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Trait-based vulnerability and tolerance thresholds of tropical mollusks in light of projected increases in climate-change stressors☆

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ABSTRACT

Extreme climate conditions increasingly threaten worldwide coastal biodiversity. We applied a trait-based approach to quantify the tolerance thresholds of 13 mollusk species from five tropical coastal habitats, using controlled experiments that simulate extreme temperature, salinity, submersion, and desiccation stress. Survival was analyzed in relation to functional traits, including isolation from ambient conditions (presence/absence of shell closure and/or operculum), respiration mode (branchial or pulmonate), shell thickness, and habitat type. Thermal safety margins (TSMs) were also projected under future climate scenarios. Species that possess isolation traits consistently survived across stress conditions. Bivalves generally tolerated higher temperatures and broader salinity ranges than gastropods, and pulmonate gastropods experienced high mortality under both prolonged submersion and desiccation. Desiccation tolerance was strongly associated with the ability to isolate. Thicker shells provided limited protection against extreme temperatures but did not protect taxa with narrow salinity tolerances. Projected TSMs indicated that species from mangrove and oyster-bank habitats will be subject to temperatures that exceed their upper thermal limits before the end of this century. Vulnerability to climate change arises from a combination of functional traits and habitat context. By addressing multiple climate-related variables, i.e., temperature, salinity, inundation, and desiccation, all of which are shifting with global climate change, this study identified combinations of traits that will confer tolerance to tropical mollusks under future conditions and identified taxa that will likely be at risk. This study fills critical data gaps for tropical habitats worldwide and provides a framework for predicting biotic responses to climate extremes.

1. Introduction

Coastal aquatic habitats are exposed to climate-driven stressors that span spatial and temporal scales (Osland et al., 2025). Climate change is projected to cause substantial and potentially irreversible effects on coastal habitats, altering both their structural and functional dynamics (Guild et al., 2025). Climate change scenarios project increasing temperatures, modifications of precipitation and evaporation regimes, and changes in salinity (Dong et al., 2025). Salinization in these habitats may occur from a combination of lower precipitation, altered hydrological connection with the ocean, higher evaporation, and/or lower freshwater inputs (Sippo et al., 2018). From a biological perspective, these climate factors are considered external multiple stressors that will challenge the physiology of organisms (Gunderson et al., 2016). It is expected that by 2050, more than 90% of the ocean will be impacted by exposure to multiple stressors (Henson et al., 2017). Species may be resistant/resilient to change in one stressor (e.g., temperature) but negatively affected by another (e.g., salinity, desiccation), resulting in myriad

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ecological responses, such as shifts in species spatial distributions, relative abundances, and even local extinctions (Dildar et al., 2025; Wernberg et al., 2025).

Increased temperatures can pose a direct threat to organisms by causing physiological stress that elevates mortality. Higher temperatures also operate indirectly, by causing salinization and prolonged desiccation (Cushway et al., 2025; Röthig et al., 2023), which can alter metabolic rates (Papadopoulos et al., 2025), affect protein production (Jeyachandran et al., 2023; Bonesteve et al., 2025), and impact other physiological processes (Mohamed et al., 2025; Vikhrev et al., 2025). Thermal tolerance studies show that coastal marine organisms live close to their upper thermal limits (Vinagre et al., 2015, 2019). To evaluate a species vulnerability to rising temperatures, it is necessary to understand its thermal tolerance and acclimation capacity, factors that are unknown for most taxa (Vinagre et al., 2018). Mollusks are informative models due to their ubiquity, diverse ecologies, and different physiological tolerances (Dong et al., 2022). They occupy many habitat types, from rocky intertidal zones to brackish lagoons and freshwater margins. Experimental data suggest that some tropical mollusk species have already reached their vulnerable Critical Thermal Maximum (CTMax) values, i.e., their upper thermal limits. The approach revealed thermal sensitivity in tropical and temperate species under projected future warming scenarios (Vinagre et al., 2019). In mollusks, the osmotic concentration of the hemolymph generally conforms to that of ambient water (Deaton, 2008). Whereas some species are stenohaline, others, particularly Bivalvia and Gastropoda, are euryhaline (Suárez-Mozo et al., 2023). This trait plays a critical role in determining the resilience of a species under fluctuating salinity conditions (Deaton, 2008), which are increasingly common in estuarine and coastal habitats impacted by climate change.

Predictions about the vulnerability of a species to climate change often do not incorporate ecological processes or individual species responses. Analysis of trait-based vulnerability may help mitigate this problem (Carlot et al., 2025). Experimental studies suggest that trophic position, behavior, and life-history traits shape species responses to climate warming (Stewart et al., 2013; Stollewerk et al., 2025). Thus, functional traits, morphological, physiological, and phenological characteristics, have emerged as variables to assess species vulnerability, providing a framework for identifying ecologically relevant information (Fordham, 2024). Linking traits to tolerance and habitat context enables ecologically grounded predictions of biodiversity responses. Most climate-based predictive models forecast dramatic losses in biodiversity in tropical regions, aligning with ecological stability theory, which posits that environmental changes beyond critical thresholds may trigger abrupt and irreversible regime shifts (Scheffer and Carpenter, 2003).

In this study, we used tropical mollusks to investigate how functional traits mediate tolerance to key environmental stressors, including submersion, desiccation, salinity fluctuations, and elevated temperatures. We assessed the vulnerability of 13 species across five coastal habitats: mangroves, oyster banks, riverine inland lagoons, rocky shores, and sandy mudflats, all within a tropical estuarine system in the southern Gulf of Mexico. By quantifying physiological responses to these stressors, we were able to estimate species-specific thermal safety margins (TSMs) under projected climate scenarios (Hijmans et al., 2024). Building on these data, we propose a trait-based framework that reflects the ecological complexities of tropical coastal systems and explores how functional traits mediate the tolerance of tropical mollusks to multiple climate stressors. A set of specific questions, hypotheses, and the methods to address them is presented in Table 1.

2. Material and methods

2.1. Model species and sampling

We worked with 13 mollusk species from five tropical coastal

Table 1

Study research questions, associated experiments addressing climate-related stressors (temperature, salinity, submersion, and desiccation), and predictions.

Question	Experiments	Prediction	References
1. How do habitat type, respiration mode, and structural isolation traits (e.g., operculum and shell closure) influence variability in thermal tolerance of tropical mollusks across aquatic and subaerial environments?	CTMax experiments	We expected that phenotypic plasticity would enable mollusks to cope with thermal fluctuations, such that species capable of tightly closing their shells or opercula would show higher survival under extreme temperature stress, despite the physiological trade-offs associated with isolation. Furthermore, we expected that habitat type modulates this response.	(Overgaard et al., 2011)
2. Does habitat-driven salinity variability predict the tolerance of species to extreme salinity?	Salinity tolerance experiment	We expected that marine mollusks from habitats with high salinity variability would exhibit higher tolerance to extreme hypo- and hypersaline conditions compared to species from habitats with relatively stable salinity. The resistance of mollusks to extreme salinity is primarily based on the reduction of water-salt exchange with the external environment, achieved through hermetization of the mantle cavity, which effectively isolates the soft tissues from abrupt osmotic changes.	(Berger and Kharazova, 1997; Deaton, 2008)
3. Will survival under prolonged submersion in mollusk species relate to their respiration mode and/or presence of isolation traits (such as an operculum and/or shell closure) and/or to habitat-related exposure to such stress?	Submersion tolerance experiment	We expected that species with gill-based respiration would tolerate prolonged submersion due to efficient aquatic gas exchange, whereas pulmonate species would show limited tolerance. We expected that isolation traits would extend survival by conserving water and reducing osmotic stress, but	(Bjelde et al., 2015)

(continued on next page)

Table 1 (*continued*)

Question	Experiments	Prediction	References
		at the cost of increased reliance on anaerobic metabolism.	
4. Will survival under prolonged desiccation in mollusk species relate to structural isolation traits (such as an operculum and/or shell closure) and/or habitat-related exposure?	Desiccation tolerance experiment	We expected that resistance to desiccation would come at a physiological cost, involving reduced gas exchange and the accumulation of CO_2 and nitrogenous wastes.	(Marshall and McQuaid, 2020)
5. Which tropical mollusk species are projected to exceed their thermal safety margins under future climate scenarios?	Thermal safety margins (TSMs) estimation using climate projections	We expected that vulnerability to exceeding thermal safety margins will depend on both functional traits and habitat context. Species from varying or stressful environments are expected to be more resilient due to higher phenotypic plasticity, consistent with a "use it or lose it" strategy, whereas generalists are "jack of all trades, master of none".	(Huey and Hertz, 1984; Calosi et al., 2010; Overgaard et al., 2011)

habitats in southern Mexico (Supplementary material 1): mangroves, rocky shores, oyster banks, riverine inland lagoons, and sandy mudflats (Fig. 1). Species were selected based on their high relative abundances, ecological relevance, and commercial or regulatory importance. This included commercially exploited oyster species (*Crassostrea rhizophorae* and *Crassostrea virginica*), the gastropod *Melongena bispinosa*, and *Isognomon alatus*, a species listed under Mexican environmental regulation (NOM-059-SEMARNAT; SEMARNAT, 2010), with an aim to capture a broad range of functional traits, habitat preferences, and physiological tolerances (Fig. 2).

