

Eco-Evolutionary Dynamics in Mangrove Nurseries: How Habitat Warming May Shape Behavioral Thermoregulation and Physiological Tolerance

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Abstract

Mangrove ecosystems serve as nursery grounds for fish, elasmobranchs and crustaceans, providing food, shelter and structurally complex habitat, which promotes the survival and recruitment of young fish and elasmobranch. Concurrently, the warm shallow waters of mangroves may have marked diurnal temperature fluctuations and heat extremes that push the resident organisms into or out of their physiological optimum. These thermal stresses could be exacerbated by warming climate and more frequent marine heatwaves. But the effects of warming are also influenced by the intrinsic ability to tolerate it, and by the ability of organisms to regulate their thermal environment behaviourally. This narrative review is intended to review the potential changes in the balance of behavioural thermoregulation, physiological plasticity and selection of thermal traits in mangrove nursery organisms due to warming. Fishes, elasmobranchs, and crustaceans show evidence of using mangrove-associated microhabitats, aggregating, changing behaviour and switching between aquatic and terrestrial habitats to decrease thermal exposure. Physiological responses consist of metabolic adjustment, changes in respiratory performance, and activation of cellular stress pathways. But these responses should not be considered as an automatic process of evolution. There is the possibility that a behavioral buffering effect can also lower exposure to extreme temperatures and thus attenuate selection against the physiological thermal limits, as mentioned in the Bogert effect. In contrast, changes in mangrove structure could eliminate thermal refugia, thereby enhancing thermal tolerance selection. There is evidence of local adaptation at the mangrove crab population level, while direct evidence of evolutionary change over multiple generations is rare. We hypothesize that Mangrove habitat structure acts as an ecological filter, influencing the kind of buffering response, behavioral or physiological, to warming. For long-term climate change resilience of mangrove nursery populations, a combination of microhabitat temperatures, organismal body temperatures, behavior, physiology, fitness and heritable variation will be crucial.

1. Introduction

Mangroves are intertidal ecosystems that are of high productivity and are home to a wide variety of fishes, crustaceans, molluscs and elasmobranchs, as well as offering food, shelter and nursery functions (Faunce & Serafy, 2006). These form a mosaic of shallow pools, tidal channels, submerged roots, shaded areas, exposed mudflats and burrows. Such features may affect the avoidance of predators, foraging opportunity, movement, and recruitment of juveniles. Coastal habitats are especially valuable for their nursery function due to the potential effect of early life conditions on growth, survival, recruitment, and ultimately the abundance of adults (Beck et al., 2001). The climate warming impacts on species may also influence the demography of movement from juvenile to adult habitats (Gillanders et al., 2003). Long-term monitoring within marine nurseries has shown that warming can change the abundance of species, but also their functional structure and composition of the communities (McLean et al., 2018), suggesting that climate change may affect the function of nurseries at the community level, as well as at the species level.

The mangrove environment in particular is of special interest for the thermal-ecology aspect as it can have pronounced temperature fluctuations over short periods. Significant fluctuations in temperature can occur across short distances in shallow water, under high solar radiation, with limited circulation, under tidal exposure and due to air-water interactions. Early studies of fish species in hyperthermal ponds on mangrove islands showed that species are not equally tolerant of high temperatures and that some are quite tolerant of high temperature and can survive (Heath et al., 1993).

Meanwhile, the temperature registered in a mangrove channel is not an organism's temperature. The animal may be able to move from exposed water to shaded water, from one depth to another, into a burrow, towards other animals of the same species or to change its activity time. Therefore, behavioral thermoregulation can play a significant role in altering thermal exposure. This is especially relevant in a warming climate. Behavioral avoidance of temperatures close to the physiological limits of organisms may mean that increases in the environment's temperature do not necessarily lead to greater physiological tolerance. On the other hand, with habitat loss, there may be less thermal refuge for people, meaning that they may be faced with temperatures more extreme than their physiological tolerance. This results in the question of how the interplay between ecology and evolution will manifest in the center of the system, namely: Is the buffering of warming due to behavioral thermoregulation or due to increased thermal stress and selection of thermal traits?

The answer to this question must differentiate three processes which are related but fundamentally different: behavioural plasticity, physiological plasticity and evolutionary adaptation. Behavioral plasticity refers to a change in behaviour of an organism in response to environmental conditions. Physiological plasticity refers to reversible modification of metabolic, respiratory, cellular or molecular function after exposure to the environment. Evolutionary adaptation, however, depends upon the heritable variation and differential reproductive success between generations. This is significant, because a substantial amount of the existing mangrove literature shows behavioral or physiological responses, but not evolutionary change. This narrative review therefore is able to synthesize evidence for mangrove-associated fishes, elasmobranchs, and crustaceans and provides mechanistic insight through comparative studies in other tropical ectotherms that can provide insight into the proposed eco-evolutionary framework.

