NEWS AND VIEWS

PERSPECTIVE

The hidden landscape: Evidence that sea-level change shaped the present population genomic patterns of marginal marine species

Greer A. Dolby ⓘ

Center for Mechanisms of Evolution, Biodesign Institute, School of Life Sciences, Arizona State University, Tempe, AZ, USA

Correspondence
Greer A. Dolby, Center for Mechanisms of Evolution, Biodesign Institute, School of Life Sciences, Arizona State University, Tempe, AZ, USA.
Email: gadolby@asu.edu

Oftentimes, to understand the genetic relatedness and diversity of today's populations requires considering the ancient landscape on which those populations evolved. Nowhere is this clearer than along Earth's coastline, which has been in its present-day configuration for only about 6.5% of the past 800,000 years (Dolby et al., 2020; Miller et al., 2005). During ice ages when glaciers expanded in the Northern Hemisphere, they stored enough of the planet's water to drop global sea level by ~120 m below present levels ("lowstand", Figure 1a), and there have been at least eight of these 100,000-year cycles preceding today. When glaciers melted, ocean water reflooded shorelines, shifting and re-forming marginal marine habitats globally and shaping the relatedness of populations (Dolby et al., 2016). In a From the Cover article in this issue of *Molecular Ecology*, Stiller et al. (2020) integrate population genomic analysis of leafy seadragons in southern Australia with estimates of available seabed area to reveal that the expansion of habitat that accompanied this reflooding led to strong demographic expansions. With statistical models, they also show that western populations were eliminated and then recolonized because the continental shelf there is narrow, leaving little available habitat when sea level was low (Figure 1b). Their results document the dynamic and interrelated nature of a hidden, changing landscape and the evolution of species inhabiting it.

Palaeontologists have long studied the effect of changing sea levels on biodiversity (e.g., Olsson, 1961), but it was only recently that genetic work suggested estuarine fish populations were isolated in refugia due to lower sea levels, and that the shape of the continental shelf could control the distribution of these refugia (Dolby et al., 2018). In the present study, Stiller et al. (2020) used an R package and an available digital elevation model (ETOPO1) to calculate the amount of seabed area during lowstand (120 m below sea level) and how that area changed as sea level rose to its present-day level. To study population genomic history, they used data of 857 variable ultraconserved elements (UCEs) from 68 leafy seadragons (*Phycodurus eques*, Syngnathidae; Figure 2; Stiller et al., 2017) distributed along the southern coast of Australia. Target enrichment of UCEs is a reduced representation method where probes are designed in conserved parts of the genome to allow them to work across species.

Although UCEs generally yield fewer loci than restriction-associated DNA sequencing (RADseq) methods, their strengths are that UCE probes can be designed to target orthologous regions that are independent (i.e., unlinked) and nongenic ("neutral"; Alfaro et al., 2018) in very distantly related species, providing data sets that can be compared and used broadly by the community. While normally applied to deeper-time phylogenetic questions, this study shows that UCEs can be informative for shallow-time phylogeographical questions too.

One particular strength of Stiller et al.'s (2020) study was the authors' integration of the two data types. They compared the heterozygosity of populations against the change in habitat size to show that wide-shelf regions had more lowstand habitat, as expected (Figure 1c; Dolby et al., 2020), which resulted in higher population heterozygosity (Figure 1d). They also employed approximate Bayesian computation (ABC), which is a powerful way to use independent evidence (e.g.,

