




Opposing genetic patterns of range shifting temperate and tropical gastropods in an area undergoing tropicalisation

Karolina M. Zarzyczny^{1,2}  | Michael E. Hellberg³ | Elena B. Lugli² | Moira MacLean¹ | David A. Paz-García⁴  | Marc Rius^{5,6} | Ethan G. Ross^{1,7} | Erick X. Treviño Balandra⁴  | James Vanstone¹ | Suzanne T. Williams²  | Phillip B. Fenberg^{1,2} 

¹School of Ocean and Earth Science, National Oceanography Centre, University of Southampton, Southampton, UK

²Department of Science, Natural History Museum, London, UK

³Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, USA

⁴Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, Mexico

⁵Centre for Advanced Studies of Blanes (CEAB, CSIC), Blanes, Spain

⁶Department of Zoology, Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Johannesburg, South Africa

⁷School of Biological Sciences, University of Aberdeen, Aberdeen, UK

Correspondence

Karolina M. Zarzyczny, School of Ocean and Earth Science, National Oceanography Centre, University of Southampton, Southampton, UK.
Email: k.m.zarzyczny@soton.ac.uk

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Abstract

Aim: The poleward range expansion of tropical species, and range contraction of temperate species (known as tropicalisation) has mainly been studied from an ecological perspective, with little research on its genetic consequences. Here, we used distributional and genetic data to document the consequences of tropicalisation in rocky shore gastropods and assess more broadly the future implications of tropicalisation on phylogeographic patterns.

Location: Nineteen sampling sites along >3000 km of the eastern Pacific rocky intertidal zone, from the tip of the Baja California Peninsula to southern California.

Taxon: Temperate gastropods: *Lottia conus*, *L. strigatella*, *Fissurella volcano* and *Tegula gallina*.

Tropical gastropods: *Fissurella rubropicta*, *Nerita funiculata* and *N. scabricosta*.

Methods: We determine historical and modern distributions of tropical and temperate species by combining historical records with current field surveys. Using a section of the cytochrome oxidase subunit I gene, we utilised comparative phylogeography, analysis of molecular variance, F_{ST} pairwise comparison, mismatch distributions of haplotype differences and neutrality tests to detect genetic signatures of tropicalisation and to better understand its consequences.

Results: We identified range contractions in two temperate species and range expansion in all three tropical species. We detected genetic signatures of range expansion in the tropical species through unimodal distributions of pairwise haplotype differences and strongly negative values for the F_u and $L_i D$ and F^* statistics. We found population subdivision and phylogeographic breaks in three temperate species, although the geographic location of the breaks differed among species.

Main Conclusions: Genetic signatures and field surveys indicate recent range expansions in tropical species, supporting tropicalisation along the studied coastline. Conversely, we found phylogeographic breaks in temperate species, suggesting that tropicalisation may cause genetic erosion of evolutionary distinct lineages with

range-contraction. The different locations of the phylogeographic breaks among temperate species suggests that some barriers are species specific.

KEYWORDS

biogeographic barriers, Eastern Pacific, Gulf of California, landscape genetics, range shifts, rocky shores, tropicalisation

1 | INTRODUCTION

Tropicalisation is characterised by the poleward range expansion of tropical species combined with contraction of temperate species (Vergés et al., 2014, 2016; Wernberg et al., 2012) and is occurring in marine ecosystems at mid- to low-latitude biogeographic transition regions (Horta e Costa et al., 2014). Until recently, tropicalisation has mostly been studied from an ecological perspective, with a focus on interspecific interactions, particularly changes in herbivory (Kumagai et al., 2018; Vergés et al., 2016; Zarzyчны et al., 2022) and consequent phase-shifts (Peleg et al., 2020; Vergés et al., 2019). For example, studies of intertidal ecosystems have shown shifts from saltmarshes to mangrove-dominated ecosystems (Guo et al., 2017) and changes in species composition on rocky shores (Hawkins et al., 2009; Mieszkowska et al., 2021). However, few studies have addressed the genetic consequences of tropicalisation (but see Arenas et al., 2012; Coleman et al., 2020; Fifer et al., 2022; Gurgel et al., 2020). Unravelling the genetic composition of expanding tropical or contracting temperate populations has the potential to advance our understanding of how species may respond to continuing warming (e.g. species ability to adapt and acclimate to future conditions) and how their distributions may ultimately be affected. However, to our knowledge, no studies simultaneously investigate the genetic consequences of both range expanding and contracting species in a region undergoing tropicalisation.

Drawing from phylogeography and tropicalisation studies, we can unravel at least two general predictions regarding the effects of tropicalisation. First, for phylogeographic structure to exist, barriers to gene flow between populations must remain in place over many generations (Avice, 1987). Tropicalisation is expected to result in communities that consist of a mix of recently expanded species that have tropical origins and resident temperate species that have a long history of occupying the region undergoing tropicalisation (Horta e Costa et al., 2014). As a result, we predict that temperate species in a region undergoing tropicalisation are more likely to exhibit phylogeographic breaks (Zink et al., 2001) as temperate populations would have more time to be subjected to any barriers to gene flow than expanding tropical species (Edwards et al., 2022; Fenberg et al., 2014; Riddle et al., 2000). Furthermore, such temperate species exhibiting phylogeographic breaks may be at risk of losing unique genetic diversity as their ranges contract in response to contemporary climate change (Fenberg et al., 2014).

Second, populations of recently expanded tropical species have had less time to be subjected to historical barriers to gene flow

within the region of expansion (Zink et al., 2001). As such they are less likely to exhibit deep phylogeographic breaks in the region of tropicalisation, instead being more likely to exhibit genetic evidence of range expansions (Domínguez et al., 2023; Excoffier, 2004). Range expansions are often characterised by founder effects, where a limited number of individuals from a source population establish a new population with only a subset of original genetic diversity (Slatkin & Excoffier, 2012). This process decreases genetic diversity at the leading edge of the species range compared to populations at the range centre (Slatkin & Excoffier, 2012). Given the impact of founder effects, genetic diversity and the number of unique haplotypes within the expanded range of tropical species should be relatively low (Slatkin & Excoffier, 2012) unless sufficient gene flow between the source and the range-expanding populations persists (Ramos et al., 2018). For example, a range-expanding gastropod, shows reduced genetic diversity in its recently expanded range (Fenberg et al., 2014). However, to our knowledge, such pattern of reduced genetic diversity has not yet been observed in tropical, recently range-expanding species. We therefore predict that tropical species will not display phylogeographic breaks but may show evidence of reduced genetic diversity in the recently expanded range.

Here, we focused on temperate and tropical grazing gastropods that are co-distributed along a rocky coastline undergoing tropicalisation. To this end, it is helpful to focus on a single taxonomic and functional group with broadly similar dispersal capabilities, living within the same habitat and region. This removes potential confounding factors such as depth, substrate type, and broad scale factors such as regional oceanography. We used comparative phylogeography combined with multi-species historical records from the literature, museum collections, and field surveys to understand how tropicalisation influences the distribution of genetic diversity in a transition between tropical and temperate ecoregions. Specifically, we tested for the presence of phylogeographic breaks in four temperate and three tropical species and for genetic signatures of recent range expansion in the tropical species. We were particularly interested in unravelling whether temperate gastropods are at risk of the genetic erosion of evolutionary distinct lineages and whether tropicalisation leaves a genetic footprint on tropical species. We predicted that temperate gastropods would display phylogeographic breaks and structure arising from past vicariant events and the variable physical environment of the peninsula. In addition, we expected that tropical species would not display phylogeographic breaks due to their recent expansion into the region but would demonstrate genetic evidence of recent range expansion.