Functional traits were selected to represent key axes of sensitivity to climate-related stressors, including thermal exposure, desiccation, submersion and salinity variability. Morphological and ecological traits were prioritized to ensure a standardized and comparative framework across species. The functional traits considered included: ability to isolate from ambient conditions (morphological-functional - presence/absence of shell closure and/or operculum), respiration mode (physiological-functional - branchial or pulmonate), and shell thickness (morphological-functional trait, measured in mm) was quantified using digital calipers. In gastropods, shell thickness was measured at the outer lip of the aperture, whereas in bivalves it was measured on one valve at the ventral margin. Measurements were taken at standardized anatomical locations within each taxonomic group. For each species, shell thickness values were averaged across measured individuals and used as species-level trait values in subsequent analyses.

Trait information was compiled from the literature (Brusca et al., 2022; Ponder and Lindberg, 2012). Species analyzed were *Ischadium recurvum* (Rafinesque, 1820), *Isognomon alatus* (Gmelin, 1791), *Crassostrea rhizophorae* (Guilding, 1828), *Crassostrea virginica* (Gmelin, 1791), *Rangia flexuosa* (Conrad, 1839), *Lampanella minima* (Gmelin, 1791), *Cerithideopsis pliculosa* (Menke, 1829), *Nerita tessellata* Gmelin, 1791, *Vitta virginea* (Linnaeus, 1758), *Melampus coffea* (Linnaeus, 1758), *Echinolittorina lineolata* (A. d'Orbigny, 1841), *Melongena bispinosa* (R. A. Philippi, 1844), and *Siphonaria pectinata* (Linnaeus, 1758) (Fig. 2).

2.2. Acclimation conditions

After collection, specimens were transported to the "El Carmen" Research Station of the Instituto de Ciencias del Mar y Limnología (UNAM). Organisms were acclimated for 15 days in aerated aquaria (36 × 22 × 21 cm) filled with ecosystem-specific water. Environmental conditions were maintained at 25 °C, 7 mg/L O_2, and habitat-specific salinity. For mangrove, sandy mudflats, and rocky shore species, salinity was maintained at 28 PSU; for oyster bank species, salinity was maintained at 12 PSU, and for riverine inland lagoon species, salinity was maintained at ~0 PSU. Encrusting organisms were manually removed from the shells before acclimation. Feeding was adjusted to dietary requirements: filter feeders received microalgae (*Tetraselmis*, *Nannochloropsis*, *Isochrysis*), carnivores received commercial fish flakes, and grazers were fed with nori (*Pyropia* sp.) and microalgae.

2.3. Tolerance experiments

Four experiments evaluated species-specific tolerance to temperature, salinity, prolonged submersion, and desiccation (Supplementary material 2). All tests followed controlled laboratory procedures adapted from Capparelli et al. (2022). Tolerance limits for each variable were defined as values at which the mollusks lost motor function, detached their foot from the surface, or lost attachment ability (for gastropods), kept their valves open and relaxed their foot muscle simultaneously (for bivalves), or failed to move after being pricked (Vinagre et al., 2015, 2018, 2019). Behavioral responses during thermal trials (e.g., detachment, loss of attachment) were monitored as indicators of acute thermal stress and were used to determine upper thermal tolerance limits.

Tropical mangrove and shallow coastal ecosystems are increasingly exposed to extreme hydroclimatological variability, including prolonged drought, flooding, and disruptions of natural tidal cycles. These processes can lead to extended periods of continuous submersion or aerial exposure lasting from several weeks to up to approximately three months (Capparelli et al., 2022), as well as pronounced salinity fluctuations driven by evaporation, restricted water exchange, and variable freshwater inputs. Field observations from tropical coastal systems (Supplementary Material 3) have documented hypersaline conditions, with surface-water salinities exceeding 60 psu and porewater salinities approaching ~90 psu (Suárez-Mozo et al., 2025), imposing severe physiological stress on benthic and intertidal organisms. The frequency, duration, and intensity of these stressors are expected to increase under ongoing climate change. Informed by this environmental context, the experimental treatments were designed to represent ecologically stressful scenarios, with exposure durations encompassing both short-term events and prolonged regimes approaching multi-month extremes reported for tropical coastal ecosystems.

2.3.1. Temperature tolerance in water and air

Seven individuals per species were exposed to gradually increasing temperatures to determine their upper thermal limit (CTMax). For water temperature, individuals were placed in beakers filled with water and submerged in a thermostatic bath, starting at 25 °C and increasing by 1 °C/min until the upper thermal limit was reached (Capparelli et al., 2022). For air temperature, individuals were placed in beakers without water and heated in the same thermostatic bath. Temperature inside the beakers was monitored using digital thermometers.

2.3.2. Salinity tolerance

Five individuals per species were exposed to seven salinity concentrations, ranging from distilled water (<0.1 PSU) to concentrated seawater: 0, 14, 28, 42, 56, 70, and 84 PSU. Four hundred mL of water of

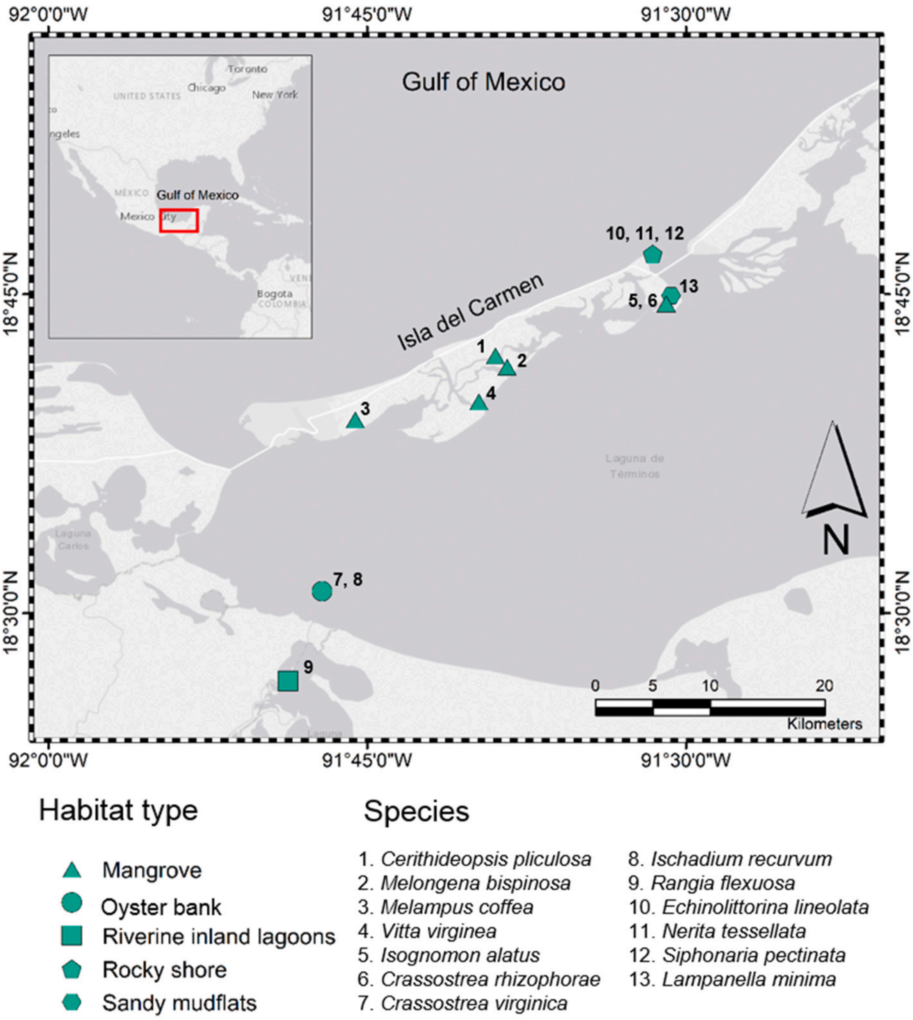


Fig. 1. Sampling locations across coastal habitats in the southern Gulf of Mexico. Symbols represent coastal habitat types: mangrove (triangle), oyster bank (circle), riverine inland lagoons (square), rocky shore (pentagon), and sandy mudflats (hexagon). Numbers correspond to the locations of the 13 representative mollusk species collected in each habitat.

each concentration was added to plastic containers to ensure the specimens were completely covered.