wileyonlinelibrary.com/journal/mec
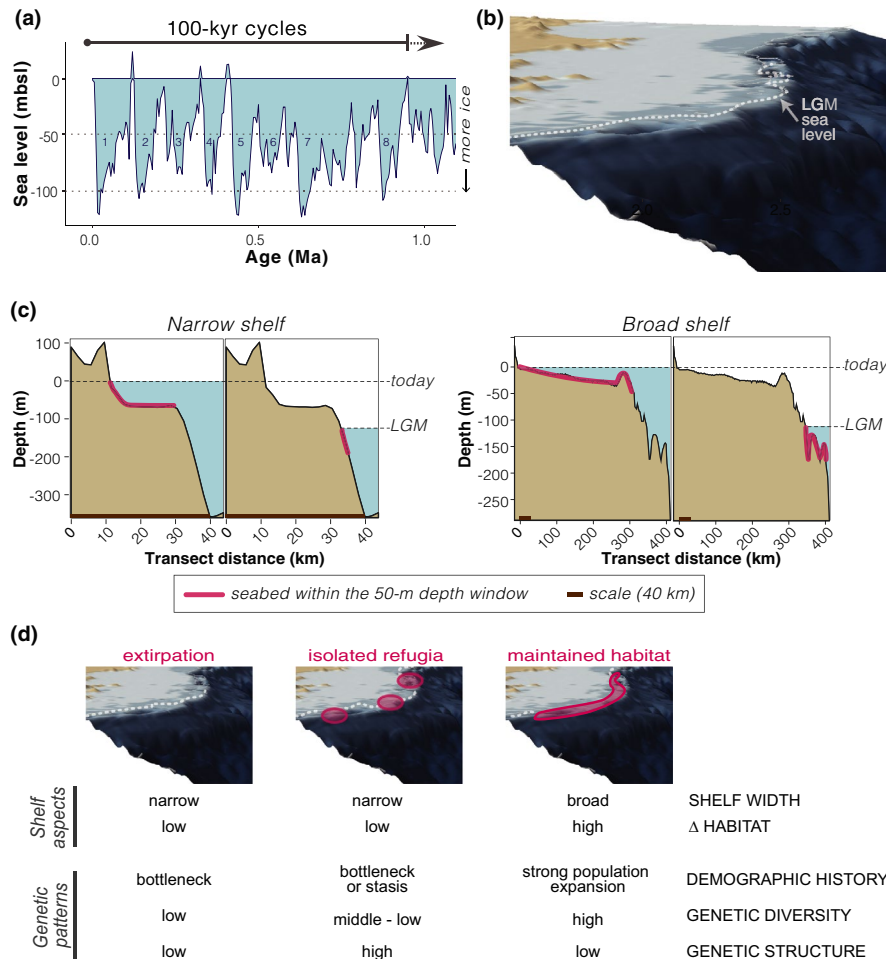
FIGURE 1 Summary of sea-level change, continental shelves and isolation scenarios of marginal marine species discussed in Stiller et al. (2020). (a) There were at least eight high-amplitude sea-level oscillations that (b) lowered sea level to ~120 m below sea level (mbsl; estimated by grey dashed line; land is beige). (c) These had different effects on narrow (left) versus wide (right) shelves. The amount of habitable seabed area is shown in pink from the western (narrow) and eastern (broad) regions from Stiller et al. (note the difference in scale). (d) Different genetic expectations are based on the width of the continental shelf. Stiller et al. found that the eastern (wide) shelf sustained habitat when sea level was low, leading to higher genetic diversity, stronger population structure and stronger expansions when sea level rose and increased habitat area. Western (narrow shelf) populations were probably extirpated and recolonized. This differs from prior work that showed that some isolated refugia on narrow shelves can survive and lead to diverged populations (Dolby et al., 2018). Habitat type and species differences may play a role

ecological, geological) to test competing evolutionary hypotheses. Generally, this approach requires setting parameters based on the organism and genetic data collected (e.g., generation time, mutation rate), and constructing a set of scenarios for which genetic data are simulated repeatedly, with each simulation drawing parameter values from those user-defined distributions. Summary statistics are generated for each simulated data set and these are compared to determine which historical scenario is most compatible with the observed data set.

Using ABC, Stiller et al. (2020) were able to show that the GIS-based palaeohabitat reconstructions described the relatedness of populations better than the Leeuwin Current, which flows in the opposite direction. They also showed that the steeper western range was probably extirpated and recolonized from the east, leading to the stepwise relatedness of populations, lower population structure and lower genetic diversity observed in western populations (Figure 1d). Perhaps most importantly,

however, they showed for the first time that the huge habitat expansion that occurs when wide continental shelves are flooded led to a strong demographic expansion in the leafy seadragon populations. The demographic expansion was stronger here than in the narrow western shelf where habitats tend to be smaller and change less in size (Dolby et al., 2020; Stiller et al., 2020). These results exemplify how populations evolve in tandem with the landscapes they inhabit.