2 | MATERIALS AND METHODS

2.1 | Study region

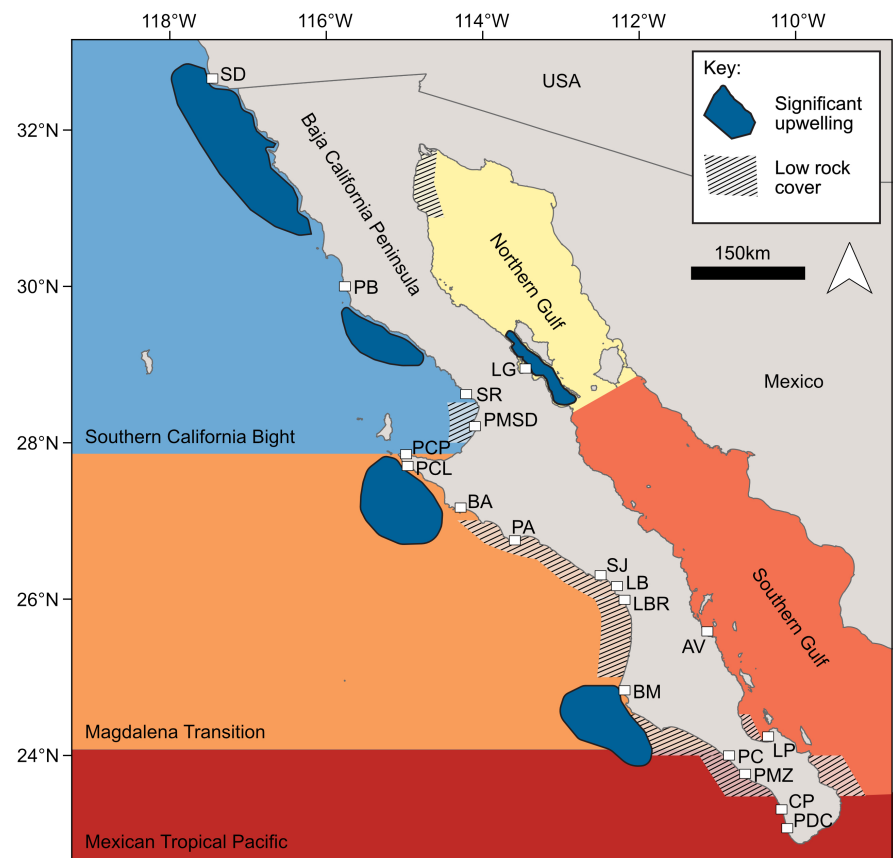
The Baja California Peninsula separates the eastern Pacific Ocean from the Gulf of California and is a major region of phylogeographic research (e.g. Edwards et al., 2022; Lindell et al., 2006; Riddle et al., 2000). Its geography, combined with the influence of the California Current System (Checkley & Barth, 2009), and coastal upwelling (Fenberg et al., 2015; Zaytsev et al., 2003) makes the peninsula a temperate-tropical transition region, hosting species of both affinities (Lluch-Belda et al., 2003). The peninsula stretches across four distinct marine biogeographic regions (Figure 1): the Southern California Bight, the Mexican Tropical Pacific on the eastern Pacific coast (Blanchette et al., 2008; Fenberg et al., 2015; Spalding et al., 2007) and the Northern and Southern Gulf regions within the Gulf of California (Riginos & Nachman, 2001). Between the Southern California Bight and the Mexican Tropical Pacific is a biogeographic transition zone, the Magdalena Transition, where the southern range limits of many temperate species (Cavanaugh et al., 2019; Reid, 1996) meet the northern range limits of many tropical species (Keen, 1971; Reid, 2002). Within this transition region, several taxa exhibit phylogeographic breaks, including plants (Lira-Noriega et al., 2015), mammals (Leaché et al., 2007), reptiles (Harrington et al., 2018; Leaché et al., 2007), birds (Zink et al., 1997), fish (Riginos, 2005) and invertebrates from terrestrial (Crews & Hedin, 2006) and marine (Fenberg et al., 2014; Hurtado et al., 2010;

Peterson et al., 2013) ecosystems. The mosaic of sandy beaches and rocky shores along the coasts of Baja California Peninsula further influences the biogeographic structure and species richness gradient of the rocky shore gastropods (Fenberg & Rivadeneira, 2019). Rocky habitat is abundant in the northern portion of the peninsula, with sandy beaches forming large gaps along the southern coasts (Figure 1) (Fenberg & Rivadeneira, 2019). Areas of significant upwelling persist along the eastern Pacific coast (Zaytsev et al., 2003) and within the Gulf of California (López et al., 2006; Santamaría-del-Angel et al., 1994; Figure 1). This combination of biogeographic structure, climate, habitat availability and oceanography make Baja California an exemplar study system for genetic consequences of tropicalisation.

2.2 | Study species

We focused on abundant and co-existing temperate (*Lottia conus*, *L. strigatella*, *Fissurella volcano* and *Tegula gallina*) and tropical (*Nerita scabricosta*, *N. funiculata* and *F. rubropicta*) rocky intertidal gastropod grazers. We classified species as tropical or temperate based on whether the mid-point of their latitudinal distribution falls within a temperate or subtropical/tropical region (Fenberg & Rivadeneira, 2019). Larval durations for each study species are given in Table 1. Based on their respective genera, *Lottia* spp., *Fissurella* spp. and *T. galina* are expected to have a lecithotrophic larval type. For *Nerita* spp. the larval type and duration are unclear, with some

FIGURE 1 Marine biogeographic regions of the Baja California Peninsula, adapted from Spalding et al. (2007), Fenberg et al. (2015), Blanchette et al. (2008) and Riginos and Nachman (2001). Low rock cover is defined as <20% rock cover per 0.5° and is shown for the peninsula only (Fenberg & Rivadeneira, 2019). Regions of significant upwelling are adapted from López et al. (2006), Santamaría-del-Angel et al. (1994), and Zaytsev et al. (2003). The 19 study sites are marked with white rectangles where SD=San Diego, PB=Punta Baja, SR=Santa Rosalillita, PMSD=Punta Morro Santo Domingo, PCP=Punta Caballo de Piedra, PCL=Punta Clambey, BA=Bahía Asunción, PA=Punta Abreojos, SJ=San Juanico, LB=La Bocana, LBR=Las Barrancas, BM=Bahía Magdalena, PC=Punta Conejo, PMZ=Punta Marquez, CP=Cerritos Point, PDC=Pozo de Cota, LP=La Paz, AV=Agua Verde, and LG=La Gringa. Site coordinates and survey dates are listed in Table S1.



studies suggesting the members of the genus can have short lived dispersal (Kano, 2006), and others suggesting they have long dispersal potential (Lesoway & Page, 2008; Underwood, 1974). In general, more research is required on larval dispersal of tropical eastern Pacific gastropods (Fenberg & Rivadeneira, 2019).

2.3 | Sample and data collection

We collected whole snails from 16 sites on the eastern Pacific coast between Pozo de Cota (23.0°N) and San Diego, California (32.7°N) between 2017 and 2022. These sites span the three eastern Pacific ecoregions (Figure 1). We also sampled three sites in the Gulf of California, between La Paz (24.1–24.3°N) and La Gringa (29.1°N). Snails were preserved in 70% ethanol in the field and transferred to absolute ethanol in the laboratory for processing and storage at room temperature.

2.4 | DNA extraction, amplification and sequencing

We extracted DNA from foot tissue using the DNeasy Blood and Tissue Kit following the manufacturer's instructions (Qiagen), apart from one minor modification; tissue samples were soaked in UV-treated Milli-Q water for 30 min, followed by blotting on Kimwipe to remove excess liquid prior to using the kit to soften the tissue and remove ethanol. For all species, we amplified a fragment of Cytochrome Oxidase Subunit I (COI). We chose COI as a genetic marker for our study for two reasons. First, as a mitochondrial DNA (mtDNA) marker, COI is non-recombining and highly variable in comparison to nuclear markers (Ballard & Whitlock, 2004) making it useful for distinguishing closely related populations and species. Second, COI has been widely used for phylogeographic and population genetics studies of marine and terrestrial species within our study region (Dawson et al., 2011; Fenberg et al., 2014; Hurtado et al., 2007; Riddle et al., 2000). This makes the molecular result of our study directly comparable with others from the Baja California peninsula, a hotspot of phylogeographic research using COI data (Supplementary Material S1). For example, future comparative phylogeographic studies can use the commonly calibrated molecular clock of COI to infer evolutionary and phylogeographic patterns along the peninsula. Furthermore, by focussing on a common marker across our study species, we can more clearly compare differences in molecular results between temperate and tropical species to detect phylogeographic differences without confounding issues, like differences in mutation rate across multiple markers. In addition, many historical phylogeographic studies in the region relied on mtDNA and are now only available as online DNA sequences (i.e. on GenBank). These studies can be re-sampled in the future using the same markers (usually COI) to identify temporal genetic change as tropicalisation progresses. However, we acknowledge that it is important to interpret phylogeographic and population genetics analyses inferred from a single genetic marker with caution, as relying solely on a single

genetic marker increases the likelihood of bias introduced by various evolutionary processes (Ballard & Whitlock, 2004).