2. Mangrove Nurseries as Thermally Heterogeneous Environments

2.1 Thermal heterogeneity

Mangrove nurseries are thermally non-uniform with temperature fluctuations that could be considerable on relatively small spatial and temporal scales. Each of these factors contributes to creating unique thermal microhabitats due to the interaction they have with shallow water, intense solar radiation, tidal fluctuation, variable water depth, canopy cover, sediment exposure, freshwater inputs, and local hydrodynamics. Thus, mangroves in the same mangrove system could be subjected to very different temperatures according to their position and activity. Initial studies on fishes in hyperthermal ponds on mangrove islands were conducted to establish thermal tolerances and preference for fishes in those ponds and allowed for the determination of the inter-specific differences in thermal preference and tolerance; these studies confirmed that fishes in mangrove islands can survive over a wide range of temperatures (Heath et al., 1993). Recent studies have focused on the importance of the structures providing thermal refuge, especially via shading and water flow. For instance, mosquitofish that reside in mangrove channels shifted from open water conditions to under the awnings of *Rhizophora mangle* in response to temperatures when they became stressful, illustrating how habitat structure can alter thermal exposure (Hendy et al., 2020). This spatial heterogeneity is also ecologically relevant since environmental temperature does not always correspond to the temperature experienced by an individual organism. Animals might choose cooler microhabitats, thereby subjecting their bodies to less body-temperature exposure without having to change their body-temperature limits immediately. Therefore mangrove structural complexity is an important ecological indicator of thermal resilience and could impact the nature of buffering and/or the intensity of physiological stress and selection generated by warming.

2.2 Environmental temperature versus body temperature

The body temperature of an individual ectotherm may differ from the environmental temperature. Body temp is a function of environment, solar radiation, water flow, substrate, body size, physiology and behavior (Kearney et al., 2009). Thus, the thermal load for organisms in the same nursery can vary as a function of microhabitat use and/or activity patterns. This distinction becomes significant when assessing climate vulnerability since physiological changes depend on the temperature of the organisms rather than just surrounding temperatures (Kearney et al., 2009). This relationship can be modified through behavioral thermoregulation, whereby movements to cooler or warmer habitats minimize exposure to a stressful habitat. Mosquitofish is a good example: As water temperature rose above threshold, individuals migrated to cooler sites under mangrove vegetation where temperatures were significantly reduced (Hendy et al., 2020). Burrowing, aggregation, or transiting between aquatic and terrestrial microhabitats may be similar habitat selection for crabs. So, warming does not mean only an increase in physiological stress directly. Rather, the biological impact of warming is related to the presence, accessibility and persistence of cooler refugia in the thermal landscape. Regional temperatures can therefore be misleading indicators of thermal exposure. The next steps to fully grasp how warming affects mangrove organisms include incorporating environmental sensors, animal movements, and body-temperature measurements into physiological assessments.

2.3 Mangrove structure as thermal infrastructure

Mangrove structural complexity can act as a thermal infrastructure to create temperature gradients within microhabitats. Solar heating, water movement, evaporative cooling and heat exchange can be modified by canopy cover, aerial roots, submerged roots, channels, pools, sediment surfaces, and burrows. Such features may enable organisms to lower their temperature without altering their physiological tolerance. The example of fishes associated with mangrove forests gives rise to this mechanism. Mosquitofish were found to shift their movement towards the vegetation to cool areas under *Rhizophora* mangle when water temperatures were stressful, showcasing the immediate thermal refuge provided by vegetation. (Hendy et al., 2020) Refuges can be significant in extreme heat situations where moving can limit exposure to the heat. But the effectiveness of structural buffering is dependent on the habitat condition and spatial connectivity. Loss of mangrove, loss of mangrove canopy, changes to water flow, and mangrove fragmentation can also limit the number and quality of refuges, which can result in greater thermal exposure even if regional temperatures are the same. This establishes an important connection between habitat protection and thermal resilience. However, the existence of a cooler microhabitat does not automatically mean that they are protected, as they may have to make trade-offs in feeding, predation, competition, oxygen, salinity, or reproduction in refugia. The structure of mangroves should therefore be considered as a climate warming mitigator rather than a panacea. The interaction between mangrove structural complexity, thermal heterogeneity, and organismal behavior is illustrated in Fig. 1.

