilians-Universität München, Planegg-Martinsried, Germany

[2]Department of Biology, CSU Dominguez Hills, Carson, California, USA

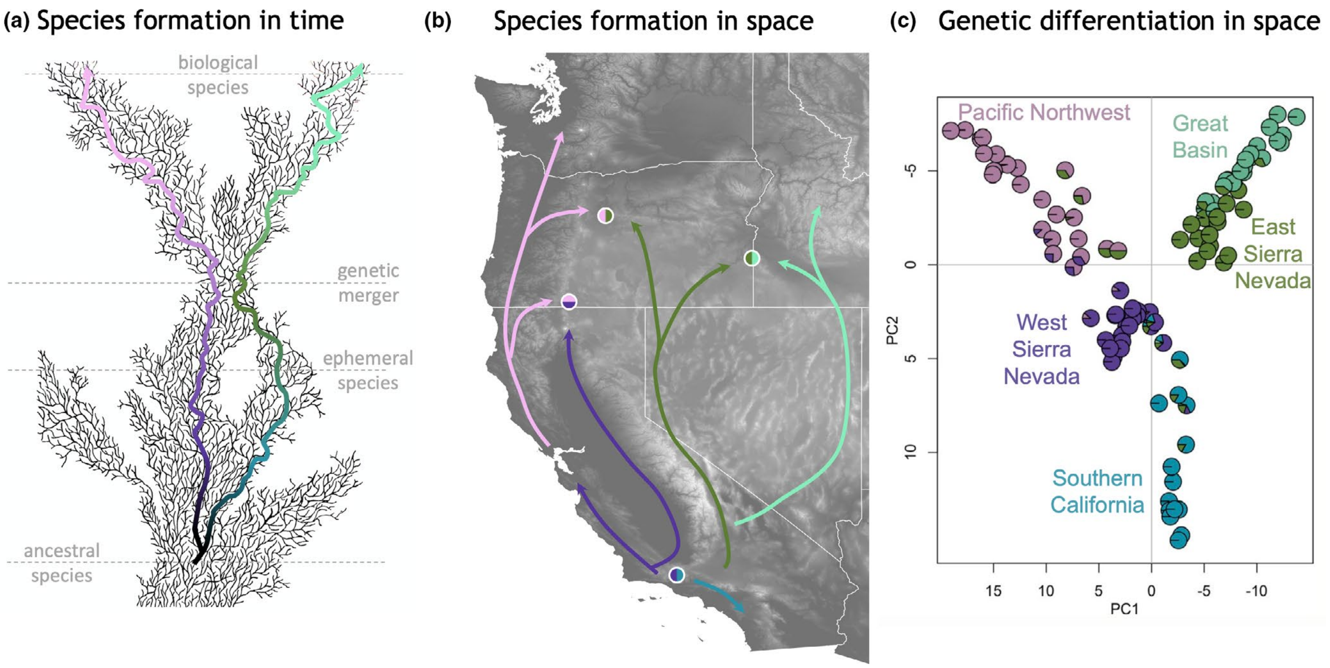
Correspondence
Ricardo J Pereira, Division of Evolutionary Biology, Faculty of Biology II, Ludwig-Maximilians-Universität München, Planegg-Martinsried, Germany.
Email: ricardojn.pereira@gmail.com

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 reverse differentiation through introgression (Figure 1a); only a few evolve complete reproductive isolation and persist in sympatry. In this issue of *Molecular Ecology*, Bouzid et al. (2021) showed how new analytical methods, when applied to genomic data, allow us to more precisely determine whether or not species formation follows the paths outlined by Darwin and Dobzhansky (Figure 1b). The authors studied 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 about 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 fully reproductively isolated taxa. 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 about species formation.

KEYWORDS
gene flow, hybridization, polytypic species, ring species, speciation

1 | TALE 1: THE FRACTAL NATURE OF SPECIES

The first tale told by *Sceloporus 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 areas of low population density. These two processes reinforce 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 these lizards are abundant throughout a large range that transverses a wide range of elevations, habitats, and climatic regimes. In this study, Bouzid et al. (2021) sampled comprehensively throughout the *S. occidentalis* range. In doing so, they identified two major lineages within the species: one ranges along the coast east into the Sierra Nevada and the second extends east of the Sierra Nevada across the arid Mojave and Great Basin deserts (Figure 1b). Within these lineages, they further identified genetic discontinuities that are coincident with previously glaciated mountain ranges and with steep ecological gradients in temperature



(a) Species formation in time (b) Species formation in space (c) Genetic differentiation in space

FIGURE 1 Ephemeral ring diversification in *Sceloporus occidentalis*. (a) As envisioned by Dobzhansky, evolutionary lineages can either merge through gene flow or acquire complete reproductive isolation (adapted from Dobzhansky, 1958). (b) Lineages of *S. occidentalis* diversify conditioned by historical and current geographic barriers, in some cases establishing secondary contact and introgression. (c) As a result, 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 (PCA from Bouzid et al. (2021) based on 6944 unlinked SNPs, with individuals colour-coded to populations from the admixture model ($K = 5$) and pie frequencies showing admixture proportions)

and aridity. Concordance of genetic breaks with climatic and topographic transitions probably results from two, nonmutually 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. (2021) hypothesized, 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 coincident with 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 is a byproduct of drift and selection. Whether that divergence presages the formation of new species remains an open question addressed in Tale 2.