1 | A HIDDEN LANDSCAPE AND NEW QUESTIONS

Growing evidence suggests that sea-level change has dramatically affected the evolution of marginal marine species (Keyse et al., 2018; Noguerales et al., 2020; Stiller et al., 2017, 2020; Thomaz
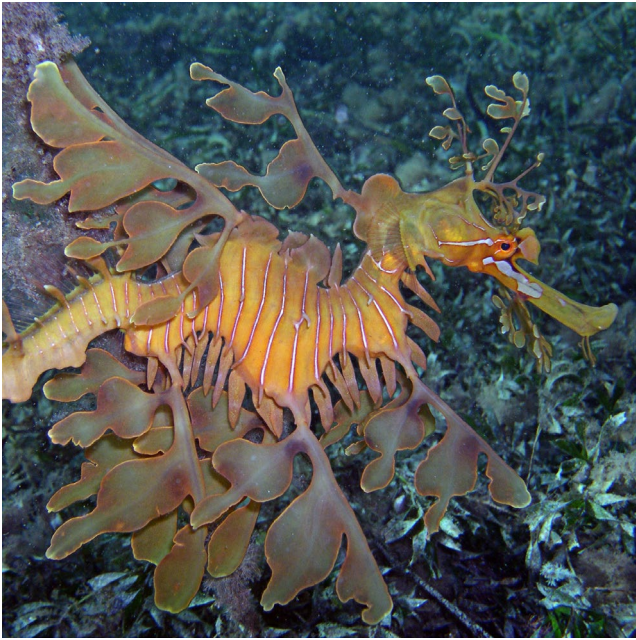
FIGURE 2 A leafy seadragon (*Phycodurus eques*) in Wool Bay, South Australia. Seadragons are uniquely camouflaged to disappear among their shallow-water kelp and seagrass habitat. Photo credit: Greg Rouse

& Knowles, 2020). One of the most important lessons from this study is that to understand present patterns of coastal species requires looking beyond the present-day landscape to consider the "hidden" coastline and how it changed during ice age cycles. Not only that, but we need to consider that the present land–sea configuration is a short-lived snapshot of what has been a landscape in flux. The ability to estimate palaeohabitat with excellent age control (e.g., Miller et al., 2005) may make these good systems for assessing other population or metapopulation dynamics, including founder effects and the "surfing" of alleles and the increased mutation load in populations at the front of a species expansion (Excoffier & Ray, 2008; Gilbert et al., 2018). Additionally, (re)colonizing habitat means species may face new predation pressures, diet resources and abiotic conditions that can also shape phylogeographical patterns (Graciá, 2020; Ortego & Knowles, 2020). Testing for signatures of selection or local adaptation, including changes in copy number that can affect phenotype, may also be fruitful (Dorant et al., 2020).

As emerging evidence refines our knowledge, new questions emerge. Stiller et al. examined a brooding species with low dispersal. At what level of dispersiveness is a species no longer affected by isolation in refugia? Also, although most phylogeographical studies focus on the effects from the Last Glacial Maximum to present, there were at least eight (and perhaps 11) major 100,000-year glaciations (Figure 1a; Miller et al., 2005; PAGES, 2016). Are the genetic effects of sea-level oscillations overprinted with each cycle, or are the genetic effects cumulative? Does the age of the first oscillation matter or only the most recent one? Finally,

palaeontologists have studied how sea-level change shapes biodiversity over deep geological time (Tennant et al., 2016), but can our emerging knowledge about its genetic impacts tie into these higher order (deeper-time) patterns of diversification and richness? Much is left to learn about the nature and extent of this relationship; the results of Stiller et al. (2020) show it is an exciting time to explore this data-rich setting.

ORCID

Greer A. Dolby https://orcid.org/0000-0002-5923-0690

REFERENCES

Alfaro, M. E., Faircloth, B. C., Harrington, R. C., Sorenson, L., Friedman, M., Thacker, C. E., Oliveros, C. H., Černý, D., & Near, T. J. (2018). Explosive diversification of marine fishes at the Cretaceous-Palaeogene boundary. *Nature Ecology & Evolution*, 2, 688–696.