2.3.3. Submersion tolerance

The experiment simulated extreme conditions that occur mainly in habitats such as mangroves, oyster banks, and riverine inland lagoons during periods of exceptionally high tides, intense rainfall, and sea-level rise, leading to prolonged inundation. Groups of five individuals per species were kept fully submerged in 4 L of water for 12 days, with salinity monitored daily. After the exposure period, survival was assessed by observing movement within 24 h.

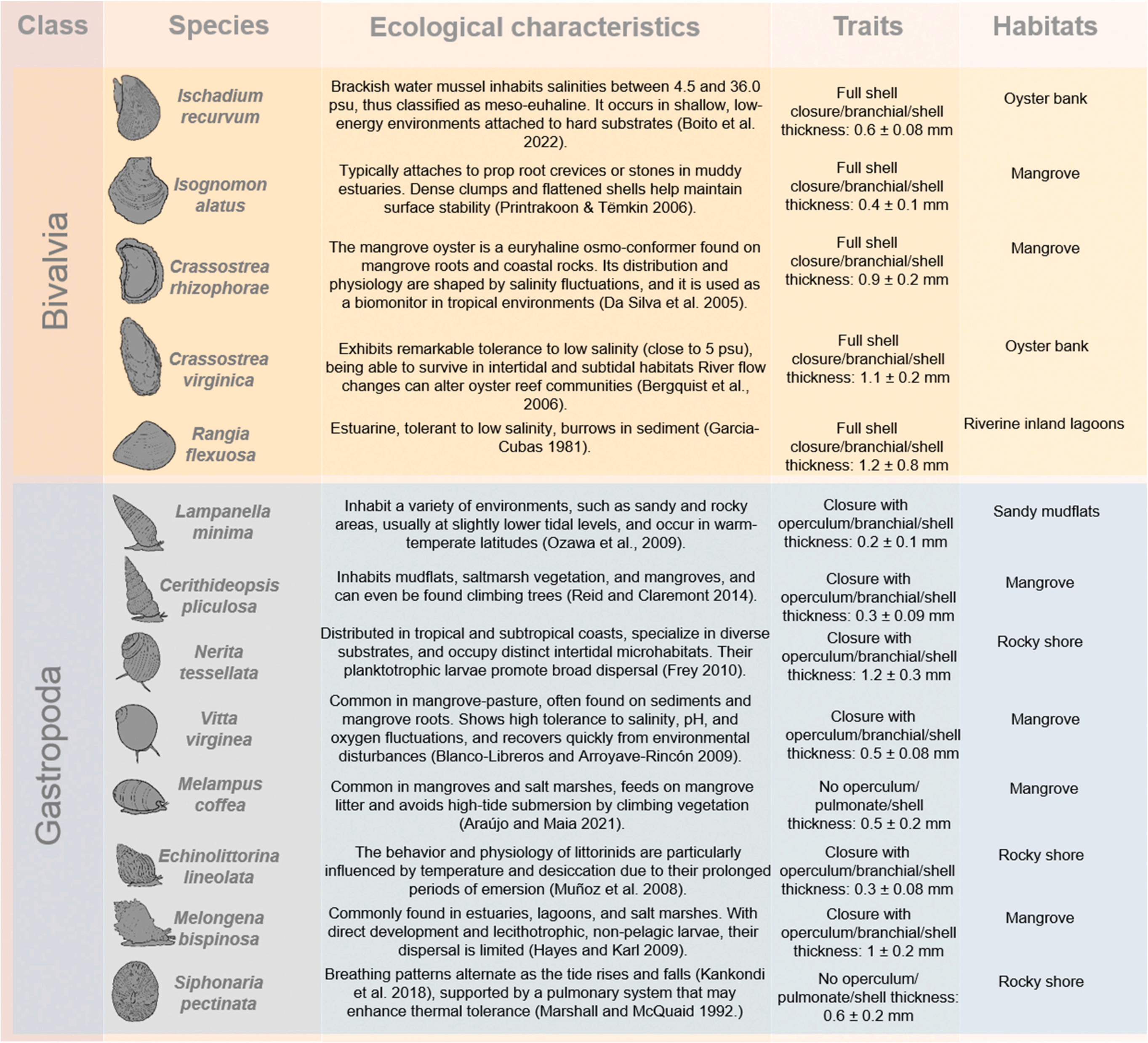
2.3.4. Desiccation tolerance

The experiment simulated prolonged subaerial conditions that occur mainly in habitats such as rocky shores, mangroves, and sandy mudflats when organisms may be exposed during the dry season, during extended low tides, or because of habitat isolation. Four exposure durations were tested (1, 2, 3, and 15 days), with groups of seven individuals per duration (28 individuals per species). After each exposure period, survival was assessed by rehydrating the specimens and observing movement within 24 h.

2.4. Data analyses

Differences in tolerance among classes and habitats were tested using PERMANOVA. We analyzed separately: (1) Tmax air, (2) Tmax water, (3) mortality after submersion, (4) mortality after desiccation, and salinity, using a two-factor design with class (Bivalvia, Gastropoda) and habitat (mangrove, inland lagoons, oyster bank, sandy mudflats, rocky shore) as fixed factors. Euclidean distance matrices were computed, and PERMANOVA was run with Type III sums of squares and 999 permutations (Anderson, 2017) in PRIMER v7 with PERMANOVA+ (Clarke and Gorley, 2015). Functional traits were tested depending on the stressor: shell closure and operculum for desiccation, and respiratory mode (branchial vs. pulmonate) for submersion, using a separate PERMANOVA.

To assess morphological influences on mortality under desiccation and salinity, we fitted generalized linear mixed models (GLMMs) with binomial error distribution using glmmTMB (Brooks et al., 2017) in R (R Development Core Team, 2024). The submersion dataset was excluded due to quasi-complete separation and small sample size. Data were aggregated by operculum, shell closure, shell thickness (fixed), and treatment and species (random). Model diagnostics with DHARMa (Hartig, 2022) using 1000 simulated residuals confirmed assumption validity for temperature and moderate deviations for salinity (Supplementary material 4).



