

REVIEW

Are eastern and western monarch butterflies distinct populations? A review of evidence for ecological, phenotypic, and genetic differentiation and implications for conservation

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Abstract

Monarch butterflies are a species of conservation priority due to declining overwintering populations in both eastern and western North America. Declines in western overwintering monarchs—more than 99.9% since monitoring began—are especially acute. However, the degree to which western monarchs are a distinct biological entity is uncertain. In this review, we focus on phenotypic and genetic differentiation between eastern and western monarchs, with the goal of informing researchers and policy-makers who are interested in monarch conservation. Eastern and western monarchs occupy distinct environments and show some evidence for phenotypic differentiation, particularly for migration-associated traits, though population genetic and genomic studies suggest that they are indistinguishable from one another. We suggest future studies that could improve our understanding of differences between eastern and western monarchs. We also discuss the concept of adaptive capacity in eastern and western monarchs as well as non-migratory populations outside of the monarch's primary North American range. Finally, we discuss the prospect of completely losing migratory monarchs from western North America and what this entails for monarch conservation.

KEYWORDS

conservation, migration, monarch butterfly, population ecology, population genetics

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1 | INTRODUCTION

The North American monarch butterfly (*Danaus plexippus plexippus* [L.]) is an iconic species known for its distinctive coloration, association with milkweed host plants, and continent-scale seasonal migration (Gustafsson, Agrawal, Lewenstein, & Wolf, 2015). Over the past two decades, monarchs have become the focus of intense conservation attention, including a recent decision by the United States Fish and Wildlife Service

(USFWS) that a threatened listing under the U.S. Endangered Species Act (ESA) is “warranted but precluded” (USFWS, 2021: Monarch Butterfly). Under the ESA, specific populations of vertebrates are eligible for separate listings, as is the case for populations of grizzly bears (USFWS ECOS, 2020a: Grizzly Bear), gray wolves (USFWS ECOS, 2020b: Gray Wolf), and particular salmon runs (USFWS ECOS, 2020c: Chinook Salmon). For invertebrates, however, listing decisions must be made on a species- or subspecies-level basis