Primers and optimal PCR conditions varied among the species (Tables S2 and S3). PCR amplicons were then cleaned using AppMag PCR clean up beads (Appleton Woods) at 1.8× PCR reaction volume and sequenced using BigDye 3.1 on an ABI 3730 DNA Analyser at the Natural History Museum, London. For *T. gallina* only, PCR products were purified using an ethanol-EDTA precipitation protocol, and sequenced using BigDye 3.1 on an ABI Analyser 3130xl at Louisiana State University.

2.5 | Establishing historical species ranges

We estimated the historical northern range limits of tropical species and the southern limits of temperate species by using museum collections (and correspondence with curators) from the Natural History Museum of Los Angeles, Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/what-is-gbif>), primary literature searches, books, and historical surveys that include published and unpublished data up to 1996 (Keen, 1971; Fenberg & Rivadeneira, 2019; L. Groves, personal observations, November 2022; J. Slapcinsky, personal observations, February 2023; A. Kittle, personal observations, March 2023).

2.6 | Establishing modern species ranges

To determine present-day species' ranges, we surveyed 16 sites along the Eastern Pacific coast and three sites within the Gulf of California (Figure 1). We estimated the abundance for each species through two-hour, exhaustive surveys using semi-quantitative SACFOR scale (S=Superabundant, A=Abundant, C=Common, F=Frequent, O=Occasional, R=Rare, and not observed). Semi-quantitative exhaustive surveys allow for rapid abundance assessment over expansive habitats when survey time is restricted (Strong & Johnson, 2020). In the case of our study, all surveys were carried out at low tide which restricted each survey to 2h. Moreover, semi-quantitative assessments are thought to be better at detecting rare species in comparison to less expansive, quantitative methods (Strong & Johnson, 2020). All surveys were conducted between September and October 2017, March 2018, and December 2021 and January 2022.

We used the survey data to determine the modern northern range limits for tropical species, and modern southern range limits for temperate species. We confirmed modern species identification of all sampled species by barcoding a section of mitochondrial COI gene and compared the sequenced samples with GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) using Nucleotide BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). To refine the location of the range limits, we assessed independent species entries on iNaturalist (<https://www.inaturalist.org>) and GBIF (<https://www.gbif.org/what-is-gbif>). We confirmed species identification using the photographs

TABLE 1 Northern and southern limits for past and present ranges of studied rocky shore gastropods, their larval duration and the accession numbers of all unique haplotypes of each studied species.*

Species	Historical distribution	Modern distribution	Larval duration	Accession numbers
Temperate				
<i>Lotia conus</i> ^a	No reliable historical limits. At least Jalama Beach, CA (34.5° N) ¹ to Bahia Magdalena (24.5° N) ¹	At least Jalama Beach, CA (34.5° N) ¹ to Bahia Magdalena (24.5° N) ²	7–14 days ¹	Haplotypes 1–23 OQ681978–OQ682000
<i>Lotia strigatella</i>	Southern California, down to the tip of Peninsula in Cabo San Lucas (22.9° N) and along the entire Gulf of California ^{3,4}	Between San Diego and Punta Baja (30.0–32.7° N) to Pozo de Cota (23.0° N), absent from the Gulf ²	5–14 days ^{a,5}	Haplotypes 1–35 OQ682001–OQ682035
<i>Fissurella volcano</i>	Crescent City, CA (41.8° N) ⁶ to Punta Marquez (24.0° N) ⁷	At least Crescent City, CA (41.8° N) ⁶ to Bahia Magdalena (24.6° N) ²	~4 days ^{8,9}	Haplotypes 1–33 OQ682036–OQ682068
<i>Tegula gallina</i>	Point Conception, CA (34.4° N) ¹⁰ to Punta Marquez (24.0° N) ¹¹	At least Point Conception, CA (34.4° N) ⁹ to Bahia Magdalena (24.6° N) ²	2–7 days ^{a,12,13}	Haplotypes 1–63 OQ682069 - OQ682131
Tropical				
<i>Fissurella rubropicta</i>	Lagoon Head, Baja California (27.9–28.1° N) ³ to Oaxaca, Mexico (15.6–16.3° N) ³	Between Santa Rosalilita and Punta Baja (28.6–29.6° N) ² to Oaxaca, Mexico (15.6–16.3° N) ³	3–10 days ^{a,7,8,14,15}	Haplotypes 1–7 OQ682132–OQ682138
<i>Nerita scabricosta</i>	Punta San Hipolito (27.0° N) ¹⁶ to Ecuador (3.0° S–1.0° N) ³	Punta Caballo de Piedra (27.8° N) ² to Ecuador (3.0° S–1.0° N)	Unknown	Haplotypes 1–42 OQ682139–OQ682180
<i>Nerita funiculata</i>	Punta Santo Domingo (26.3° N) ¹⁷ to Peru (18.4° S–0°) ³	Punta Caballo de Piedra (27.8° N) ² to Peru (18.4° S–0°) ³	Unknown	Haplotypes 1–72 OQ682181–OQ682252

Note: As we only surveyed the Baja California Peninsula, we only provide updated northern range limits for tropical species and updated southern range limits for temperate species. 1—Coombs et al. (2017), 2—This study, 3—Keen (1971), 4—Simison and Lindberg (2003), 5—Grismer (2002), 6—Morris et al. (1980), 7—Groves and Mertz (2023a), 8—Kelly and Palumbi (2010), 9—Reynoso-Granados et al. (2007), 10—Hellberg (1998), 11—we obtained samples of *T. gallina* from Punta Marquez collected by Hellberg in 1996, 12—Guzmán del Próo et al. (2011), 13—Moran (1997), 14—Blanco et al. (2019), 15—Pérez et al. (2007), 16—Groves and Mertz (2023b) and 17—Groves and Mertz (2023c).

*Denotes the larval duration is an estimate based on data for congeneric species.

associated with the species recording and extracted the latitude and longitude data.

To estimate the coastline extent of modern range changes for species with reliable historic data, we plotted the historic and modern range limits (southern range limits for temperate species and northern range limits for tropical species) onto the coastal transect produced by Fenberg and Rivadeneira (2019). We then calculated the coastline distance between historic and modern range limits to estimate modern range change.

2.7 | DNA sequence data analysis

We visually assessed the quality of chromatograms and removed poor-quality sequences from the analysis. We used MEGA 11 (Tamura et al., 2021) to manually align the sequences for each species and trimmed non-variable, ragged ends to obtain sequences of the same length (634 bp for *L. conus*, 642 bp for *L. strigatella*, 632 bp for *F. volcano*, 614 bp for *F. rubropicta*, 639 bp for *T. gallina*, 575 bp for *N. scabricosta*, and 624 bp for *N. funiculata*). The resulting sequences (*L. conus*: $n=142$; *L. strigatella*: $n=120$; *F. volcano*: $n=114$; *T. gallina*: $n=157$; *F. rubropicta*: $n=63$; *N. scabricosta*: $n=87$; and *N. funiculata*: $n=89$; see Table S4 for site details) were used in phylogeographic analyses.

We created haplotype networks using R Studio 4.2.0 following the workflow and packages from Toparslan et al. (2020). We grouped sequences first by collection site, then by northern and southern populations as informed by the haplotype network and geographic location. We conducted an analysis of molecular variance (AMOVA) with pairwise differences and 1023 permutations for both groupings. When phylogeographic structure was not detected, we conducted an AMOVA for site groupings only. For species exhibiting significant population differentiation, we conducted a pairwise F_{ST} comparison using Arlequin (3.5.2.2; Excoffier & Lischer, 2010) to determine which sites show population structure. To reduce the chances of type I errors, we applied a Bonferroni correction to pairwise F_{ST} comparisons. Nucleotide diversity and haplotype diversity were calculated for all species, across all sites using DnaSP 6.12.03 (Rozas et al., 2017).