Class	Species	Ecological characteristics	Traits	Habitats
Bivalvia	*Ischadium recurvum*	Brackish water mussel inhabits salinities between 4.5 and 36.0 psu, thus classified as meso-euhaline. It occurs in shallow, low-energy environments attached to hard substrates (Boito et al. 2022).	Full shell closure/branchial/shell thickness: 0.6 ± 0.08 mm	Oyster bank
	Isognomon alatus	Typically attaches to prop root crevices or stones in muddy estuaries. Dense clumps and flattened shells help maintain surface stability (Printrakoon & Tëmkin 2006).	Full shell closure/branchial/shell thickness: 0.4 ± 0.1 mm	Mangrove
	Crassostrea rhizophorae	The mangrove oyster is a euryhaline osmo-conformer found on mangrove roots and coastal rocks. Its distribution and physiology are shaped by salinity fluctuations, and it is used as a biomonitor in tropical environments (Da Silva et al. 2005).	Full shell closure/branchial/shell thickness: 0.9 ± 0.2 mm	Mangrove
	Crassostrea virginica	Exhibits remarkable tolerance to low salinity (close to 5 psu), being able to survive in intertidal and subtidal habitats River flow changes can alter oyster reef communities (Bergquist et al., 2006).	Full shell closure/branchial/shell thickness: 1.1 ± 0.2 mm	Oyster bank
	Rangia flexuosa	Estuarine, tolerant to low salinity, burrows in sediment (Garcia-Cubas 1981).	Full shell closure/branchial/shell thickness: 1.2 ± 0.8 mm	Riverine inland lagoons
Gastropoda	*Lampanella minima*	Inhabit a variety of environments, such as sandy and rocky areas, usually at slightly lower tidal levels, and occur in warm-temperate latitudes (Ozawa et al., 2009).	Closure with operculum/branchial/shell thickness: 0.2 ± 0.1 mm	Sandy mudflats
	Cerithideopsis pliculosa	Inhabits mudflats, saltmarsh vegetation, and mangroves, and can even be found climbing trees (Reid and Claremont 2014).	Closure with operculum/branchial/shell thickness: 0.3 ± 0.09 mm	Mangrove
	Nerita tessellata	Distributed in tropical and subtropical coasts, specialize in diverse substrates, and occupy distinct intertidal microhabitats. Their planktotrophic larvae promote broad dispersal (Frey 2010).	Closure with operculum/branchial/shell thickness: 1.2 ± 0.3 mm	Rocky shore
	Vitta virginea	Common in mangrove-pasture, often found on sediments and mangrove roots. Shows high tolerance to salinity, pH, and oxygen fluctuations, and recovers quickly from environmental disturbances (Blanco-Libreros and Arroyave-Rincón 2009).	Closure with operculum/branchial/shell thickness: 0.5 ± 0.08 mm	Mangrove
	Melampus coffea	Common in mangroves and salt marshes, feeds on mangrove litter and avoids high-tide submersion by climbing vegetation (Araújo and Maia 2021).	No operculum/ pulmonate/shell thickness: 0.5 ± 0.2 mm	Mangrove
	Echinolittorina lineolata	The behavior and physiology of littorinids are particularly influenced by temperature and desiccation due to their prolonged periods of emersion (Muñoz et al. 2008).	Closure with operculum/branchial/shell thickness: 0.3 ± 0.08 mm	Rocky shore
	Melongena bispinosa	Commonly found in estuaries, lagoons, and salt marshes. With direct development and lecithotrophic, non-pelagic larvae, their dispersal is limited (Hayes and Karl 2009).	Closure with operculum/branchial/shell thickness: 1 ± 0.2 mm	Mangrove
	Siphonaria pectinata	Breathing patterns alternate as the tide rises and falls (Kankondi et al. 2018), supported by a pulmonary system that may enhance thermal tolerance (Marshall and McQuaid 1992.)	No operculum/ pulmonate/shell thickness: 0.6 ± 0.2 mm	Rocky shore

Fig. 2. Description of the sampled mollusk species, their functional traits (operculum, shell closure, respiratory mode, shell thickness), and preferred habitats.

2.5. *Projection scenarios of thermal safety margins*

Thermal safety margins for 2100 were calculated as the difference between each species' CTMax and projected maximum temperatures. Projections of maximum air temperature were obtained from CMIP6 using the cmip6_tile function of the geodata package (Hijmans et al., 2024). We selected 26 General Circulation Models (GCMs – ACCESS-CM2, ACCESS-ESM1-5, AWI-CM-1-1-MR, BCC-CSM2-MR, CanESM5, CanESM5-CanOE, CMCC-ESM2, CNRM-CM6-1, CNRM-CM6-1-HR, CNRM-ESM2-1, EC-Earth3-Veg, EC-Earth3-Veg-LR, FIO-ESM-2-0, GFDL-ESM4, GISS-E2-1-G, GISS-E2-1-H, HadGEM3-GC31-LL, INM-CM4-8, INM-CM5-0, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MPI-ESM1-2-HR, MPI-ESM1-2-LR, MRI-ESM2-0, UKESM1-0-LL) under four Shared Socioeconomic Pathways (SSPs: SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5) for four future periods (2021–2040, 2041–2060, 2061–2080, 2081–2100), spanning low to very high radiative forcing (~2.6–8.5 W/m^2; Meinshausen et al., 2020).

For each model–scenario–period combination, maximum temperature values (tmax; 0.5° resolution) were extracted for the coastal region of Isla del Carmen (−92° to −91.2° W, 18.5° to 18.9° N). We computed the regional median maximum temperature and subtracted it from species-specific thermal limits to classify species as vulnerable (projected Tmax > CTMax) or tolerant (projected Tmax < CTMax). Projections were visualized using LOESS smoothing (geodata and stats packages; Hijmans et al., 2024; Meinshausen et al., 2020).

3. Results

3.1. *Temperature tolerance*

Critical thermal maxima (CTMax) across the 13 studied mollusks ranged from 33.2 °C to 51.3 °C. Bivalves generally tolerated higher temperatures than gastropods (Fig. 3A), both in air and water (bivalves: 46.06 ± 7.35 °C in air, 41.70 ± 5.20 °C in water, and gastropods: 39.94 ± 1.51 °C in air, 41.04 ± 2.12 °C in water). Highest air and water temperature maxima were recorded in bivalve species *Isognomon alatus*