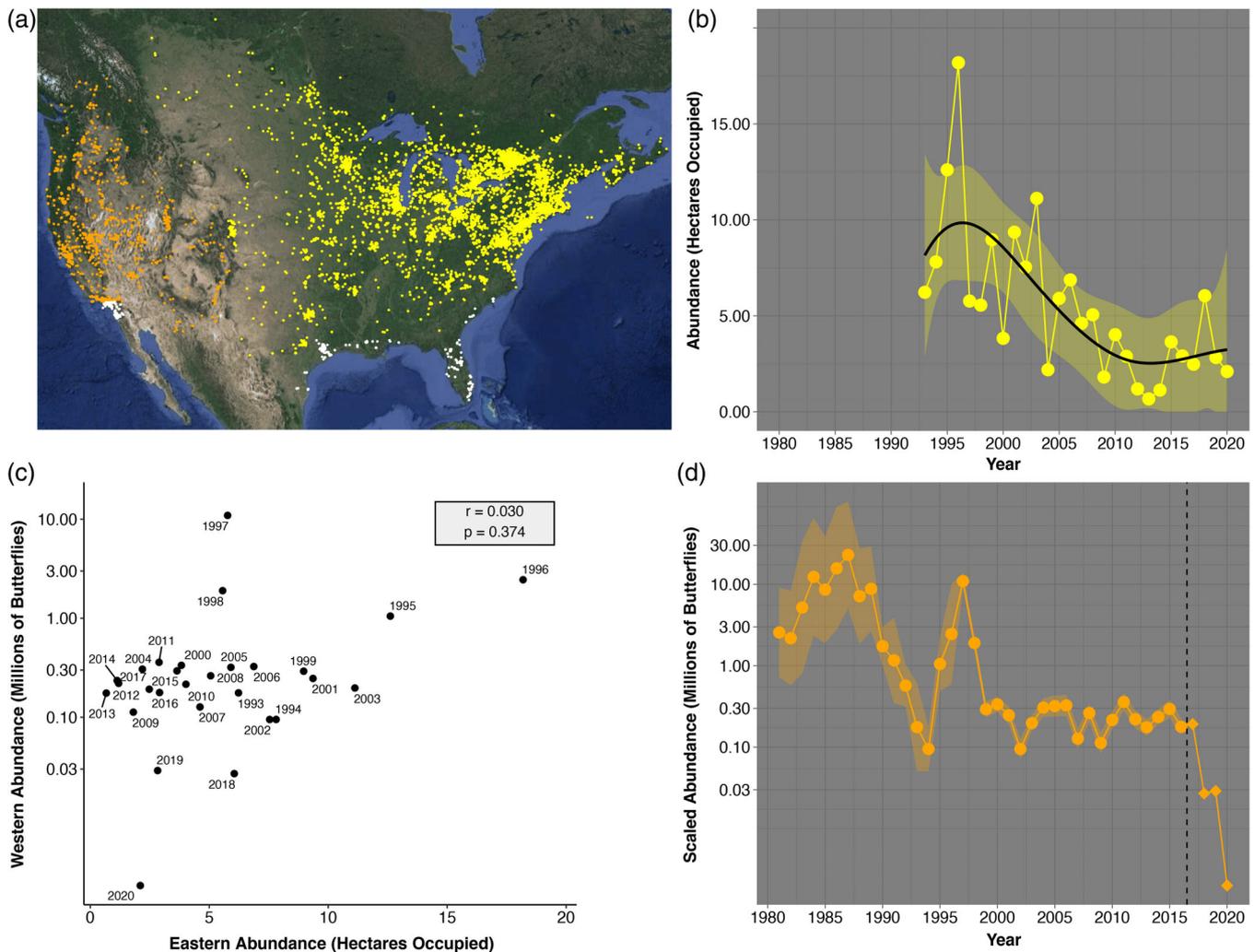


FIGURE 1 (A) Distribution of summer-breeding monarch butterflies in the United States and Canada. Points correspond to all records from GBIF ($n = 20,552$) in July and August and are separated into eastern (yellow), western (orange), and year-round breeding (white) locations. Map generated using ggmap (Kahle and Wickham 2013) and the Google Maps API. (B) Comparison of overwintering numbers for eastern and western monarchs between 1993-2020. Overwintering abundances are weakly positively correlated (also see Appendix 1). Note that axes are on very different scales. (C) Overwintering abundance for eastern monarchs from Mexico, based on data from WWF Mexico. Abundance is based on aerial estimates of forest area occupied. The trend line shows polynomial-smoothed change through time and 95% confidence intervals around this trend. Note that overwintering abundance estimates are also available for some years between 1976-1994 but are not shown here. Overwintering eastern monarch densities are likely between 21-28 million butterflies/hectare (Thogmartin et al. 2017). (D) Overwintering abundance for western monarchs from sites in California. Abundance estimates from 1981-2016 take into account sampling effort and are the same as the values presented in Schultz et al. (2017); abundance estimates for 2017-2020 are based on non-adjusted counts

(National Research Council, 1995; Western Association of Fish and Wildlife Agencies, 2019).

In the case of monarch butterflies, species-level conservation decisions require weighing evidence from two geographically and demographically distinct regions that comprise the core of the species' geographical distribution: eastern North America and western North America (Figure 1a). In addition, monarchs are established as year-round breeding populations in areas around the world, including many outlying U.S. states and territories (Ackery & Vane-Wright, 1984). This manuscript discusses whether monarch populations outside of eastern North America provide adaptive capacity—broadly defined as the ability to respond to future environmental change—for the species a whole. Here, we focus on adaptive capacity in an evolutionary rather than a demographic sense, as we consider it self-evident that the presence of monarch populations outside of eastern North America provides redundancy and reduces the risk of stochastic extinction (e.g., from extreme weather events affecting eastern overwintering locations) (Nail, Drizd, & Voorhies, 2019).

Historically, eastern and western monarchs have been regarded as distinct populations (Urquhart, 1960). Eastern monarchs overwinter in the Transverse Neovolcanic Range of central Mexico and have a summertime breeding range that covers much of the United States and southern Canada east of the Rocky Mountains. Western monarchs overwinter at hundreds of sites along a stretch of coastline in California and Baja California and have a summertime breeding range that includes parts of California and the interior west. Western monarchs occupy a large geographic area—approximately 30% of the monarch's overall North American range (Figure 1a)—but comprise a relatively small proportion of the monarch's North American population. Counts of eastern overwintering monarchs have historically been two to three orders of magnitude larger than those for western overwintering monarchs (Figure 1).

Although most conservation attention to date has focused on the larger eastern monarch population, the recent decline of western overwintering populations has been precipitous (Crone, Pelton, Brown, Thomas, & Schultz, 2019; Pelton, Schultz, Jepsen, Black, & Crone, 2019; Schultz, Brown, Pelton, & Crone, 2017). Declines in western overwintering monarchs have been mirrored by low summer breeding numbers (Espeset et al., 2016), culminating in a >99% reduction in counts of western overwintering monarchs since monitoring began. For three consecutive years, western monarch overwintering numbers have been below their quasi-extinction threshold, raising concerns about their long-term persistence (Pelton et al., 2019; Xerces Society, 2021; Figure 1d).