2 | TALE 2: THE EPHEMERAL NATURE OF SPECIES

The second tale told by *Sceloporus 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 complete reproductive isolation (Figure 1a). This process can take a long time, and populations must persist throughout. However, many populations – perhaps most populations – become locally extinct before reproductive isolation 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 become extinct either because neighbors cannot compete or because they become swamped by hybridization (Kuhlwilm et al., 2019). In *S. occidentalis*, we see early evidence for the erosion of population differentiation 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 the northwestern United States (Figure 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 the bounds of introgression 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. Furthermore, during repeated glacial cycles, *S. occidentalis* probably 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 probably 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 of other species in the same biogeographic region remain distinct upon secondary contact? Bouzid et al. (2021) presented 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 years), the cyclical ecological instability of dispersal barriers (currently arid habitats), and the high dispersal rate of this species, these conditions simply might be insufficient for reproductive barriers to evolve.

3 | WHAT CAN WE LEARN FROM SUCH FRACTAL AND EPHEMERAL LINEAGES?

In *Sceloporus occidentalis*, geographic isolation of two arms of expansion maintains genetic differentiation, whereas secondary contact between lineages leads to genetic merger and the gradual reversal of divergence (Figure 1c). This process is a clear example of Darwinian species formation, where subspecies evolve into species and back (Darwin, 1859). 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 lineages come into secondary contact, from unrestricted gene flow to apparent complete 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 selection is not strong enough to reduce gene flow genome wide. Studying such permeable boundaries between taxa remains an important task in evolutionary biology because it allows 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 species formation. Ephemeral lineages provide an opportunity to integrate 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 introgression 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 (Figure 1a), Bouzid et al. (2021) demonstrated that subspecies, varieties and races are no less valuable than are "good species"; rather, they are key for understanding the formation of well delineated species.

ACKNOWLEDGMENT

Open access funding enabled and organized by ProjektDEAL. We thank N. Bouzid, J. Patton and K. de Queiroz for comments on earlier versions of this manuscript.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this perspective.

ORCID

Ricardo J. Pereira https://orcid.org/0000-0002-8076-4822
Sonal Singhal https://orcid.org/0000-0001-5407-5567

REFERENCES

Bouzid, N. M., Archie, J. W., Anderson, R. A., Grummer, J. A., & Leaché, A. D. (2021). Evidence for ephemeral ring species formation during the diversification history of western fence lizards (*Sceloporus occidentalis*). *Molecular Ecology*, *31*, 620–631.

Darwin, C. (1859). *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 S. A. Barnett (Ed.), *A century of Darwin* (pp. 19–55). Heinemann.

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

Harrison, R. G., & Larson, E. L. (2014). Hybridization, introgression, and the nature of species boundaries. *Journal of Heredity*, *105*, 795–809. https://doi.org/10.1093/jhered/esu033

Kuhlwilm, M., Han, S., Sousa, V. C., Excoffier, L., & Marqués-Bonet, T. (2019). Ancient admixture from an extinct ape lineage into bonobos. *Nature Ecology & Evolution*, *3*(6), 957–965. https://doi.org/10.1038/s41559-019-0881-7

Pereira, R. J., & Wake, D. B. (2009). Genetic leakage after adaptive and nonadaptive divergence in the *Ensatina eschscholtzii* ring species. *Evolution*, *63*, 2288–2301.

Rosenblum, E. B., Sarver, B. A. J., Brown, J. W., Des Roches, S., Hardwick, K. M., Hether, T. D., Eastman, J. M., Pennell, M. W., & Harmon, L. J. (2012). Goldilocks meets Santa Rosalia: An ephemeral speciation model explains patterns of diversification across time scales. *Evolutionary Biology*, *39*, 255–261. https://doi.org/10.1007/s11692-012-9171-x

Roux, C., Fraïsse, C., Romiguier, J., Anciaux, Y., Galtier, N., & Bierne, N. (2016). Shedding light on the grey zone of speciation along a continuum of genomic divergence. *PLoS Biology*, *14*, e2000234. https://doi.org/10.1371/journal.pbio.2000234

Singhal, S., & Moritz, C. (2013). Reproductive isolation between phylogeographic lineages scales with divergence. *Proceedings of the Royal Society B*, *280*, 20132246. https://doi.org/10.1098/rspb.2013.2246

How to cite this article: Pereira, R. J., & Singhal, S. (2022). A lizard with two tales: What diversification within *Sceloporus occidentalis* teaches us about species formation. *Molecular Ecology*, 31, 407–410. https://doi.org/10.1111/mec.16321