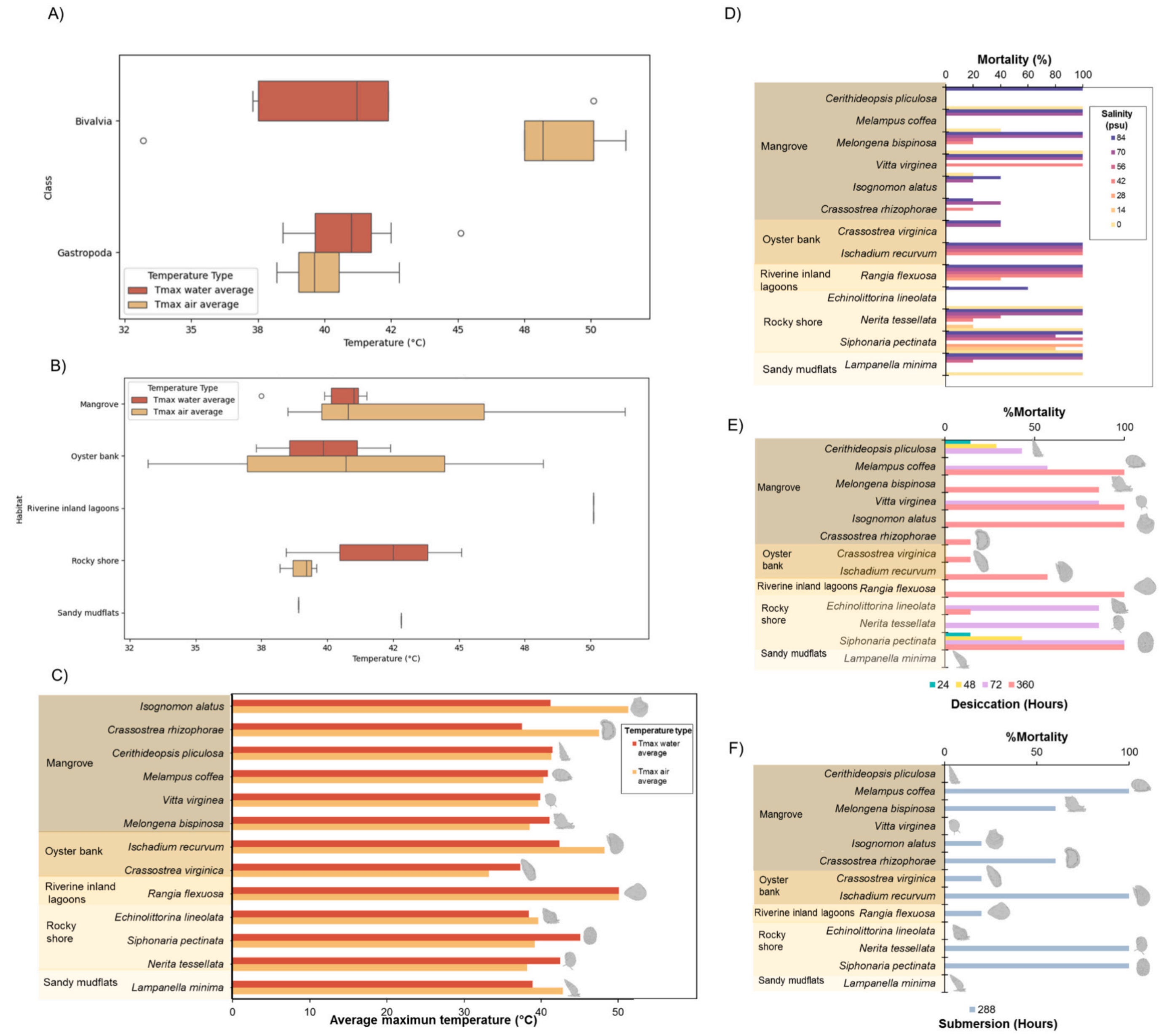


Fig. 3. Thermal, salinity, desiccation, and submersion tolerance experiments in 13 tropical mollusk species, showing maximum thermal tolerance (CTmax) in air (light orange) and water (red) A) by taxonomic class and B) by habitat type (riverine inland lagoons, mangrove, oyster bank, sandy mudflats, rocky shore), and species-specific responses grouped by habitat type (C–F): C) mean CTmax (°C) in air and water, D) mortality across seven salinity levels (0–84 PSU), E) mortality under desiccation stress (24, 48, 72, 360 h), and F) mortality after prolonged submersion (288 h). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Tmax air = 51.3 °C) and *Rangia flexuosa* (Tmax air and water = 50.1 °C), respectively (Fig. 3A). Pulmonate gastropods displayed the lowest thermal tolerance in water (*Melampus coffea*, 40.9 °C). It was the mangrove species *Isognomon alatus* that showed the highest tolerance to air temperature (51.3 °C) (Fig. 3B).

Air CTMax values differed significantly between bivalves and gastropods (Pseudo-f = 5.47, $p = 0.048$) and ecosystem-level differences, though no significant variation was detected among habitats (Pseudo-f = 0.8385, $p = 0.567$) (Fig. 3A). Some bivalves, such as *Isognomon alatus* and *Crassostrea rhizophorae* (Tmax air = 47.5 °C vs. water = 37.5 °C), reached higher thermal limits in air than in water. Several gastropods, particularly the pulmonate *Siphonaria pectinata* (Tmax air = 39.2 °C vs. water = 45.1 °C), and species with limited desiccation tolerance, such as *Nerita tessellata* (38.2 °C), *Vitta virginea* (39.6 °C), and *Melongena bispinosa* (38.5 °C), exhibited consistently lower CTMax values, especially in air (Fig. 3C). Exceptions were observed in operculate gastropods such as *Lampanella minima* and *Cerithideopsis pliculosa* (Tmax air = 41.3 °C), which showed high desiccation tolerance.

3.2. Salinity tolerances

Bivalves and gastropods differed significantly in salinity tolerance ($p = 0.011$). Bivalves tolerated a broader range (61.6 ± 30.67 PSU) than gastropods (54.2 ± 8.97 PSU). Mangrove species (*Crassostrea* spp., *Isognomon alatus*, *Melongena bispinosa*, and *Cerithideopsis pliculosa*) survived up to 40 PSU. Pulmonate and freshwater species had more stenohaline responses, with mortality under both hyposaline and hypersaline conditions. Rocky shores and sandy mudflat species were restricted to intermediate salinity (typically 14–42 PSU), except *Echinollitorina lineolata* (Fig. 3D).

3.3. Desiccation and submersion tolerances

Desiccation tolerance was highest in *Cerithideopsis pliculosa* and *Lampanella minima*, which survived 15 days (360 h) of exposure (Fig. 3E). *Crassostrea* spp. also showed high resistance (<20% mortality), whereas pulmonate gastropods that lack opercula (*Melampus coffea*, *Siphonaria pectinata*) experienced high mortality under desiccation (Fig. 3E). Shell closure explained most desiccation-related mortality ($p = 0.011$), and presence of an operculum had a marginal effect ($p = 0.056$) (Fig. 3E).

During prolonged submersion (Fig. 3F), species with branchial respiration, such as *Lampanella minima*, *Cerithideopsis pliculosa*, and *Vitta virginea*, were resilient, surviving the full duration of the submersion treatment (288 h). Pulmonate gastropods, such as *Melampus coffea* and *Siphonaria pectinata*, experienced rapid mortality, surviving only 192 and 288 h, respectively. Rocky shore species showed different patterns; *Echinolittorina lineolata* survived 288 h, whereas *Nerita tessellata* and *S. pectinata* experienced 100% mortality under submersion conditions (Fig. 3F).

3.4. Functional traits predict mortality under salinity and desiccation stress

The GLMM used to assess survival under salinity stress showed no statistically significant main effects of operculum presence or shell closure on mortality (Fig. 4A). Shell thickness showed a marginally non-significant trend ($p = 0.0870$) (Fig. 4B). The interaction between operculum presence and shell thickness also showed a marginal trend ($p = 0.0661$).

The GLMM showed that both the presence of an operculum and the capacity to isolate internal tissues via shell structures had significant effects on desiccation-induced mortality (Fig. 4). Individuals lacking an operculum had a higher mortality rate compared to those with an operculum ($p = 0.0535$) (Fig. 4D). Similarly, species lacking articulated shells that can be fully closed (Fig. 4E), such as most gastropods, had significantly greater mortality compared to bivalves capable of complete shell closure ($p = 0.0256$). Shell thickness alone (Fig. 4F) was not a significant predictor of mortality ($p = 0.2787$), nor were the interactions among traits.

3.5. Thermal safety margins (TSMs) predict climate vulnerability across tropical mollusks

Projected thermal safety margins (TSMs) across coastal habitats reveal marked interspecific differences in vulnerability (Fig. 5). In water exposure (Fig. 5A–E), TSMs remain generally positive across habitats, although species differ in the degree of decline. *Rangia flexuosa* and *Ischadium recurvum* retain the widest safety margins (>5 °C throughout the century). Mangrove species (*Cerithideopsis pliculosa*, *Melampus coffea*, *Melongena bispinosa*, and *Isognomon alatus*) and rocky-shore species (*Echinolittorina lineolata*, *Siphonaria pectinata*) show a progressive decline. For *Crassostrea virginica* and *C. rhizophorae*, temperatures are projected to cross their TSMs late in the century. *Lampanella minima* exhibits the narrowest margins, approaching critical values by mid-century.

Under subaerial exposure (Fig. 5F–J), TSMs decline more precipitously than in water. The oyster *Crassostrea virginica* is projected to decline below zero. *Melongena bispinosa* also loses its safety buffer, crossing below zero despite maintaining near-critical but positive margins in water. *Crassostrea rhizophorae*, which declines below zero in water, remains above the threshold under subaerial exposure. *Lampanella minima* retains relatively safe margins (>5 °C). Rocky-shore