How, if at all, should the decline of western monarchs be incorporated into a species-level conservation approach? The answer to this question depends partly on the degree to which eastern and western monarchs constitute ecologically and evolutionary distinct entities. Specifically, if western monarchs are distinct and have the potential to contribute non-redundant adaptive genetic variation to the species, then their decline should be weighed more heavily in a species-level listing decision.

In this review, we evaluate the current state of knowledge regarding ecological, phenotypic, and genetic differentiation between eastern and western North American monarchs. In each section, we suggest future experiments and analyses that could be done to address current gaps in knowledge. We then discuss adaptive capacity in eastern and western monarchs as well as non-migratory monarch populations outside of North America.

2 | ECOLOGICAL AND PHENOTYPIC DIVERGENCE BETWEEN EASTERN AND WESTERN MONARCHS

Eastern and western North American monarchs are geographically separated by the Rocky Mountains and occupy distinct biotic and abiotic environments. These different environments have the potential to exert divergent selection pressures and drive phenotypic differentiation. Studies have used measurements from both wild-caught and common garden reared monarchs to test for phenotypic differentiation between eastern and western monarchs. We focus on four primary ecological factors—though there may be others—that are strong candidates to drive phenotypic differentiation between eastern and western monarchs: host plant associations, thermal environments, interactions with natural enemies, and migratory behavior.

2.1 | Host plant associations

Monarchs encounter more than 100 native species of milkweed (Apocynaceae: Asclepiadoideae) host plants throughout their North American range (Woodson, 1954) and have been documented using more than 40 of these species as larval hosts (Borders & Lee-Mäders, 2018; Malcolm & Brower, 1986). Eastern and western milkweed assemblages differ greatly: the eastern species perceived to be of greatest importance to monarchs (*Asclepias syriaca*, *A. viridis*, *A. incarnata*) are confined entirely to east of the Rocky Mountains, and the primary

western hosts (*A. speciosa*, *A. fascicularis*) are either partly or entirely restricted to the west. This divergence in larval host plant assemblages has the potential to contribute to adaptive differentiation in eastern and western monarchs. Two studies to date have tested for patterns of local adaptation to host plant assemblages, both using common garden experiments (Table S1). Neither study found strong evidence for local adaptation to host plant assemblages, as measured by host plant by population interactions (Ladner & Altizer, 2005) or sympatric/allopatric contrasts (Freedman, Jason, Ramírez, & Strauss, 2020). While future studies comparing eastern and western host plants are unlikely to uncover a signature of local adaptation and are not a high research priority, obtaining a better understanding of how monarchs utilize early-season milkweeds in western North America (especially *A. cordifolia*, but also *A. californica*, *A. erosa*, and *A. vestita*) would be beneficial.

2.2 | Thermal regimes

Eastern and western monarchs occupy generally distinct thermal regimes. Summer-breeding monarchs in western

North America are typically found in areas with a broader range of daytime high temperatures, despite having a more compact geographic range (Figure 2a; see Data S1). Western monarchs also occur in areas with limited summer precipitation (Figure 2b), which may determine milkweed availability and explain why western monarch occurrence records are biased toward areas with surface water (Dingle, Zalucki, Rochester, & Armijo-Prewitt, 2005) and particular land cover patterns (Dilts et al., 2019). This pattern applies to both adult and larval monarch records (Data S1). We also note that western monarchs (including immature stages) are frequently found in areas considered outside of the climatic envelope predicted in mechanistic models of larval development (Zalucki, Brower, Malcolm, & Slager, 2015; Zalucki & Rochester, 1999).

Only one study to date has directly compared eastern and western monarchs with respect to rearing temperature (Davis, Farrey, & Altizer, 2005). This study compared eastern and western monarchs under a range of temperature treatments and found that western monarch larvae were lighter in coloration than eastern larvae regardless of temperature treatment, with this result interpreted as evidence for adaptive variation: lighter cuticular color should be favorable for living in high

