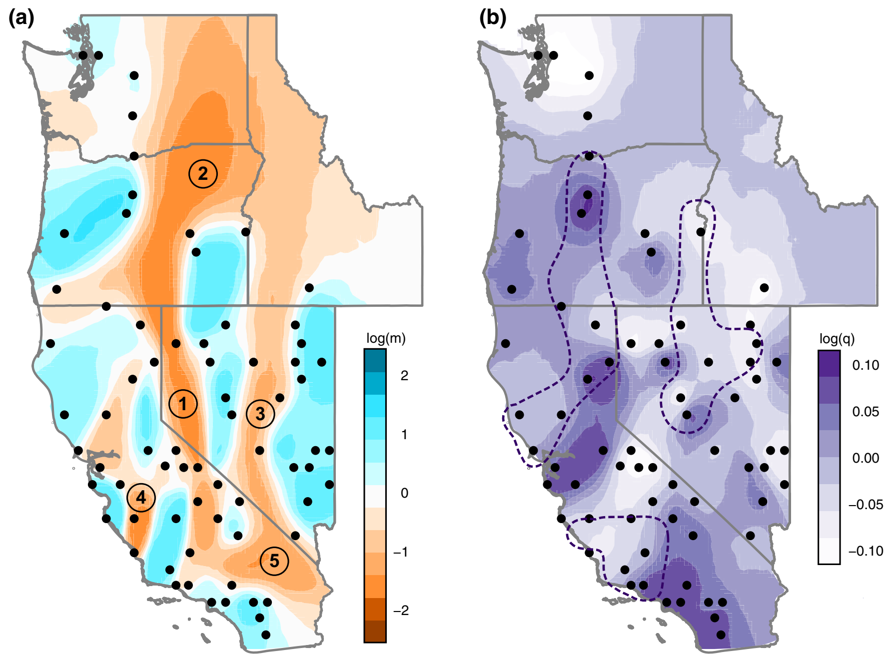

FIGURE 5 Contour maps of effective migration (*m*) and effective diversity (*q*) estimated using EEMS. (a) Barriers to migration with *m* rates lower than expected under isolation-by-distance (IBD) are shown in brown/orange; corridors of migration with high *m* rates are shown in blue. Numbers indicate significant migration barriers: (1) eastern escarpment and rain-shadow of the Sierra Nevada Range, (2) rain-shadow of the Cascade Range and the Columbia Basin in southeastern Washington, (3) central Nevada mountain ranges, (4) California Central Valley and southern Coast Ranges, (5) Mojave Desert. (b) Areas of high diversity with *q* rates higher than expected under IBD are shown in purple; areas of low *q* are shown in white. Contact zones are outlined and match those shown in Figure 2(c). Sample sites are illustrated with black dots [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our study uses SNP-based estimates of phylogeographical structure and demographic history to understand the processes that have shaped genetic diversification in *Sceloporus occidentalis*. We find evidence for genetic divergences that are hierarchical and geographically structured, resulting in spatial concordance with major ecoregions, and admixture on the margins of ecoregions. Demographic models suggest that most contemporary populations diverged in isolation before coming into secondary contact, which is consistent with isolation during Quaternary glacial cycles. The population genetic relationships and relative divergence times suggest that Pleistocene glaciation isolated populations into two major clades, which diversified on separate sides of the Sierra Nevada before reconnecting at northern latitudes following range expansion after glacial retreat. Within both clades, the most recently diverged populations occupy the outer range limits at northern latitudes in the Pacific Northwest and in the Great Basin. Arid geographical features, most notably the eastern escarpment of the Sierra Nevada, eastern Cascades, and N–S basins and ranges in Nevada, are responsible for structuring populations. Consistent with expectations of expanding populations, genetic diversity in the northern extreme of the range is low, although secondary contact between genetically distinct populations in the northern part of the range (central Oregon), presumably through range expansion through the Columbia River Basin, has created a region of unexpectedly high genetic diversity.

4.1 | Glaciation and population divergence

Until 14,000 years ago, glaciers occupied high elevations in California's Sierra Nevada and Trinity Alps and Washington and Oregon's Cascade and Klamath mountains (Moore & Moring, 2013; Porter, 1976; Rosenbaum & Reynolds, 2004; Sharp, 1960). During glacial periods, glaciers descended to lower elevations and "locked-up" terrestrial water sources, resulting in drier conditions (Guyton, 1998; Hewitt, 2000). Species persisted in isolated glacial refugia in North America—Mediterranean-type ecosystems, warm and cold deserts—during glacial periods and came into secondary contact during warmer and wetter interglacial periods (Hewitt, 2011; Swenson & Howard, 2005; Waltari et al., 2007; Wilson & Pitts, 2012). We found support for allopatric divergence with secondary contact as the predominant mode of genetic divergence in the Eastern clade and between the Western and Eastern clades, while populations in the Western clade have diverged recently and with continuous gene flow. Phylogeographical studies of many North American taxa have revealed genetic signatures of population isolation and secondary contact (Hedin et al., 2020; Lavin et al., 2018; Martínez-Solano et al., 2007; Mulcahy, 2008; Pereira & Wake, 2009; Recuero et al., 2006; Shafer et al., 2010), thus adding more evidence for divergence with secondary contact as a common process among western North America species.

The glacial history of Western North America is one likely driver of population diversification in *S. occidentalis*. Glaciation precluded