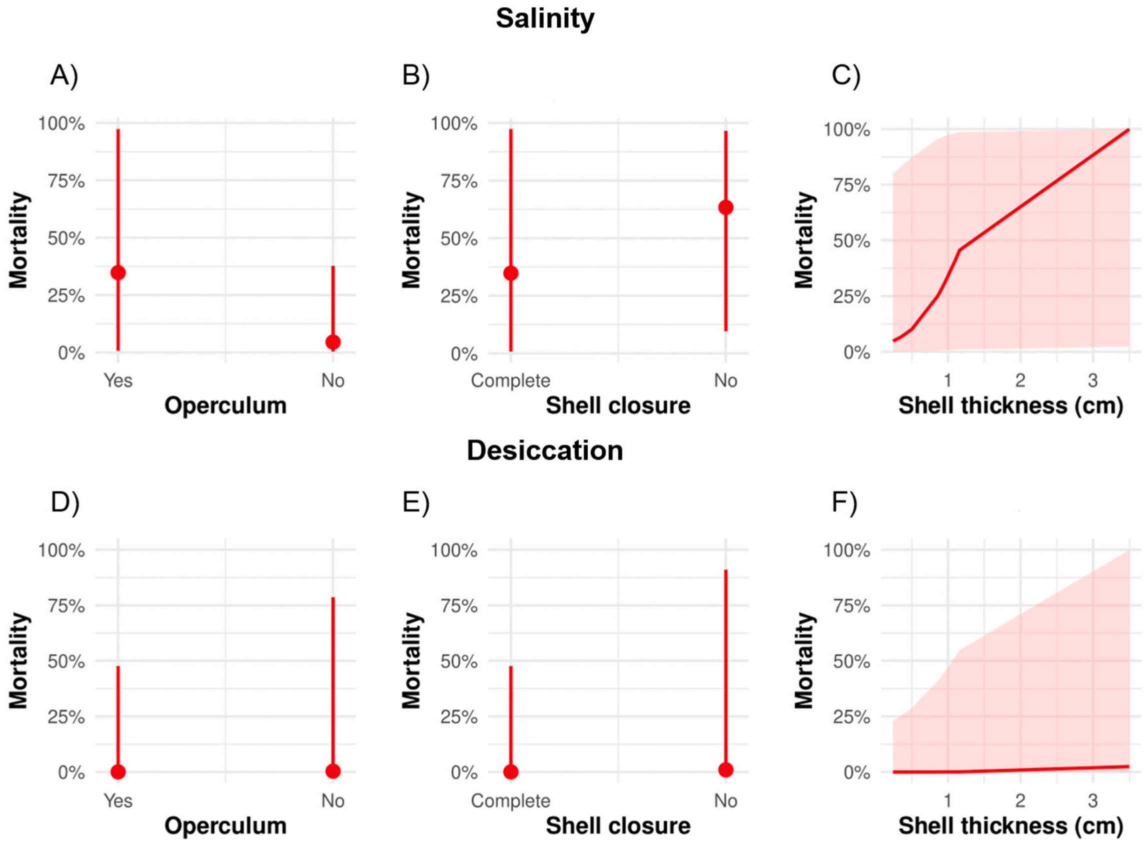


Fig. 4. Effects of morphological traits on mortality under salinity (A–C) and desiccation stresses (D–F), as estimated by generalized linear mixed models (GLMMs). Mortality is shown in relation to operculum presence, shell closure capacity, and shell thickness. Red points show model predictions with 95% confidence intervals (bars or shaded areas). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

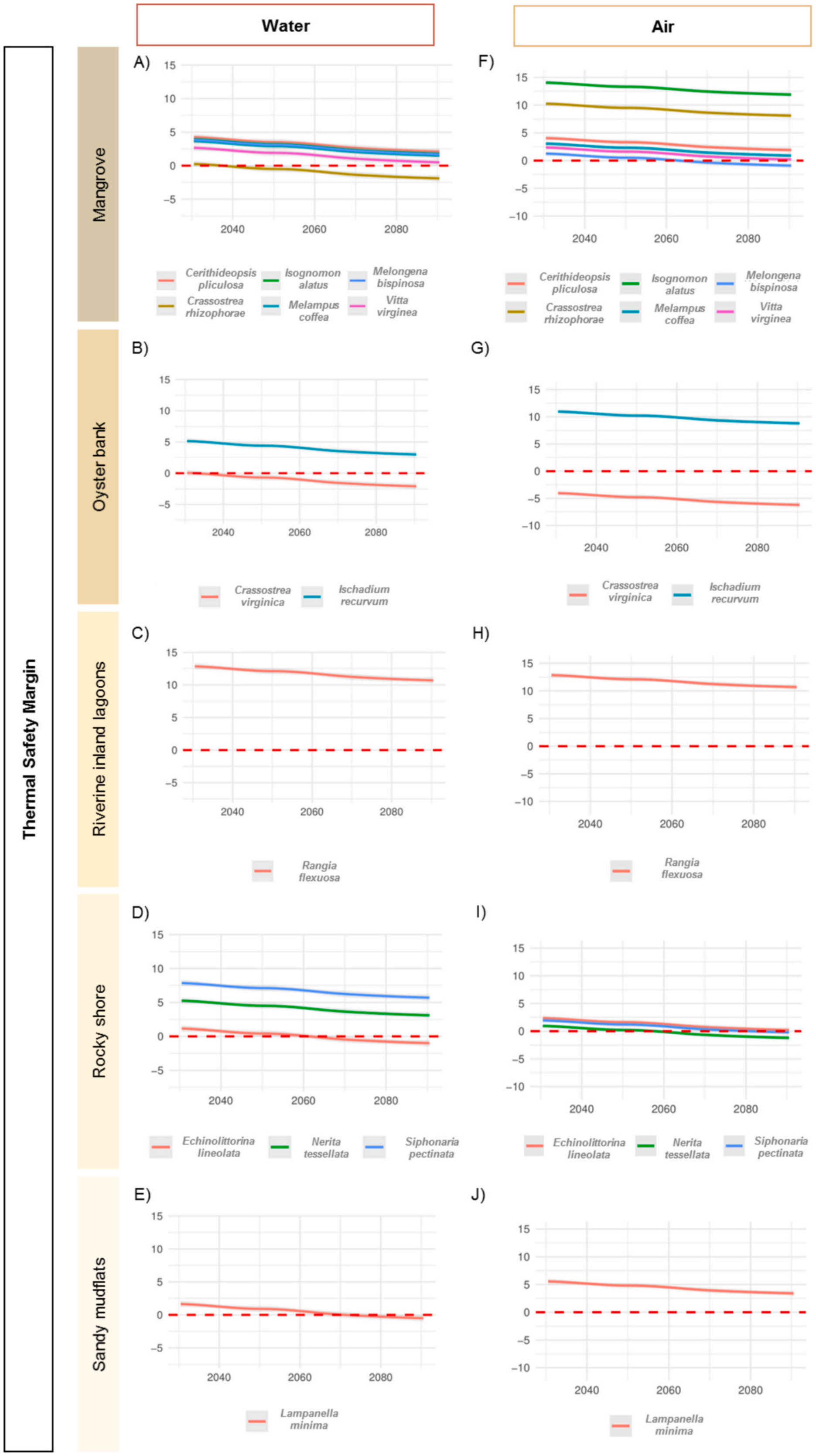


Fig. 5. Projected thermal safety margins (TSMs) for 13 tropical mollusk species across five coastal habitats. TSMs were estimated as the difference between experimentally determined upper thermal limits (CTmax) and maximum environmental temperatures projected for the periods 2021–2040, 2041–2060, 2061–2080, and 2081–2100. (A–E) TSMs in water and (F–J) in air. Zero values (red dashed line) represent the threshold of thermal tolerance; below this line, TSMs are negative, indicating that maximum temperature tolerance is exceeded. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

species *Echinolittorina lineolata* declines to near-critical levels, *Siphonaria pectinata* experiences reductions, and *Nerita tessellata* approaches and slightly crosses the zero threshold by the end of the century. As in water, *Rangia flexuosa* and *Ischadium recurvum* consistently maintain broad safety margins (>5 °C).

4. Discussion

This study showed that functional traits and ecosystem context will determine how 13 tropical mollusks respond to multiple climate-driven stressors in five coastal habitats. Structural isolation mechanisms (opercula and shell closure) and respiration mode emerged as the strongest predictors of survival under desiccation and submersion, respectively. At the same time, euryhalinity was critical for coping with salinity fluctuations. Habitat types also shape tolerance thresholds. Species from variable environments, such as mangroves and rocky shores, generally exhibited broader limits, whereas pulmonates and riverine taxa were the most vulnerable. These findings confirm that resilience arises not from a single trait but from a combination of functional traits filtered by environmental conditions, which together explain a species response to extreme temperature, salinity, and hydrological stress.

4.1. Air-water thermal limits reveal strategies across habitats

Lethal thermal tolerances in tropical mollusks remain poorly documented. Previous efforts, such as the GlobTherm database (Bennett et al., 2018), and studies by Vinagre et al. (2018, 2019), provided CTMax for a small number of temperate and tropical taxa. Our water-based CTMax values for 13 tropical species ranged from 40.9 °C (*Melampus coffea*) to 50.1 °C (*Rangia flexuosa*), extending the upper CTMax ranges (0.8 times), compared to the previous evaluation by Vinagre et al. (2018). Subaerial exposures revealed even higher CTMax (up to 51.3 °C in *Isognomon alatus*), underscoring the importance of considering both aquatic and subaerial conditions when evaluating the vulnerability of a species to climate extremes.

Bivalves consistently exhibited higher critical thermal maxima in air and water than do gastropods (Fig. 3A). This pattern may reflect differences in shell thickness, burrowing behavior, and microhabitat use. For instance, *Rangia* spp. can suppress routine metabolism and achieve limited survival, ranging from a few hours to several weeks under thermal stress (Tuszer-Kunc et al., 2020). Our study demonstrates that these species tolerate temperatures as high as 50 °C. It has been reported that at 32 °C, members of this genus can survive for several months. Previous studies indicated that upper lethal thermal limits can also be influenced by microhabitat conditions (Compton et al., 2007). Species that form clusters or possess byssal threads, such as *Isognomon alatus* and *Ischadium recurvum*, also exhibited relatively high CTMax values. However, the species that typically burrows and has a thick shell showed the highest CTMax among all taxa, suggesting that both behavioral traits (clustering or burrowing) and shell traits affect thermal tolerance.