For tropical species, we tested for evidence of a recent range expansion using a pairwise differences mismatch distribution analysis and extracted the Harpending raggedness index in Arlequin. Stationary populations are characterised by a multi-modal mismatch distribution and low raggedness (Harpending, 1994). In contrast, a population which has undergone a recent population or range expansion is expected to present a smooth, unimodal mismatch distribution. To test for signatures of a range expansion further, we calculated the sum of squared deviation with 10,000 bootstrap replicates, between pairwise differences of observed and expected distributions under a spatial expansion model as described in Excoffier and Lischer (2010). We also conducted two neutrality tests; Fu and Li's statistics, D and F^* (Fu & Li, 1993; Ray et al., 2003), to test if allelic distribution deviates from the

Wright-Fisher model, as expected for range expanding population, in DnaSP (Rozas et al., 2017). We did not test for range expansion in temperate species, as we did not obtain samples from the northern range limit of those species.

3 | RESULTS

3.1 | Species ranges

Comparing our field surveys with historical data revealed a recent range contraction of ~144 km in two temperate species: *F. volcano* and *T. gallina* (Table 1). All three tropical species have recently expanded their ranges north by as much as 480 km in about 50 years (Table 1). We also reported new baseline ranges for temperate *L. conus* and *L. strigatella*, but we are unable to confirm whether these species have undergone range contractions due to the absence of reliable historical records.

For *T. gallina* and *F. volcano*, the range contraction occurred from Punta Marquez (24.0°N) to Bahía Magdalena (24.6°N) between 1996–2022 and 1979–2022, respectively. For tropical species, *F. rubropicta* has expanded northward by ~240 km, from “Lagoon Head” (27.9°N–28.1°N) to between Santa Rosalillita and Punta Baja (29.23°N) between 1971 and 2022. *Nerita scabricosta* and *N. funiculata* have both expanded their northern range limit since the 1970's by ~288 km from Punta San Hipolito (27.0°N) and ~480 km Punta Santo Domingo (26.3°N) respectively, to Punta Caballo de Piedra (27.8°N).

Our surveys and DNA barcoding confirmed the modern southern limit of *L. conus* as Bahía Magdalena (24.6°N). Simison and Lindberg (2003) suggested the range of congeneric *L. strigatella* at the time of their study extended from Sonora (28°N), throughout the Gulf of California, and along the eastern Pacific coast, north to southern California (no exact location provided). Our field surveys and COI barcoding suggested the northern range limit of *L. strigatella* is around Punta Baja (29.6°N), and the southern range limit is Pozo de Cota (23.0°N) on the eastern Pacific coast. We did not detect any *L. strigatella* in the Gulf of California, along the studied coastline. Although we identified several specimens from San Diego that closely resemble *L. strigatella*, COI sequences confirmed these as small morphs of *L. limatula* and *L. austrodigitalis*.

3.2 | Phylogeographic structure of temperate species

We found phylogeographic breaks for three of the four temperate gastropods (Figure 2). *Lottia strigatella* and *F. volcano* both exhibited a single phylogeographic break, while *L. conus* displayed two. *Tegula gallina* was the only temperate gastropod that did not show any evidence of phylogeographic structure.

Lottia conus and *L. strigatella* displayed a phylogeographic break between La Bocana and Bahía Magdalena (~25–26°N), with a second phylogeographic break between Punta Baja and Santa Rosalillita

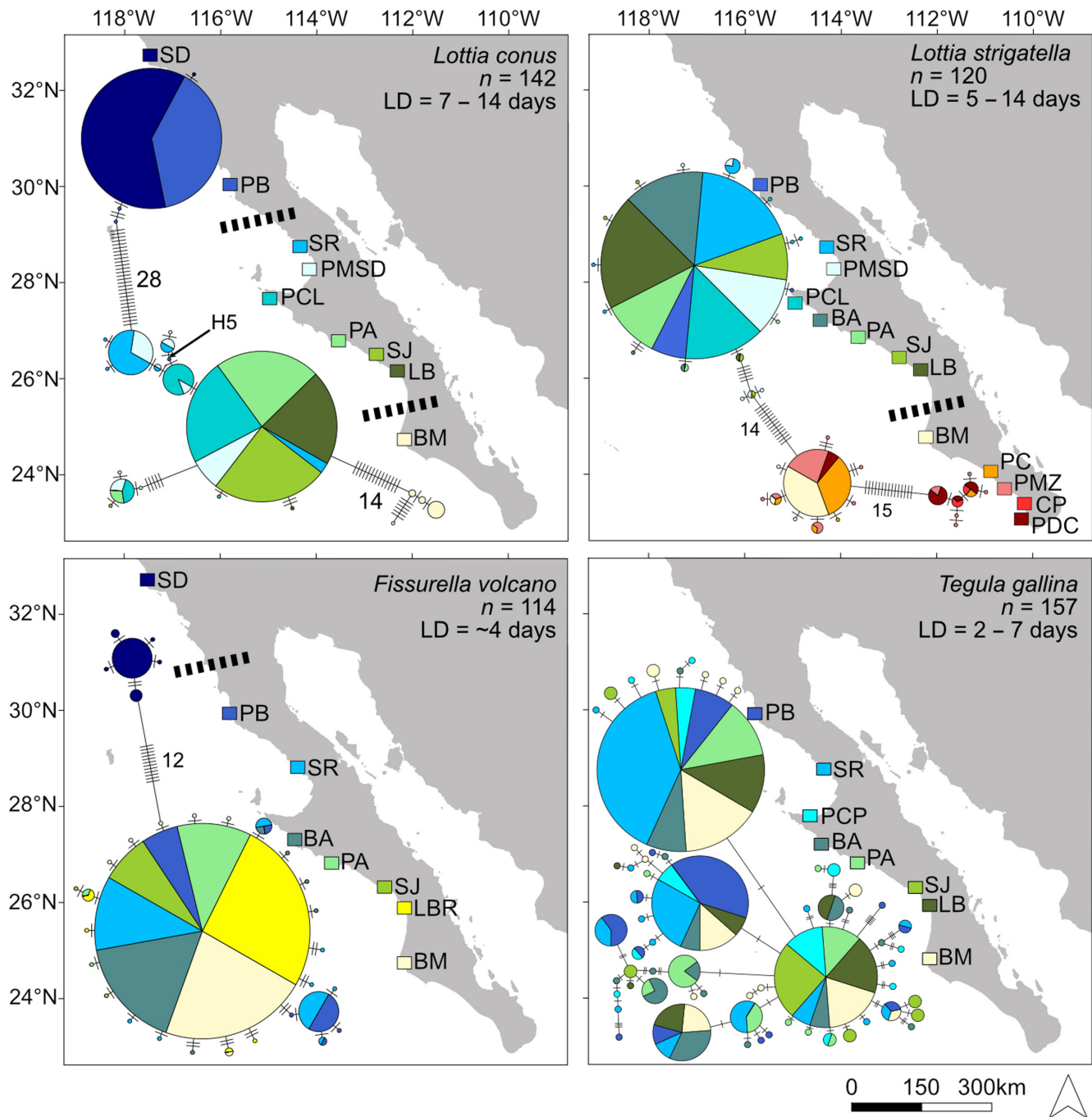


FIGURE 2 Haplotype networks of four temperate gastropod species, with three showing phylogeographic breaks along the Baja California coast. Site codes correspond to Table S1. Sizes of the haplotypes are proportional to the number of individuals. Colours within haplotypes correspond to the sites where individuals of that haplotype were sampled where SD=San Diego, PB=Punta Baja, SR=Santa Rosalillita, PMSD=Punta Morro Santo Domingo, PCP=Punta Caballo de Piedra, PCL=Punta Clambey, BA=Bahía Asunción, PA=Punta Abrejos, SJ=San Juanico, LB=La Bocana, LBR=Las Barrancas, BM=Bahía Magdalena, PC=Punta Conejo, PMZ=Punta Marquez, CP=Cerritos Point, PDC=Poza de Cota. Dashes correspond to the number of mutations separating the haplotypes. The locations of phylogeographic breaks are marked with dashed lines on the map. H5=Haplotype 5 which was closest to the southern haplotypes, yet it was found in Punta Baja, in the northern peninsula. LD=larval duration; n =sample size.