Dolby, G. A., Bedolla, A. M., Bennett, S. E., & Jacobs, D. K. (2020). Global physical controls on estuarine habitat distribution during sea level change: Consequences for genetic diversification through time. *Global and Planetary Change*, 187, 103128.

Dolby, G. A., Ellingson, R. A., Findley, L. T., & Jacobs, D. K. (2018). How sea level change mediates genetic divergence in coastal species across regions with varying tectonic and sediment processes. *Molecular Ecology*, 27, 994–1011.

Dolby, G. A., Hechinger, R., Ellingson, R. A., Findley, L. T., Lorda, J., & Jacobs, D. K. (2016). Sea-level driven glacial-age refugia and postglacial mixing on subtropical coasts, a palaeohabitat and genetic study. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20161571.

Dorant, Y., Cayuela, H., Wellband, K., Laporte, M., Rougemont, Q., Mérot, C., Normandeau, E., Rochette, R., & Bernatchez, L. (2020). Copy number variants outperform SNPs to reveal genotype–temperature association in a marine species. *Molecular Ecology*, 29, 4765–4782.

Excoffier, L., & Ray, N. (2008). Surfing during population expansions promotes genetic revolutions and structuration. *Trends in Ecology & Evolution*, 23, 347–351.

Gilbert, K. J., Peischl, S., & Excoffier, L. (2018). Mutation load dynamics during environmentally-driven range shifts. *PLoS Genetics*, 14, e1007450–e1007518.

Graciá, E. (2020). Biotic interactions matter in phylogeography research: Integrative analysis of demographic, genetic and distribution data to account for them. *Molecular Ecology*, 29, 4503–4505.

Keyse, J., Treml, E. A., Huelsken, T., Barber, P. H., DeBoer, T., Kochzius, M., Nuryanto, A., Gardner, J. P. A., Liu, L.-L., Penny, S., & Riginos, C. (2018). Historical divergences associated with intermittent land bridges overshadow isolation by larval dispersal in co-distributed species of Tridacnagiant clams. *Journal of Biogeography*, 45, 848–858.

Miller, K. G., Kominz, M. A., Browning, J. V., Wright, J. D., Mountain, G. S., Katz, M. E., Sugarman, P. J., Cramer, B. S., Christie-Blick, N., & Pekar, S. F. (2005). The Phanerozoic record of global sea-level change. *Science*, 310, 1293–1298.

Noguerales, V., Cordero, P. J., Knowles, L. L., & Ortego, J. (2020). Genomic insights into the origin of trans-Mediterranean disjunct distributions. *Journal of Biogeography*, 2, 1–13.

Olsson, A. A. (1961). *Mollusks of the tropical eastern Pacific: Particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru)*. Paleontological Research Institution, Ithaca, NY.

Ortego, J., & Knowles, L. L. (2020). Incorporating interspecific interactions into phylogeographic models: A case study with Californian oaks. *Molecular Ecology*, 29, 4510–4524.

Past Interglacials Working Group of PAGES. (2016). Interglacials of the last 800,000 years. *Reviews of Geophysics*, *54*, 162–219.

Stiller, J., da Fonseca, R. R., Alfaro, M. E., Faircloth, B. C., Wilson, N. G., & Rouse, G. W. (2020). Using ultraconserved elements to track the influence of sea-level change on leafy seadragon populations. *Molecular Ecology*, *30*, 1364–1380. https://doi.org/10.1111/mec.15744

Stiller, J., Wilson, N. G., Donnellan, S., & Rouse, G. W. (2017). The leafy seadragon, *Phycodurus eques*, a flagship species with low but structured genetic variability. *Journal of Heredity*, *108*, 152–162.

Tennant, J., Mannion, P., & Upchurch, P. (2016). Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. *Nature Communications*, *7*, 1–11.

Thomaz, A. T., & Knowles, L. L. (2020). Common barriers, but temporal dissonance: Genomic tests suggest ecological and paleo-landscape sieves structure a coastal riverine fish community. *Molecular Ecology*, *29*, 783–796.