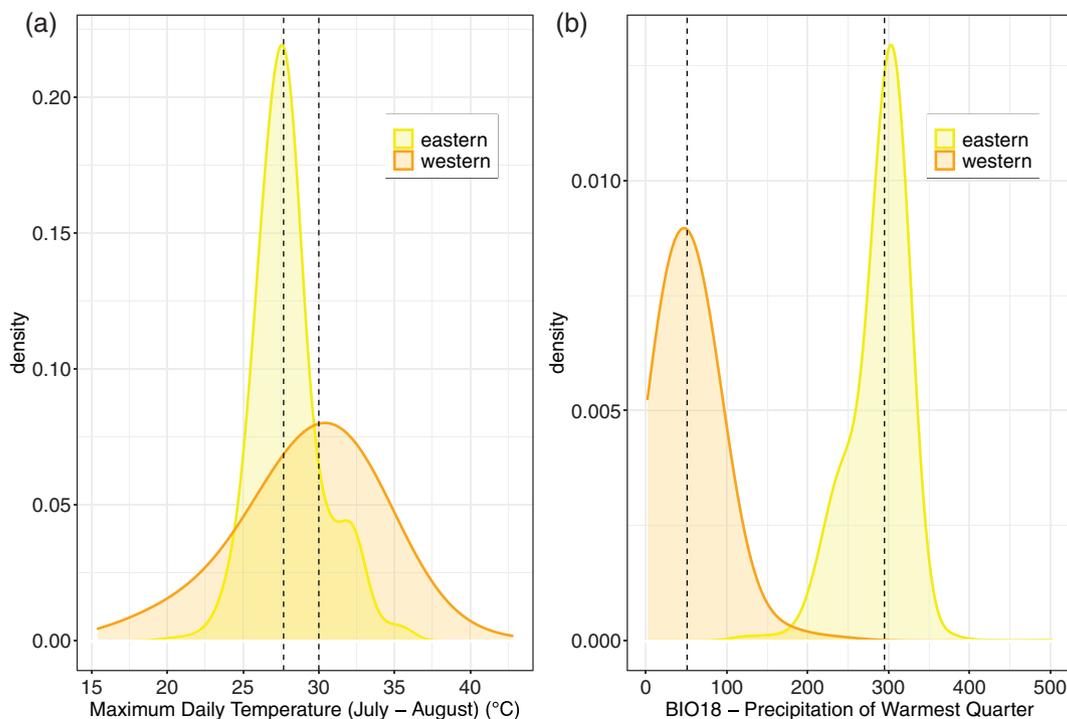


FIGURE 2 (Left) Distribution of daily high temperatures during the peak of the monarch's summer breeding season (July and August) in eastern and western North America, corresponding to the occurrence records shown in Figure 1A. Western monarchs were recorded in locations that had median summertime maximum temperatures that were 2.3°C warmer than comparable eastern locations. Results are qualitatively similar when using only records from immature monarchs (eggs, larvae, pupae) generated from iNaturalist using the iNatTools package (Hanly 2019). (Right) Summer records of monarchs in western North America come from areas that receive little summer precipitation. For details, see Appendix 1

summer temperatures (Davis et al., 2005). In addition to differences in temperature in summer breeding areas, western overwintering sites in California also tend to have slightly higher mean temperatures but lower diurnal fluctuations and lesser temperature extremes than eastern overwintering sites in Mexico (Brower et al., 2009; Brower, Williams, Fink, Zubieta, & Ramirez, 2008; Leong, 1990).

Future studies would benefit from repeating earlier studies on thermal performance using both eastern and western monarchs. For example, the often-cited estimates of developmental degree days for monarch larvae come from a genetically divergent population in Australia (Zalucki, 1982) and could be repeated using side-by-side rearing of eastern and western monarchs under conditions featuring natural insolation (Rawlins & Lederhouse, 1981). Likewise, it would be useful to identify genes that may be involved in thermal tolerance in monarchs, since these could potentially differ in frequency or level of expression between eastern and western monarchs. Genes involved in thermal tolerance may also be targets of natural selection in a warming climate (Somero, 2010).

2.3 | Interactions with natural enemies

Eastern and western monarchs likely interact with disparate assemblages of natural enemies. In eastern North America, various studies have reported on the effects of predation and parasitism by Tachinid flies (Oberhauser, 2012), fire ants (Calvert, 2004), ladybugs (Koch, Hutchison, Venette, & Heimpel, 2003), and other arthropods (Hermann, Blackledge, Haan, Myers, & Landis, 2019; Oberhauser et al., 2015; Prysby, 2004; Rayor, 2004). Few studies have focused on natural enemies in western monarchs, and this would be a useful avenue for future research.

The best-studied interaction between monarchs and their natural enemies is with the protozoan parasite *Ophryocystis elektroscirrha* (OE). Common garden cross-infection experiments with OE showed no differences in tolerance or resistance between eastern and western monarchs (de Roode, Yates, & Altizer, 2008), despite evidence for (a) higher natural prevalence of OE in western compared to eastern North America (Altizer & de Roode, 2015); (b) genetic variation among monarch genotypes for tolerance and resistance (de Roode & Altizer, 2010; Lefèvre, Williams, & de Roode, 2011); (c) variation among OE strains in virulence (de Roode et al., 2008; de Roode & Altizer, 2010); (d) evidence that monarch populations in Hawaii and South Florida do show evidence for divergence in OE tolerance and resistance (Sternberg, Li, Wang,

Gowler, & de Roode, 2013). Together, these results suggest that differences in virulence among OE genotypes are capable of selecting for genetically-based differences in tolerance and resistance in monarch populations, though such differences are not observed in eastern versus western monarchs.