(~28.6–29.6° N) in *L. conus*. We also detected a phylogeographic break for *F. volcano* between Punta Baja and San Diego (~29.6–33.0°N). The populations separated by the phylogeographic breaks were significantly differentiated (Table S5; AMOVA, $p < 0.001$). We detected weak (albeit significant, AMOVA, $p < 0.010$, Table S5)

subdivision among all eight populations of *T. gallina*. We also detected significant population differentiation among sites for *L. conus*, *L. strigatella* and *F. volcano* (Table S5; AMOVA, $p < 0.001$).

We detected population structure between the sites for *L. conus*, *L. strigatella* and *F. volcano* (Figure 3; Pairwise F_{ST} , $p < 0.05$). We did

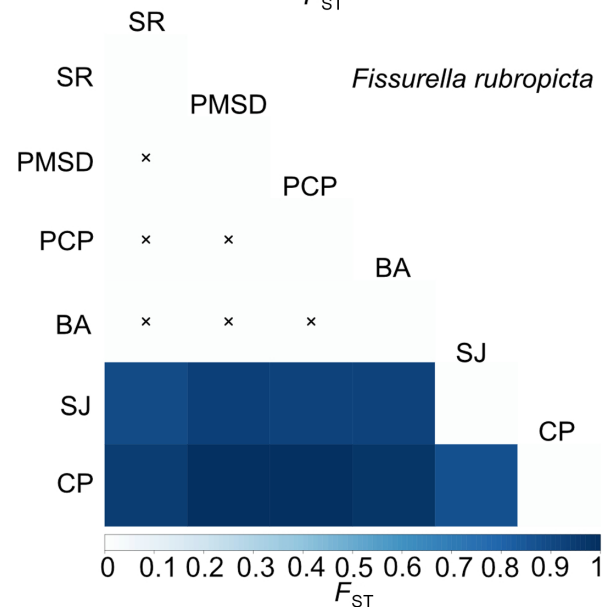
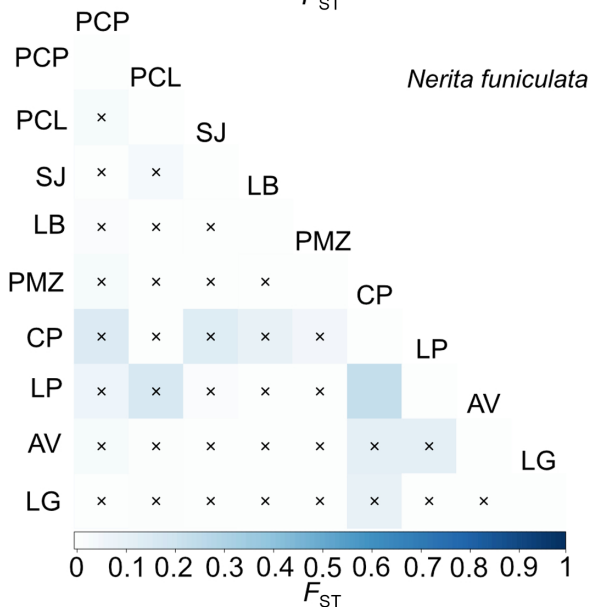
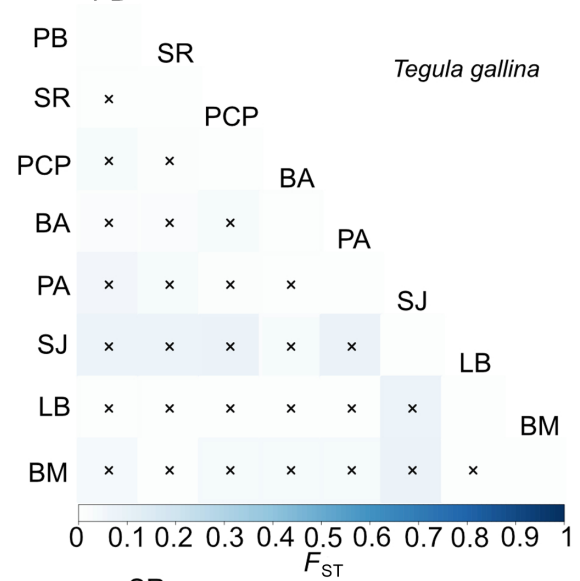
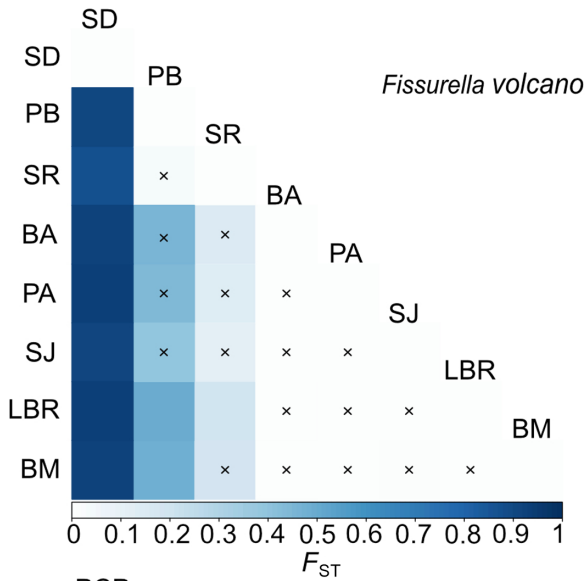
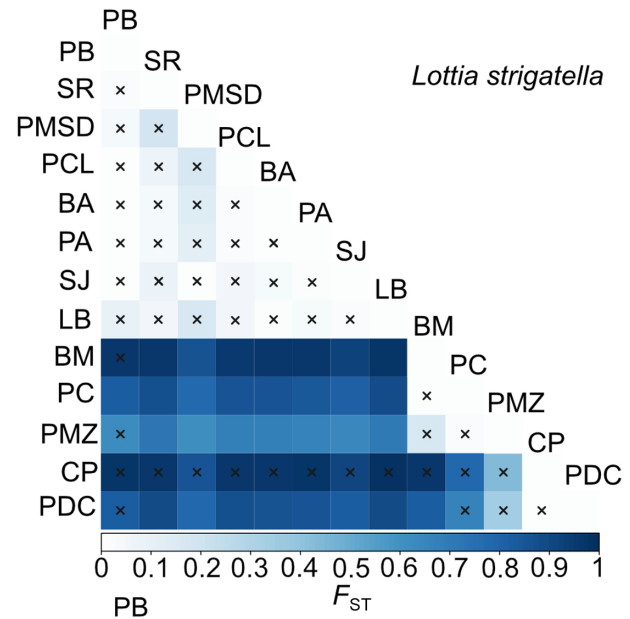
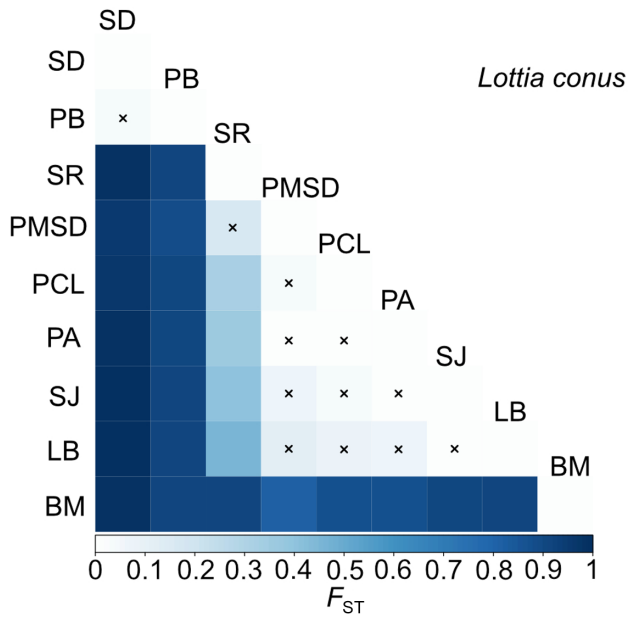


FIGURE 3 A heatmap showing the pairwise F_{ST} comparison between populations grouped by the site of sample collection where SD=San Diego, PB=Punta Baja, SR=Santa Rosalillita, PMSD=Punta Morro Santo Domingo, PCP=Punta Caballo de Piedra, PCL=Punta Clambey, BA=Bahía Asunción, PA=Punta Abreojos, SJ=San Juanico, LB=La Bocana, LBR=Las Barrancas, BM=Bahía Magdalena, PC=Punta Conejo, PMZ=Punta Marquez, CP=Cerritos Point, PDC=Poza de Cota, LP=La Paz, AV=Agua Verde, and LG=La Gringa. The blocks are ordered by the order of the sites along the coastline. Dark blue square indicates $F_{ST}=1$, and white square indicates $F_{ST}=0$. A cross in the square indicates no significant population structure between the two populations, determined by the F_{ST} pairwise comparison where Bonferroni corrected $p > 0.05$. Heatmaps were plotted using a modified R script from The Banta Lab (<https://sites.google.com/site/thebantalab/tutorials>).

not detect any population structure between the sites for *T. gallina* (Figure 3; $p > 0.05$).