Air CTMax was highest in intertidal species that inhabit mangroves and rocky shores, suggesting local adaptation to episodic subaerial exposure during low tides (Helmuth et al., 2002). Most species appear to mitigate effects of thermal stress behaviorally by synchronizing their activity and inactivity with tidal or diel cycles (Ng et al., 2021). Our results show that CTMax in air tends to be higher than in water, particularly for intertidal species (*Isognomon alatus*, *Ischadium recurvum*, *C. rhizophorae*, *Siphonaria pectinata*, *Lampanella minima*, and *Echinolittorina lineolata*), reflecting adaptations to subaerial exposure during low tides (Miller and Denny, 2011). Similarly, semi-terrestrial species like fiddler crabs tolerate higher temperatures in air than in water, likely because of oxygen limitation in warm aquatic conditions, whereas higher oxygen availability in air reduces the energetic cost of respiration (Capparelli et al., 2025). Terrestrial exposure, however, creates challenges like dehydration and osmotic stress, though individuals may use air-exposed microhabitats to lower body temperature and support physiological functions (Capparelli et al., 2022).

Additionally, it is important to consider that not only the surrounding air and water will warm, but substrates also can reach higher temperatures because of direct insolation. Such conditions exacerbate the risk of thermal stress, particularly for slow-moving species. The high CTMax values observed in species from mangroves and rocky shores suggest that behavioral thermoregulation strategies, such as seeking shade, lifting or reorienting the shell, or aggregating, may be essential for survival under future climate conditions (Ng et al., 2021).

4.2. Contrasting responses to salinity stress among tropical mollusks

Coastal habitats are undergoing progressive salinization, caused mainly by human activities, but compounded by climate change effects on precipitation, evaporation, and sea-level rise (Herbert et al., 2015; Moreira et al., 2023). These disturbances alter hydroperiods, reduce vegetation cover, and cause both elevated salinity and temperature (Capparelli et al., 2025), imposing substantial physiological costs related to osmoregulation, respiration, and behavior (Barrios-Figueroa and Urbina, 2023; Dildar et al., 2025). Future climate scenarios predict more frequent ENSO events, rainfall extremes, and heatwaves, all of which drive rapid salinity fluctuations (Valjarević et al., 2020; Suárez-Mozo et al., 2025).

Euryhaline bivalves and mangrove-associated gastropods exhibited the broadest salinity tolerance. *Isognomon alatus*, *Crassostrea rhizophorae*, *Crassostrea virginica*, and the gastropod *Echinolittorina lineolata* were among the most tolerant species to hypersaline conditions, up to 84 PSU. *C. virginica* is known to thrive across a wide range of salinity (McFarland et al., 2022). Species inhabiting estuarine and intertidal zones tend to exhibit higher salinity tolerance, in part because of their exposure to seasonal precipitation-driven changes. In our case, however, hypersaline conditions proved more favorable for mollusks than were low salinities that approached those of freshwater (Fig. 3D). Salinity stress is caused by the osmotic difference between the environment and an organism, which can trigger physiological imbalances (Dildar et al., 2025). Mollusks may respond through behavioral mechanisms such as valve closure, reduced movement, and withdrawal (Reyes-Martínez et al., 2020). However, these are often temporary solutions, and mortality occurs once cellular volume regulation fails (Verdelhos et al., 2015). In hypersaline mangrove zones of the southern Gulf of Mexico, species richness and abundance are low, with some mollusks restricted to less saline, undisturbed sites, highlighting that species that are unable to tolerate high salinity face strong ecological constraints (Suárez-Mozo et al., 2025).

Our findings indicate that the responses of some species to salinity stress are influenced by both their osmotic regulatory mechanisms and habitat type. *Rangia flexuosa* lacks structural and physiological mechanisms to withstand osmotic stress (0–28 PSU), rendering it especially vulnerable to salinity fluctuations. This species may serve as a sentinel of freshwater ecosystem stability under changing climate conditions, as its decline in transitional zones could signal a shift toward more marine-like conditions. The pulmonate gastropod *Siphonaria pectinata* displayed low hypersalinity tolerance despite being an osmoconformer, with hemolymph salt concentration tracking that of the local seawater (McAlister and Fisher, 1968). Although this species tolerates moderate salinity variations (20–40 PSU), survival dropped sharply beyond this range, consistent with previous reports. Our experiments confirmed survival only between 14 and 42 PSU, reinforcing its sensitivity to extreme salinity fluctuations.

4.3. Tolerance to submersion and desiccation in the face of sea-level change

Alterations in flooding regimes, driven by sea-level rise, intense droughts, and episodic inundation events, are becoming increasingly frequent as a consequence of global climate change, particularly in low-elevation tropical regions (McGranahan et al., 2007). The southern Gulf of Mexico is vulnerable, with projections indicating that sea level could rise by up to 2 m under RCP8.5 scenarios by 2100 (Sánchez-García et al., 2023). Considering this scenario, certain species and ecosystems may be more vulnerable to sea-level change.

Our experimental results show that tolerance to prolonged submersion was primarily determined by respiratory mode. Pulmonate species such as *Melampus coffea* and *Siphonaria pectinata* experienced high mortality when submersed. *Melampus* typically climbs onto mangrove roots as the tide rises, avoiding submersion (Proffitt and Devlin, 2005), and similar vertical escape behavior has been reported for other mangrove gastropods such as *Cerithideopsis* spp. (Collin and Ochoa, 2016). Comparable escape strategies have also been observed in fiddler crabs, which climb mangrove trunks or roots during extreme flooding and heatwave events (Capparelli et al., 2024). *Siphonaria* spp. cope by possessing accessory gills that facilitate gas exchange during immersion (Kankondi et al., 2018). Ongoing changes in flood regimes in degraded mangroves may disrupt these behavioral strategies (Capparelli et al., 2025), exposing pulmonate species to longer immersion events and increasing their vulnerability.

Across all species, our results indicate that desiccation was associated with weight loss (Supplementary Material 5), likely as a consequence of water loss, which may accelerate mortality (Maia and Troncoso, 2024). McAlister and Fisher (1968) showed that *S. pectinata* could survive up to 72 h of desiccation when attached, with mortality resulting from water loss and mantle rupture. In our experiments, mortality of *S. pectinata* reached 100% after 72 and 360 h of exposure (Fig. 3E), corroborating the limited ability of this species to cope with prolonged desiccation. Gastropods with gills and opercula were more tolerant of prolonged submersion and desiccation, indicating that structural and physiological isolation from the environment is key for coping with desiccation. Similarly, terrestrial fiddler crabs (*Minuca rapax* and *Leptuca panacea*) reduce water loss and maintain internal stability through gill-chamber retention of water (Capparelli et al., 2022). Our GLMM results show that individuals possessing these traits exhibit significantly lower mortality under desiccation stress (Fig. 4).

As climate change intensifies, droughts and heatwaves will become more frequent, magnifying the impacts desiccation and flooding stress. Sessile taxa such as mussels are exposed, but aggregation can buffer against heat through increased thermal inertia (Wagner et al., 2024). This mechanism may explain the survival of species that form dense aggregations (*Crassostrea* spp., *Isognomon alatus*, *Ischadium recurvum*), which only showed mortality under long periods (360 h) of desiccation.

4.4. Functional traits act as ecological filters under climate-driven stressors

No single trait determines tolerance; instead, combinations of morphological, physiological, behavioral, and ecological traits shape responses to extreme environmental conditions. Traits such as shell thickness, shell closure capacity, operculum presence, and tolerance to temperature, desiccation, and salinity extremes act as selective filters under climate change scenarios. Species that possess these traits are more likely to persist (Cushway et al., 2025), potentially reshaping community composition and ecosystem functioning. Isolation mechanisms are among the most effective survival strategies in mollusks. Bivalves close their shell to avoid adverse environmental conditions, and some gastropods use opercula to reduce water loss and protect internal tissues. However, prolonged isolation restricts oxygen and food intake, forcing reliance on less efficient anaerobic metabolism (Tuszer-Kunc et al., 2020).