A potentially interesting follow-up study would be to compare the virulence estimates of eastern and western OE genotypes from de Roode et al. (2008) with present-day estimates. A prediction might be that OE virulence has increased in western North America in the last decade, coincident with increases in the prevalence of year-round breeding in California (Crone & Schultz, 2021; Satterfield, Villablanca, Maerz, & Altizer, 2016).

2.4 | Migration-associated traits and behaviors

The most conspicuous difference between eastern and western monarchs is the scale of their seasonal migration. Mark-recapture studies with eastern monarchs show that they generally fly between 1,500–3,000 km during their fall migration to Mexico, with some individuals covering more than 4,000 km (Flockhart et al., 2017). By contrast, tagging studies with western monarchs have found maximum flight distances of ~1,400 km (James & Kappen, 2021), with typical flight distances of <800 km (James et al., 2018). Studies using stable isotope data corroborate these differences in migration distance between eastern and western monarchs (Flockhart, Brower, et al., 2017; Hobson, Wassenaar, & Taylor, 1999; Wassenaar & Hobson, 1998; Yang, Ostrovsky, Rogers, & Welker, 2016). In particular, the eastern overwintering monarchs in Flockhart, Brower, et al. (2017) had an average migration distance (based on the distance to centroid metric) of 2,995 km; Yang et al. (2016) do not provide migration distance estimates, though a substantial proportion of western overwintering monarchs appear to originate in coastal California, suggesting that average western migration distances may be closer to ~500 km. This would represent an approximately six-fold difference in average migration distance between eastern and western monarchs.

Migration acts as a strong selective filter for migratory monarchs, favoring individuals with larger and more elongated forewings (Altizer & Davis, 2010; Flockhart et al., 2017; Yang et al., 2016). Researchers have generally found that western monarchs have slightly smaller and less elongated forewings than eastern monarchs, potentially as a result of divergent selection due to differences in migration distance (Altizer &

Davis, 2010; Freedman & Dingle, 2018; Li, Pierce, & de Roode, 2016). Studies that have directly compared eastern and western monarchs—both wild-caught and common-garden reared—are shown in Table S2. Eastern monarchs have consistently larger forewings than western monarchs across all studies and comparisons (Table S2). However, these differences are relatively modest in comparisons using wild caught individuals (eastern monarchs are between 1–8% larger), and even less pronounced for common-garden reared monarchs (~1%). Future studies could focus on accounting for the sources of environmental variation (e.g., rearing temperature, host plant identity, photoperiod conditions) in

migration-associated traits that could potentially explain phenotypic differences between eastern and western monarchs. Environmental contributions to migration-associated traits may be particularly important for understanding differences observed between wild-caught eastern and western monarchs, especially in light of studies showing that larval host plant species can influence adult monarch size (Decker, Soule, de Roode, & Hunter, 2019; Freedman, Jason, et al., 2020; Pocius et al., 2017). Environmental differences were also suggested as the reason for the significantly higher flight endurance of eastern compared to western monarchs (Talla et al., 2020).

TABLE 1 Summary of studies that have directly compared eastern and western monarchs to compare patterns of genetic differentiation

Study	Number and location of monarchs sampled	Type of sequencing/number of loci analyzed	Brief summary of findings
Brower and Boyce (1991)	28 total: <ul style="list-style-type: none"> • 12 eastern (Sierra Chincua) • 12 western (Natural Bridges SP) • 1 Tobago • 3 Trinidad 	Allozymes/13 fragments used in analysis	No differentiation between any samples. Based on subsequent studies, lack of differentiation between North American and Caribbean samples likely an artifact of low statistical power.
Shephard, Hughes, and Zalucki (2002)	1,194 total: <ul style="list-style-type: none"> • 152 eastern (100 Michoacan, 52 Kalamazoo) • 160 western (50 San Diego, 55 Santa Barbara, 55 San Luis Obispo) • 855 Australia • 48 Hawaii 	Allozymes/7 fragments used in analysis	No differentiation between eastern and western samples, with the possible exception of San Diego. Substantial gene flow inferred between Santa Barbara and Kalamazoo samples.
Lyons et al. (2012)	262 total: <ul style="list-style-type: none"> • 100 eastern (St. Marks, FL) • 100 western (Pismo Beach, Santa Barbara) • 46 Hawaii • 16 New Zealand 	Microsatellites/17 sequenced, 11 used in analysis	No differentiation between eastern and western samples. Hawaii and New Zealand clearly distinct from North America. Note that Pierce et al. (2014) included the same North American monarchs and found the same results.
Zhan et al. (2014)	92 total: <ul style="list-style-type: none"> • 25 eastern (MA, NJ, FL, TX, MX) • 3 western (CA) • Various other locations in Central America, South America, Pacific, Atlantic 	Whole genome resequencing/ ~10 million SNPs with average genome-wide coverage >95%	No differentiation between eastern and western samples. Substantial differentiation between North America and all other locations, including South Florida.
Talla et al. (2020)	43 total: <ul style="list-style-type: none"> • 14 eastern (MA, NJ, FL, TX, MX) • 29 western (Big Sur, Oceano, Carpinteria) 	Whole genome resequencing/ ~20 million SNPs with average genome-wide coverage >95%	No differentiation between eastern and western samples. Overall genome-wide $F_{ST} \sim 0.001$, with no fixed differences between samples. *Note that eastern samples are the same as those used in Zhan et al. (2014).