Both nucleotide and haplotype diversity were lower in the northern population, compared with the southern population of *L. strigatella* (Figure S1). For *L. conus*, the nucleotide diversity appears to be similar across the north, central and south regions but haplotype diversity is much lower in the north, in comparison to central and southern regions (Figure S1). Both *F. volcano* and *T. gallina* displayed similar nucleotide and haplotype diversity throughout the sampled range (Figure S1).

3.3 | Phylogeographic structure of tropical species

Nerita funiculata and *N. scabricosta* did not display any obvious phylogeographic breaks within the haplotype networks (Figure 4a,b). *Fissurella rubropicta* did not display any deep phylogeographic breaks (Figure 4c). However, populations from the two southern sites (Cerritos Point and San Juanico) are significantly differentiated from the northern populations (Figure 3; $p < 0.05$) albeit the sample sizes in the two southern sites were low (Table S4). We did not detect any population differentiation between the sites for *N. scabricosta* but we did identify weakly significant differentiation for *N. funiculata* (Table S5; $p < 0.05$), including significant pairwise F_{ST} pairwise comparison between Cerritos Point and La Paz (Figure 3; $p < 0.05$).

Given population differentiation for *F. rubropicta*, mismatch distribution and neutrality tests were only conducted on the northern population of this species. All tropical species showed a unimodal distribution of pairwise haplotype differences (Figure 4d), suggesting recent range expansion. The left-skewed mismatch distribution for *F. rubropicta* and *N. scabricosta* suggests a more recent range expansion (Harpending, 1994; Jenkins et al., 2018). Additionally, both of those species did not display significant sum of squared deviation and the raggedness statistic was low for *N. scabricosta* indicating a good fit of the spatial expansion model ($p > 0.05$; Table 2). The distribution of the pairwise differences deviated significantly from the spatial expansion model for *N. funiculata* ($p < 0.02$; Table 2) but the raggedness value was low and weakly significant ($p < 0.05$; Table 2). Moreover, the sum of squared deviation value for *N. funiculata* was significantly higher than expected ($p < 0.05$), displaying a poor fit against the spatial expansion model.

Although mismatch distributions and Fu and Li's neutrality tests have their limitations (Grant, 2015), together with our survey data

they can provide collective information on past population dynamics. The allelic distribution for all three tropical species displayed significant deviation from the Wright-Fisher model, as determined by the Fu and Li's D , and Fu and Li's F^* neutrality tests (for both *Nerita* species $p < 0.02$, for *F. rubropicta* $p < 0.05$; Table 2). Moreover, all three species presented with strongly negative D and F^* statistics, suggestive of range expansion (Table 2).

4 | DISCUSSION

In this study, we assessed phylogeographic patterns of multiple temperate and tropical species in a region undergoing tropicalisation and simultaneously investigated the potential genetic consequences on range expanding and contracting species. We hypothesised that in a region undergoing tropicalisation, temperate species would display phylogeographic breaks, as they had more time to be subjected to any historical barriers to gene flow (Edwards et al., 2022; Fenberg et al., 2014; Riddle et al., 2000). Conversely, we expected that range expanding tropical species would not exhibit deep population subdivision over the area of expansion as they are less likely to have been subjected to historical barriers to gene flow, given their relatively short time occupying the region (Zink et al., 2001). Furthermore, we predicted that tropical species may exhibit genetic evidence of range expansions (Domínguez et al., 2023; Excoffier, 2004).

As hypothesised, we detected deep phylogeographic structure for most (three out of four) temperate species but not in any tropical species. While all three tropical species have recently expanded northward, only one (*F. rubropicta*) revealed a genetic signature of a recent range expansion, with the other two maintaining a high level of genetic diversity within their recently expanded ranges. Ongoing tropicalisation may result in an enhanced risk of the genetic erosion of evolutionary distinct lineages of temperate species, but studies using more genetic markers are needed. Conversely, the range expansion of tropical species may not always result in populations primarily characterised by low genetic diversity, especially if dispersal ability is high.

4.1 | Genetic patterns of temperate species and future consequences

Under projected carbon emission scenarios, taxa globally are expected to undergo range shifts or contractions (Alsos et al., 2012;