Gregarious behavior in *Echinolittorina peruviana* enhances desiccation tolerance and aggregated individuals keep opercula open longer than solitary ones, suggesting interactive physiological benefits in stressful environments (Muñoz et al., 2008; Rojas et al., 2013). Mangrove-associated gastropods modulate their vertical position in response to tidal cycles. They climb onto trunks or branches above the inundation zone during high tides and descend to forage during low tides. This dynamic positioning may help mitigate the effects of high temperatures and low humidity during the dry season, and vertical mobility could offer a temporary refuge against sea level rise. In *Cerithideopsis* spp., these environmental conditions may also influence reproductive cycles (Collin and Ochoa, 2016). Other gastropods like *Achatina achatina* enter estivation and undergo metabolic depression during prolonged dry periods. While in this state, their lipid reserves are depleted, and oxidative damage can accumulate (Chukwuka et al., 2014). Some snails also form an epiphragm, a temporary barrier to prevent desiccation (Esue and Ademolu, 2025). During immersion, littorinid snails retract their feet and seal the shell aperture with mucus, minimizing evaporative water loss and limiting heat transfer from the substrate (Ng et al., 2021).

Infaunal bivalves like *Rangia* spp. respond to stress by adjusting the depth to which they burrow and by closing their shells (Hopkins and Andrews, 1970). *Rangia flexuosa* displayed the highest thermal tolerance among the studied species, likely aided by its thick shell, highlighting a potential advantage under warming scenarios. Experimental studies on oysters showed that individuals with slower growth rates developed thicker shells, suggesting a tradeoff between growth and shell protection (McAfee et al., 2017). Intraspecific variability was also observed in oyster beds between *Crassostrea virginica* and *Ischadium recurvum*, possibly indicating competitive interactions or differing tolerances, although their ecological dynamics in Laguna de Términos, southern Gulf of Mexico, remain poorly understood.

4.5. Tolerance to climate change scenarios

Temperature is a key driver of ectotherm physiology (Davenport and Davenport, 2005), and predicting climate change impacts requires understanding how thermal stress alters organismal performance. Although air and water temperatures are commonly used as proxies, actual body temperature depends on multiple interacting factors (Seuront et al., 2018), a critical consideration for tropical species already near their thermal limits (Vinagre et al., 2015). Our results highlight the contrasting vulnerability of tropical mollusks depending on whether they are exposed to aquatic or subaerial conditions (Fig. 5). Whereas most species are predicted to retain positive thermal safety margins (TSMs) in water throughout this century, subaerial exposure yielded predicted declines, with several taxa approaching or crossing critical thresholds. Indeed, predictions of climate impacts based solely on air or water temperatures often differ markedly from those that include body temperature (Helmuth et al., 2002).

Recent advances, including the development of open-access climate models, long-term high-quality datasets, and improvements in physical and biological monitoring, have greatly enhanced our ability to quantify atmospheric and oceanic warming (Ukoba et al., 2025). However, a critical gap remains: fine-scale monitoring that captures organism-specific body temperatures and microhabitat variability, and how these scale up to shape global biodiversity responses. Bridging this gap is essential for predicting dynamics under climate change. In particular, marine heatwaves (MHWs) are strongly influenced by fine-scale spatial variability in coastal environments (Capparelli et al., 2024). This variability affects how individual organisms and ecosystems respond to thermal stress, introducing uncertainty into thermal safety margin estimates derived from regional climate projections. Additionally, inter-individual variation in thermal tolerance and differences among climate scenarios may further modulate projected safety margins, highlighting the need for detailed, localized monitoring to accurately assess and predict ecological impacts (Starko et al., 2024). Consequently, projected safety margins should be interpreted as indicative ranges rather than fixed thresholds.

4.6. *Perspectives on tropical coastal vulnerability*

Most climate change projections focus on temperature and ocean acidification, whereas critical variables in estuarine and coastal ecosystems, such as salinity (Valjarević et al., 2020), flooding (Rey et al., 2025) and desiccation (Marks et al., 2025) remain largely overlooked. Experimental findings are rarely validated under field conditions (Capparelli et al., 2025), which limits our ability to capture ecological complexity and identify synergistic interactions among multiple factors. Thermal tolerance has been shown to shift in the presence of other stressors, such as low oxygen concentrations or high salinity, underscoring the importance of considering key physiological variables (Xie et al., 2023). The lack of long-term time series of environmental conditions in lagoons and estuaries, in contrast to the abundance of open ocean data, often leads to generalizations that neglect the heterogeneity of local microhabitats and weaken long-term predictive capacity. To address this limitation, modeling approaches that estimate the probability of ecosystem persistence under high parameter uncertainty provide a valuable alternative (Buelow et al., 2025).

Species functional traits also shape their responses to climate change. Sessile organisms such as oysters must endure harsh environmental conditions, whereas mobile species may tolerate extreme temperatures, given their ability to escape (van der Grient et al., 2025). We must account for the interplay among multiple stressors and functional traits if we are to be able to predict more accurately biological vulnerability in coastal ecosystems. Species lacking effective isolation mechanisms or broad salinity tolerance, such as pulmonates and riverine species, emerge as priority targets for conservation-oriented monitoring, as they are likely to respond rapidly to increasing thermal and hydrological variability. Conversely, habitat-forming and mangrove-associated species may function as effective sentinels of ecosystem change, given that their tolerance thresholds are projected to be exceeded under future climate scenarios.

5. Conclusions

Our study revealed that mollusk survival under climate-driven stressors cannot be explained by a single factor, but rather, is controlled by a combination of morphological, physiological, and behavioral traits, and habitat characteristics. At a broad taxonomic level, bivalves generally exhibited higher tolerance than gastropods; however, closely related species, such as oysters, displayed contrasting thermal safety margins and different responses to aerial versus aquatic exposure. Likewise, species co-occurring within the same habitat did not necessarily share similar tolerance limits, whereas some taxa occupying distinct habitats converged in their tolerance limits.

1. Thermal tolerance variability (Question 1). As predicted, structural isolation traits (shell closure, operculum) and respiration mode strongly influenced thermal tolerance. Bivalves and taxa with the ability to close their shells consistently displayed higher thermal limits, supporting the idea that phenotypic plasticity linked to isolation provides advantages under extreme heat stress, despite associated physiological tradeoffs.
2. Salinity tolerance reflects habitat context (Question 2): Salinity tolerance was strongly habitat-dependent. Mangrove and oyster bank mollusks displayed broader salinity ranges, whereas pulmonates and riverine lagoon species were more stenohaline, confirming that exposure to salinity variability predicts resilience to future fluctuations.
3. Survival under prolonged submersion (Question 3). As expected, respiration mode played a key role in survival. Branchial species tolerated prolonged immersion, whereas pulmonates exhibited rapid mortality. Isolation traits contributed partially to survival, although their effectiveness was limited under prolonged submersion.
4. Resistance to desiccation (Question 4). Survival under prolonged subaerial exposure was tightly linked to the presence of an operculum and shell closure capacity, confirming our predictions. Shell thickness alone was not a significant predictor of survival in the face of drying.
5. Future thermal safety margins (Question 5). Climate projections revealed that habitat-forming species (e.g., *Crassostrea* spp.) and several mangrove taxa are likely to experience temperatures that exceed their thermal safety margins, before the end of this century. Some bivalves (*Ischadium recurvum* and *Rangia flexuosa*) are projected to retain broader safety margins, consistent with a “use it or lose it” strategy. That is, resilience will be favored in taxa that are regularly exposed to fluctuating conditions.

Overall, our findings demonstrate that no single trait determines for tolerance to climate change. Instead, it is a combination of functional traits, interacting with habitat context, which together shape a species capacity to withstand rising temperature, salinity fluctuations, and hydrological extremes. This trait-based approach can be extended to other taxonomic groups and ecosystems, provide insights into biodiversity responses under ongoing climate change, and enabling prioritization of conservation efforts.

CRediT authorship contribution statement

Nancy Yolimar Suárez-Mozo: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luis Enrique Angeles-Gonzalez:** Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation. **Gabriel M. Moulatlet:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Ana Dianel Hernández-Ceballos:** Writing – review & editing, Methodology, Formal analysis. **Fernando Díaz:** Writing – review & editing, Validation, Supervision, Investigation. **Catarina Vinagre:** Writing – review & editing, Visualization, Validation, Investigation, Conceptualization. **Mariana V. Capparelli:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Data availability

Data will be made available on request.

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