3 | GENETIC STUDIES OF DIFFERENTIATION BETWEEN EASTERN AND WESTERN MONARCHS

3.1 | Population genetics

Researchers have been investigating the potential for genetic differentiation between eastern and western monarchs since at least 1991. As early as 1995, researchers cautioned against human-assisted movement of eastern and western monarchs across the continental divide, in part because of the perceived risk of gene flow potentially disrupting patterns of local adaptation (Brower et al., 1995). The current consensus—developed over the last 9 years and with the advent of novel sequencing methods—is that there is a lack of genetic differentiation between eastern and western monarchs.

Recent research strongly suggests that eastern and western monarchs form a genetically indistinguishable population that spans most of their North American range. The exception to this pattern is in South Florida, where monarchs are predominantly non-migratory (Brower, 1961; Zhan et al., 2014). This result is summarized in Table 1 (also reviewed in Pierce, Altizer, Chamerlain, Kronforst, & de Roode, 2015) and is robust to the kind and number of markers analyzed (i.e., microsatellites versus single nucleotide polymorphisms from whole genome sequencing) and consistent across studies. The most comprehensive study on the topic is from Talla et al. (2020), who used whole genome resequencing for 14 eastern and 29 western monarchs and found no evidence for any genetic differentiation, including no fixed differences between east and west and no windows of elevated F_{ST} in genome-wide comparisons. While these studies are consistent with genetic panmixia between eastern and western monarchs, an alternative interpretation is recent divergence but with ongoing low levels of gene flow.

Existing studies have included comparisons from a mix of breeding, migrating and overwintering monarchs. Future research could directly compare overwintering eastern and western monarchs only, since this should provide the best opportunity for detecting allele frequency shifts associated with selection imposed by long-distance migration. Seasonally variable selection pressures can drive oscillating allele frequency changes in natural populations (Behrman et al., 2018; Bergland, Behrman, O'Brien, Schmidt, & Petrov, 2014). If the differences in fall migration distance between eastern and western monarchs result in differences in selection intensity, this could potentially lead to a transient signature of

divergent selection between overwintering populations. By contrast, butterflies sequenced during summer breeding are the offspring of adults that randomly mate at overwintering sites and during spring return migration (Eanes & Koehn, 1978), which would reduce any signal of divergent selection associated with fall migration distance.

While current evidence suggests little genetic differentiation between eastern and western monarchs, studies that include non-migratory monarchs from South Florida, the Caribbean, Central and South America, the Atlantic, and the Pacific do all find clear evidence for genetic differentiation in these peripheral populations (Lyons et al., 2012, Pierce et al., 2014, Zhan et al., 2014, Hemstrom et al., in review). This pattern suggests that existing methods are capable of detecting genetic differentiation among more divergent monarch lineages, including for monarchs in South Florida, which are genetically distinct from eastern monarchs despite a large influx of eastern migrants each year (Knight & Brower, 2009, Vander Zanden et al., 2018). The genetic differences between North American and non-North American monarchs are also generally accompanied by more pronounced phenotypic differences than those observed between eastern and western monarchs (Freedman, Dingle, Strauss, & Ramírez, 2020; Li et al., 2016). However, it is possible that expanded sampling involving hundreds or thousands of monarchs sampled across a large number of markers could reveal subtle patterns of genetic differentiation between eastern and western monarchs that present studies have not detected.