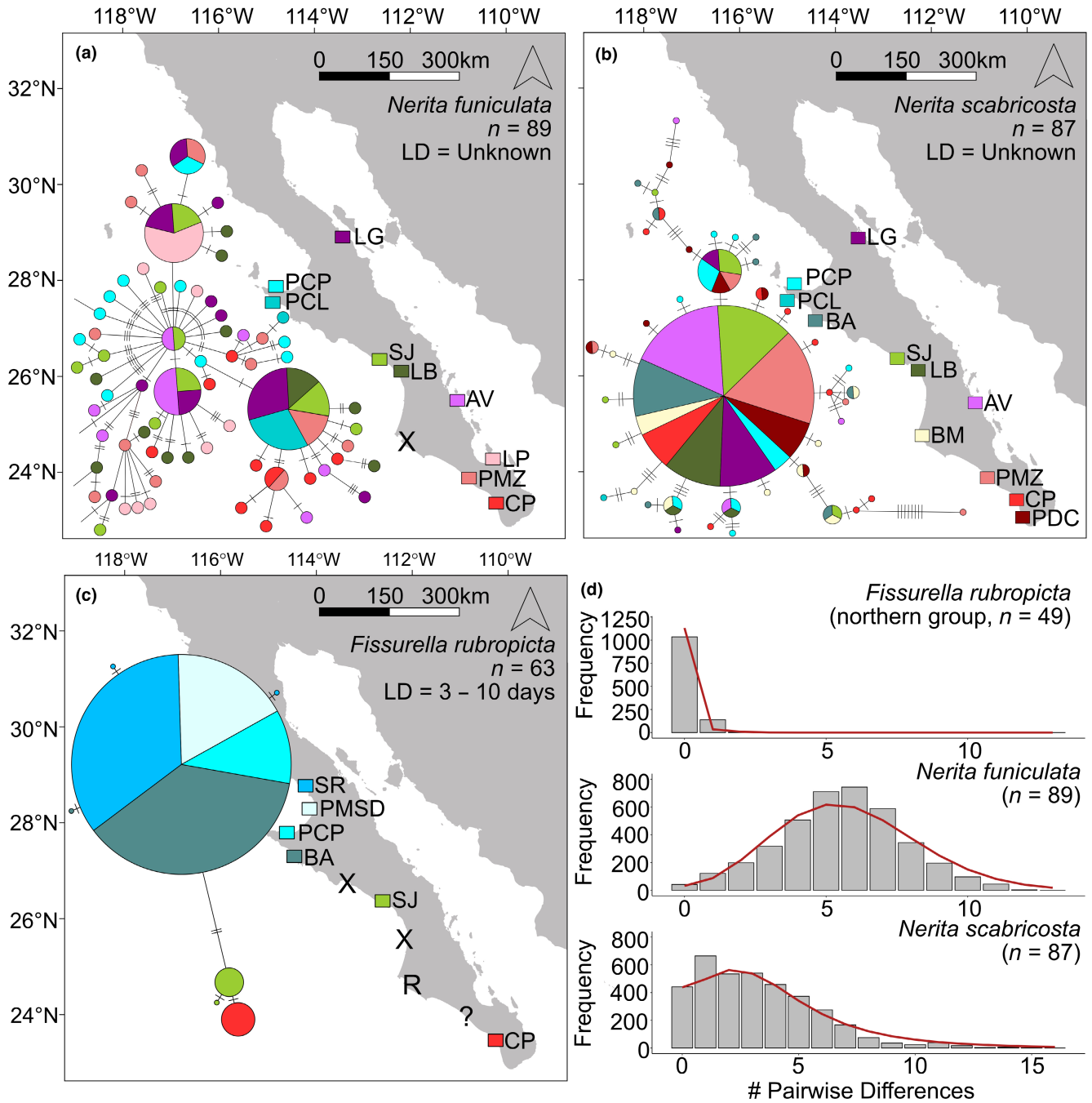


FIGURE 4 (a–c) Haplotype networks of three tropical gastropod species. Site codes correspond to Table S1. Sizes of the haplotypes are proportional to the number of individuals whilst the haplotype colour corresponds to sampled SR=Santa Rosalillita, PMSD=Punta Morro Santo Domingo, PCP=Punta Caballo de Piedra, PCL=Punta Clambey, BA=Bahía Asunción, SJ=San Juanico, LB=La Bocana, BM=Bahía Magdalena, PMZ=Punta Marquez, CP=Cerritos Point, PDC=Pozo de Cota, LP=La Paz, AV=Agua Verde, and LG=La Gringa. Dashes represent the number of mutations separating the haplotypes. LD=larval duration; *n*=sample size, X=species not detected, R=species is rare, ?=presence of the species is uncertain. (d) Mismatch distribution of pairwise haplotype differences for the three tropical species. Grey bars depict the observed distribution; red line indicates the expected distribution modelled under spatial expansion as in Excoffier and Lischer (2010).

Cavvaro et al., 2023; Sopniewski et al., 2022). Landscape genetic analyses of temperate plants show that species exhibiting genetic differentiation among populations are more vulnerable to the loss of genetic diversity resulting from range contraction (Alsos et al., 2012). Consistent with our prediction, the temperate limpets

L. conus, *L. strigatella* and *F. volcano* displayed clear genetic differentiation between northern and southern populations.

The deep phylogeographic breaks identified within the temperate species indicate persistent barriers to gene flow, albeit at different locations for different species. The breaks for *L. conus* and

TABLE 2 Fu and Li's *D* and *F** statistics show the allelic distributions of the three tropical species deviate from the Wright-Fisher model.

Species	<i>Fissurella rubropicta</i>	<i>Nerita funiculata</i>	<i>Nerita scabricosta</i>
Population	Northern group	Entire sampled range	Entire sampled range
<i>n</i>	49	89	86
Neutrality tests			
Fu and Li's <i>D</i> test	-3.01012*	-3.80294**	-3.45463**
Fu and Li's <i>F</i> * test	-3.04517*	-3.67367**	-3.47352**
Spatial expansion			
Rag	0.59498 NS	0.01469*	0.00845 NS
SSD	0.00011 NS	0.00263**	0.00233 NS

Note: Raggedness index (Rag) and sum of square deviations (SSD) were conducted with 10,000 boot replicates between the observed and expected mismatch distributions, under a spatial expansion model. Not significant (NS) Rag and SSD indicate a good fit of the observed values to the spatial expansion model.

Abbreviation: NS, not significant.

* $p < 0.05$; ** $p < 0.02$.

F. volcano were located north of Punta Eugenia, a mid-peninsular break hotspot for several taxa of Baja California (Dolby et al., 2015; Riddle et al., 2000). Meanwhile, haplotype 5 of *L. conus* was closest to the southern haplotypes, yet it was found in Punta Baja, in the northern peninsula (Figure 2). This outlier haplotype may suggest recent gene flow between the northern and southern populations or that insufficient time has passed since isolation for the two distinct haplogroups to sort (You et al., 2022). Meanwhile, the southern phylogeographic break for *L. conus* and *L. strigatella* coincided with the Loreto break, previously documented only for terrestrial species (Harrington et al., 2018; Lindell et al., 2005).

The potential causes of barriers to gene flow in this region are a source of controversy and debate which extends beyond the scope of our study (e.g. Grismer, 2002; Riddle et al., 2000). Here, we focus only on upwelling and large habitat gaps as potential barriers to gene flow (Fenberg et al., 2015; Knutsen et al., 2022; Krumhansl et al., 2023), as these have implications on coastal marine populations currently experiencing tropicalisation. However, we explore historical vicariant events and the phylogeographic patterns of our studied gastropods in the Supporting Information (Data S1).

Both upwelling (Fenberg et al., 2015) and large habitat gaps (Knutsen et al., 2022; Krumhansl et al., 2023) can create barriers to larval dispersal. Habitat availability and fragmentation affect dispersal success of plants and animals and consequently influence genetic diversity (Gibbs, 2001; Wort et al., 2019). However, rocky shore habitats for *L. conus* and *F. volcano* are abundant where the phylogeographic breaks occur (Figure 1; Fenberg & Rivadeneira, 2019), suggesting that habitat gaps are not responsible for the population structuring we see in these species. The phylogeographic pattern may be better explained by strong upwelling in this region (Figure 1), as associated offshore flow could transport planktonic larvae away from the coast (Menge & Menge, 2013), thus preventing larval dispersal alongshore (Zaytsev et al., 2003). For example, on the Gulf side of the peninsula, phylogeographic breaks of coastal fish and molluscs are associated with upwelling near Bahía de Los Angeles (-29° N) (Deng & Hazel, 2010; Riginos &

Nachman, 2001). Strong upwelling also occurs both north and south of Punta Baja (Figure 1), with both upwelling zones coinciding with the phylogeographic breaks. As gene flow persists between Punta Baja and southern sites for *F. volcano*, the larvae of this species can cross the upwelling region, south of Punta Baja. It is unclear whether the larger upwelling region located between San Diego and Punta Baja is acting as a barrier to gene flow for *F. volcano*. However, for upwelling to create a barrier to dispersal, the timing of larval release and seasonal patterns of upwelling would need to coincide—which is currently unknown for our studied species.

Tegula gallina did not show any evidence of phylogeographic structure (Figure 2). As we were unable to obtain *T. gallina* samples north of Punta Baja, we cannot exclude the presence of a phylogeographic break coinciding with that of *F. volcano*. However, given the consistently high haplotype diversity (Figure S1), the lack of population structure between sites, and the highly complex haplotype network (Figure 2), we do not expect the presence of a phylogeographic break in this species along the Baja Peninsula. The geographic origin of *T. gallina* is unknown but its sister species *T. rugosa* is geographically restricted to the warmer Gulf waters (Hellberg et al., 2012). Thus, *T. gallina* may not be a truly temperate species. A better understanding of the evolutionary history of this species, and its fossil record, are needed to test this hypothesis. Alternatively, high genetic diversity and absence of population structure in *T. gallina* could be attributed to its high abundance and large population size, as has been suggested for other taxa (e.g. Williams & Benzie, 1996). *Tegula gallina* was very abundant at the sites where we confirmed its presence, more so than any other species. Large populations can harbour more genetic variation than small ones and take longer to sort variation between populations should they become isolated (Lande & Barrowclough, 1987).

Many rocky shore gastropods, including *T. gallina* and *F. volcano*, have undergone a contraction at the southern end of their range in recent decades (this study, Table 1; Hawkins et al., 2009; Mieszkowska et al., 2021), although whether this is true for *L. conus*,

and *L. strigatella* is not known due to the absence of reliable historical species records. The southern populations of temperate species displaying phylogeographic breaks may be at risk of genetic erosion as tropicalisation progresses. If significant range contraction occurs, unique genetic diversity held by the southern populations may be lost unless gene flow between the populations to either side of phylogenetic breaks resumes. Such risk is more apparent for *L. conus* which experiences two phylogeographic breaks, with one break close to its southern range limit at Bahía Magdalena. The second phylogeographic break for *L. conus*, and the breaks for *L. strigatella* and *F. volcano* occur further north on the peninsula and would require a range contraction of 4–5° in latitude for significant genetic erosion to occur. As *T. gallina* does not display a phylogeographic break, it is unlikely to be affected. Genetic erosion could occur as a direct effect of thermal stress, where genetically unique populations became locally extinct as they are unable to cross barriers to dispersal (Buonomo et al., 2018). On the other hand, genetic erosion could also occur due to altered interspecific interactions. For example, range expanding tropical predators can exert strong selection pressure on naïve prey (Fenberg et al., 2023; Ingeman, 2016) and can cause local extinction of prey populations.

While mtDNA is mostly neutrally evolving (Ballard & Whitlock, 2004), some evidence suggests COI can harbour adaptive variation (Little et al., 2018) and may experience natural selection (Ballard & Kreitman, 1995). Although caution is necessary when inferring population genetic patterns from a single genetic marker (Ballard & Whitlock, 2004), patterns revealed by COI are frequently reflected within other (including nuclear) genetic markers (Avice, 1994; Zink & Barrowclough, 2008). Most temperate gastropods displayed phylogeographic breaks, and some species showed greater genetic diversity in the southern portions of their range (Figure S1). If this pattern of genetic diversity is reflected by other genetic markers, tropicalisation may have evolutionary consequences in the future. High genetic diversity facilitates the resilience of populations facing disturbances by enhancing the adaptive potential (Wernberg et al., 2018). Such adaptive potential is particularly important for ecosystem resilience against the effects of climate change and increasing environmental stress (Hughes & Stachowicz, 2004; Wernberg et al., 2018). Our study suggests that as tropicalisation progresses, loss of genetic diversity could lead to reduced evolutionary potential, leaving populations of temperate species more vulnerable to future environmental stressors (Nicastro et al., 2013; Wernberg et al., 2018). Thus, the conservation of high diversity populations of temperate species should be a priority for the management of regions undergoing tropicalisation. However, more studies using multi-loci approaches should be utilised to support our findings.

4.2 | Genetic patterns of tropical species

We detected no strong phylogeographic breaks (Figure 4a–c) and found evidence of range expansions in all three species using field studies and genetic evidence for one species. This suggests that

there are few modern barriers to gene flow for these species within our study region. This also suggests that continued range expansion could be rapid as tropicalisation progresses.

While there are no deep breaks in any of the tropical species, *F. rubropicta* showed some phylogeographic structure, separating northern and southern haplogroups by only two mutational differences (Figure 4c). The northern haplogroup is dominated by a single haplotype, which is a likely result of a stepwise range expansion and localised dispersal around Bahía Asunción (Figure 4c). The southern haplogroup appears to have low genetic diversity but this may be an artefact of the low sample size in the south ($n=14$), in comparison to the north ($n=49$; Figure 4c; Table S4). This low sample size can be attributed to the patchy distribution of this species in the southern portion of the peninsula (Figure 4c), which may be related to the low habitat availability in the south (Figure 1). Meanwhile, both *Nerita* species exhibited a greater number of haplotypes in comparison to *F. rubropicta*, which could be attributed to greater larval dispersal potential and higher population abundances in comparison to *F. rubropicta*, but more research on larval development of the *Nerita* species is required (Table 1).

Range expansions are typically expected to result in reduced genetic diversity at a species' leading range margin (Domínguez et al., 2023; Pujol & Pannell, 2008), which has been widely observed in many taxa (usually as a result post-glacial range expansion), including flowering plants (Ehrich et al., 2007; Pujol & Pannell, 2008), sea snakes (Lukoschek et al., 2007), crabs (Deli et al., 2019) and snails (Hellberg et al., 2001). Using this logic, we would expect range expanding populations of tropical species with low diversity to eventually replace genetically unique populations of temperate species within regions undergoing tropicalisation. Our results provide equivocal support for this hypothesis, with one tropical species having relatively low genetic diversity at its leading edge (for *F. rubropicta* the newly occupied sites Punta Caballo de Piedra, Punta Morro Santo Domingo and Santa Rosalillita are largely dominated by a single haplotype) and the other two not showing a reduction in genetic diversity (*N. scabricosta* and *N. funiculata*). In fact, an increasing number of studies assessing modern range expansions have not detected a reduction in genetic diversity within the new range. For example, microsatellite analysis of a range expanding damselfly identified only a marginal reduction in genetic diversity (Swaegers et al., 2013). Similar absence of major reduction in genetic diversity has been observed in European beech populations (Lander et al., 2021) and an invasive fish (Bernos et al., 2023).

Colonising species can evade a reduction in genetic diversity if high gene flow persists between the source and newly settled populations (Wallingford et al., 2020). Species which have avoided reduction in genetic diversity during modern-day range expansions are often high-dispersing species which are able to maintain gene flow to the leading edge of their range (Lander et al., 2021; Swaegers et al., 2013). Naturally, dispersal ability is correlated with greater dispersal potential which allows species to track climate change and thus keep pace if suitable habitat is available (Hughes et al., 2007). Therefore, the factors which facilitate range expansion of species,

are also the same factors which allows species to maintain high levels of gene flow and thus, allow species to maintain relatively high levels of genetic diversity. We suggest that a similar explanation is causing the genetic patterns found in *N. scabricosta* and *N. funiculata* (Figure 4). It is also likely that both *Nerita* species experienced a sudden spatial expansion during the Pleistocene warming (Hurtado et al., 2007) and are now undergoing further range expansion in response to current climate change (as supported by our field surveys), while maintaining high levels of gene flow in the recently expanded range. Furthermore, suitable rocky shore habitat for grazing is plentiful north of their current range limits (Figure 1), indicating that continued expansion would not be habitat limited.

4.3 | Conclusions

Marine tropicalisation research has largely focussed on documenting species range shifts and its ecological impacts (Kumagai et al., 2018; Vergés et al., 2016; Zarzyчны et al., 2022), whereas the potential genetic impacts of tropicalisation have not yet been well studied. Here, we used a comparative phylogeographic approach to highlight that ongoing tropicalisation may lead to erosion of genetic diversity within southern haplogroups of temperate species as their ranges contract in response to climate change. Conversely, tropical range expanding species can maintain relatively high levels of genetic diversity, possibly due to higher dispersal capabilities. However, to fully capture the potential genetic consequences of tropicalisation, we highlight the need for (i) greater understanding of the ecological and biological factors that affect tropical versus temperate species dispersal in transition regions, and (ii) the assessment of modern gene flow rates by assessing single-nucleotide polymorphisms and multi-locus studies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Genetic data for all unique haplotypes are available on GenBank (Accession numbers OQ681978-OQ682252).

ORCID

Karolina M. Zarzyчны  <https://orcid.org/0000-0003-1675-2090>

David A. Paz-García  <https://orcid.org/0000-0002-1228-5221>

Erick X. Treviño Balandra  <https://orcid.org/0000-0002-1185-586X>

Suzanne T. Williams  <https://orcid.org/0000-0003-2995-5823>

Phillip B. Fenberg  <https://orcid.org/0000-0003-4474-176X>

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BIOSKETCHES

Karolina M. Zarzychny is a marine biologist and molecular ecologist interested in tropicalisation of rocky shore communities and shallow marine reefs. All co-authors have special interests ranging from biogeography to molecular ecology and evolution, with some specialising in coastal ecosystems of the north-eastern Pacific and Gulf of California.

Author Contributions: Phillip B. Fenberg conceived the initial concept. Phillip B. Fenberg and KMZ designed the research, selected the species, and conducted the fieldwork. Karolina M. Zarzychny performed the laboratory work, analysed the genetic data and wrote the manuscript. Ethan G. Ross conducted preliminary analyses on one of the species. David A. Paz-García provided in country support and local expertise. David A. Paz-García, Moira MacLean and Erick X. Treviño Balandra contributed to the fieldwork. Phillip B. Fenberg, Marc Rius, Suzanne T. Williams and Michael E. Hellberg guided the laboratory work and genetic analysis. Phillip B. Fenberg, James Vanstone and Elena B. Lugli contributed to the laboratory work. All authors contributed to the final manuscript.

SUPPORTING INFORMATION

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

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