3.2 | Migration rates between east and west

Given their divergent overwintering destinations, it may at first be difficult to see how eastern and western monarchs could form a single genetic population. Mark-recapture studies (Billings, 2019; Morris, Kline, & Morris, 2015), behavioral observations (Brower & Pyle, 2004; Pyle, 1999) and museum records (Dingle et al., 2005) suggest that at least some western monarchs travel to Mexican overwintering sites in the autumn. Billings (2019) compiled results from 3 years of mark-recapture studies conducted in Arizona. Of the 3,194 tagged and released monarchs, 32 were recovered at California overwintering sites and 12 were recovered at Mexican overwintering sites. Likewise, there is speculation that Mexican overwintering monarchs might recolonize western North America in the spring (Brower & Pyle, 2004). When monarch populations in the east and west were larger,

occasional movement across the Rocky Mountains was recorded (Pyle, pers. comm.). None of the more than 2 million monarchs tagged east of the Rockies between August–November have ever been recovered in the west (O. Taylor, unpublished data); however, this may reflect (a) low general recovery rates ($\sim 1\%$) for tagged monarchs (Taylor et al., 2019); (b) low rates of movement from Mexican overwintering sites to western North America; (c) limited human population density in areas where these monarchs might be recovered (i.e., southern Arizona and New Mexico). It is also important to note that even small numbers of migrants between east and west—the classic rule of thumb suggests one migrant per generation (but see Mills & Allendorf, 1996)—would be sufficient to prevent genetic differentiation from developing in a large, outcrossing species like monarchs.

4 | ADAPTIVE CAPACITY IN MONARCHS

4.1 | Adaptive capacity in North American monarchs

The concept of adaptive capacity refers broadly to the ability of populations or species to adapt to future environmental change. North American monarchs possess high levels of genetic diversity, as indicated by high estimates of effective population size ($N_e \approx 2 \times 10^6$) (Zhan et al., 2014). This high level of standing diversity should be associated with robust evolutionary potential. Eastern and western monarchs appear to harbor comparable levels of genetic diversity, as seen in measures of allelic richness using microsatellites (Pierce et al., 2014), the ratio of heterozygote to homozygote genotypes (Zhan et al., 2014), and various other measures (Talla et al., 2020, Hemstrom et al. in review). The lack of fixed genetic differences between eastern and western North America suggests that there are no strongly selected genetic variants that contribute to adaptation specifically to eastern or western North American environments (Talla et al., 2020). Experiments that reciprocally translocate eastern and western monarchs and assess their ability to exhibit appropriate migration-associated behaviors (e.g., directional orientation) would help to establish whether eastern and western monarchs are actually interchangeable. A number of previous studies have involved transplanting eastern monarchs westward (Mouritsen et al., 2013; Urquhart & Urquhart, 1977), though the inferences that can be drawn from these studies may be limited (see Brower et al., 1995; Brower & Pyle, 2004; Oberhauser et al., 2013).

4.2 | Adaptive capacity in non-migratory monarch populations around the world

Many non-migratory, year-round breeding populations of monarchs have become established in locations around the world over recent evolutionary history (Pierce et al., 2014; Vane-Wright, 1993; Zalucki & Clarke, 2004; Zhan et al., 2014). These sites include multiple locations that fall under the purview of USFWS: American Samoa, Guam, the Northern Mariana Islands, Hawaii, Puerto Rico, and the U.S. Virgin Islands. Year-round breeding populations are also present in South Florida, coastal Georgia and the Carolinas, the Gulf Coast states, and southern California. Whether these recently-derived non-migratory populations can act as meaningful reservoirs of genetic diversity and adaptive capacity remains an open question (Reppert & de Roode, 2018).

A recent review by Nail et al. (2019) suggested that the monarch's global distribution provides the species with adaptive capacity. While this may be true in a demographic sense—having widely distributed populations around the world reduces the risk of a stochastic extinction event for the species as a whole—recent research suggests that non-migratory populations may not provide adaptive capacity in an evolutionary sense. Derived monarch populations have reduced allelic richness (Pierce et al., 2014) and effective population sizes (Zhan et al., 2014, Hemstrom et al. in review), suggesting a loss of standing genetic diversity associated with founding bottlenecks in these populations. The reduction in genetic diversity in these peripheral populations could conceivably compromise their ability to adapt to future environmental change.

A number of recent studies have addressed the question of adaptive capacity in non-migratory monarchs. Freedman et al. (2018) found that non-migratory monarch populations from Queensland retain migration-associated traits such as induction of reproductive arrest, suggesting that the loss of migration may be due to a lack of relevant seasonal cues, rather than an inability to sense and/or integrate those cues. However, two recent studies (Tenger-Trolander & Kronforst, 2020; Tenger-Trolander, Lu, Noyes, & Kronforst, 2019) found that commercially-reared monarchs whose breeding history precludes seasonal migration can lose their ability to consistently directionally orient, a critical part of their ability to complete migration. These studies suggest that some aspects of monarch migration are phenotypically plastic and may be shielded from selection and maintained in non-migratory populations, while other migration-associated traits might be selected against and lost. Another recent study showed that non-migratory

monarchs from Costa Rica have less narrowly tuned peripheral neurons associated with the ability to detect green light, which is thought to be an important celestial navigational cue in temperate regions (Nguyen, Beetz, Merlin, & El Jundi, 2021). Finally, non-migratory monarch populations tend to have high prevalence and abundance of infection with OE (Altizer, Oberhauser, & Brower, 2000; Bartel, Oberhauser, De Roode, & Altizer, 2011; Satterfield, Maerz, & Altizer, 2015). Despite having greater tolerance and resistance to OE, non-migratory populations' parasite loads may render them less capable of completing long-distance flights (Bradley & Altizer, 2005). Together, these results call into question the notion that derived non-migratory monarch populations are adequate stand-ins for their migratory North American ancestors if the goal is to conserve functional genetic diversity.

5 | WHAT LESSONS CAN BE LEARNED FROM DECLINES IN WESTERN MONARCHS?

One year after approximately 300,000 monarchs were recorded at overwintering sites in California in 2016, Schultz et al. (2017) proposed a quasi-extinction threshold of approximately 30,000 monarchs and suggested a 72% risk of extinction within the next 20 years. In 2018, western overwintering numbers fell below the quasi-extinction threshold for the first time. By 2020, fewer than 2,000 monarchs were recorded from California overwintering sites. The reasons for this extremely rapid decline are not entirely clear and are hard to disentangle from time series data (see Crone et al., 2019), though climate change—and especially autumnal warming—has been implicated broadly in the decline of western North American butterflies (Forister et al., 2021). The lack of recovery in western monarchs between 2018–2020 is also consistent with possible Allee effects. The rapid loss of western monarchs highlights that adoption of mitigation measures to stem declines cannot be reactive; ongoing efforts to restore overwintering sites in California, while well-intentioned, would have been more useful if implemented preemptively.

Despite the looming extirpation of *migratory* monarchs from the western U.S., a potentially growing population of year-round resident monarchs has established in coastal California (Crone & Schultz, 2021; Satterfield et al., 2016), particularly in urban areas with cultivated, non-native milkweed (especially *A. curassavica*). While likely several orders of magnitude smaller than historical migratory populations, these year-round breeding populations may prevent a complete extirpation of monarchs from western North America. It is currently unclear whether year-round breeding

populations in California as well as the U.S. Gulf Coast and Florida may act as demographic sources or sinks for migratory monarchs. There is some evidence of monarchs interrupting their migration and joining year-round breeding populations in both eastern (Satterfield et al., 2018) and western (James & Kappen, 2021) North America. The distinction between outright extinction versus loss of migration is important and has been noted previously: indeed, the 2014 petition to list monarchs under the ESA highlights that while species-level extinction is unlikely, the phenomenon of long-distance migration is at risk (also see Wells, Pyle, & Collins, 1983, Brower & Malcolm, 1991). From an evolutionary perspective, migration is likely a derived condition within the *Danaus* clade containing monarchs (Zhan et al., 2014). Even though migration is not uncommon among other Danaine butterflies (Ackery & Vane-Wright, 1984), monarchs are unique in the scale and scope of their migration. Future research into partial migration—whereby animal populations are composed of a mixture of resident and migratory individuals (Chapman, Brönmark, Nilsson, & Hansson, 2011)—may provide a glimpse into an uncertain future for migratory monarch butterflies.

6 | CONCLUSIONS

Eastern and western monarchs are geographically and demographically distinct, though there is only modest evidence for phenotypic differentiation and no current evidence for genetic differentiation between them. Policy-makers who are considering how to contextualize the decline of western monarchs will need to decide whether to adopt a parsimonious or precautionary approach in their decision-making. A parsimonious approach based on presently available genetic data would suggest that western monarchs do not constitute a distinct population: at present, there are no diagnostic criteria that could reliably be used to distinguish an eastern from a western monarch. A precautionary approach would recognize the potential for western monarchs to provide adaptive capacity and would involve treating the two populations as distinct based on their phenotypic and demographic differences. The rapid decline of western migrants highlights the need for conservation practitioners to consider sudden state changes and to decide whether conservation efforts should focus exclusively on migratory monarchs.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

All authors were involved in conceiving of the ideas presented in this manuscript. Micah G. Freedman performed data analyses and wrote the first draft. All authors contributed to editing and revising the manuscript.

ETHICS STATEMENT

The authors certify that the material presented here is original work which has not been previously published. This research did not involve the use of animal or human subjects.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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