3. Behavioral Thermoregulation

3.1 Microhabitat selection

Behavioural thermoregulation refers to the way organisms linked to mangroves can minimise exposure to stressful temperature. Fish and crustaceans do not simply react to their surroundings, but they can also modify their behavior or thermal environment by changing their thermal habitat use, activity or location. Possible responses are movements towards shaded water, deeper channels, burrows, or to areas where there is more tidal

exchange, as well as aggregation and alteration of daytime activities. These behaviors may help conserve body temperature without immediate adjustments of physiological thermal limits. Mosquitofish are a good example of this approach: exposed channels to shaded undercover in *Rhizophora* mangrove when conditions are stressful (Hendy et al., 2020). The fiddler crab also displays behavioural responses to extreme heat such as aggregation and movement between microhabitats (Capparelli et al., 2024). Behavioral thermoregulation can thus be effective at quickly protecting against short-term deviations from the thermal norm and may be especially important for juveniles who have less physiological capacity. But, with behavioral responses come ecological compromises. Access to food sources, competition/predation pressures, and reproductive opportunities may be affected by moving to cooler habitats. Thus, the effectiveness of behavioral thermoregulation is dependent upon the availability of appropriate refugia and the cost of reaching and/or occupying those refugia. These trade-offs need to be understood to determine how sustainable nursery populations may be with continued warming under the context of behavioral flexibility.

3.2 Behavioral buffering and the Bogert effect

Behavioral thermoregulation doesn't necessarily operate outside of evolutionary processes. Behavioral plasticity allows organisms to escape from stressful temperatures, thereby minimizing exposure to temperatures that would otherwise impose a selection pressure on physiological thermal limits. The Bogert effect posits that organisms can use their thermoregulatory behavior to cope with the environment, thereby decreasing selection on physiology (Huey et al., 2003). This is evident in the case of tropical lizards, which differ in their ability to compensate for thermal heterogeneity of their environment through behaviour and some thermal characteristics are evolutionarily conserved (Muñoz et al., 2014). This evidence is from terrestrial systems but the mechanism offers a conceptual framework of mangrove nurseries. Structurally complex mangroves can offer thermal refugia that can keep organisms cooler than their tolerated CT_{max}, so decreasing selection for increased CT_{max}. Behavioral options, on the other hand, may be lost due to habitat degradation, and exposure to extreme temperatures may be higher, thereby reinforcing selection on physiological tolerance. Importantly, the Bogert effect is a theory of behavior and evolution, not proof that behavior thermoregulation precludes adaptation globally. However, some behavioural characteristics, such as habitat preference, movement capacity, activity timing and risk-taking may still be selected. Therefore, behavioral thermoregulation could increase resilience and change how warming affects the evolution of a population.

3.3 Limits to behavioral buffering

Availability and accessibility of thermal refugia are important factors in determining how well behavioral thermoregulation will work. The mangrove organisms are not only dependent on temperature, but also on the presence of predators, competitors, food resources, varying salinities, oxygen gradients and tides. Thus, a shift in habitat to cooler areas could be beneficial for thermal safety and be energetically or ecologically costly. The case of fiddler crabs living in disturbed mangroves is an example of this. Crabs also showed aggregation and behavioural responses during heatwaves, but their thermal safety margin was still not sufficiently high to indicate that behavioural buffering will not be adequate when approaching the physiological limits of thermal tolerance (Capparelli et al., 2024). Behavioral options may be limited due to habitat degradation caused by lower canopy cover, less hydrological connectivity, less complexity of roots and less shaded or deeper microhabitats. However, in such situations, an organism might not be capable of regulating its temperature with thermoregulatory behavior. The result will be a higher exposure to heat which could have an impact on eating, growth, movement, reproduction, and survival at lower temperatures before the lethal level is reached. However, the ability to respond

behaviorally flexibly is not a bottomless pit to take care of the climate. The behaviorally flexible response can only be effective if the thermal refuges are available in quality, quantity and persistence, and their accessibility is not too high (Fey et al., 2019). Conservation of mangroves could contribute to maintaining biodiversity, nursery role, and behavioral choices to deal with thermal variability.

4. Physiological Thermal Tolerance

Physiological thermal tolerance refers to the ability of mangrove associated organisms to tolerate temperatures that cannot be avoided by behavior. Thermal tolerance refers to several physiological mechanisms such as metabolic control, respiratory function, cellular mechanisms of stress and homeostasis maintenance at higher temperatures. They include critical thermal maximum, upper thermal limits, thermal safety margins, metabolic rate, and expression of heat-shock proteins. These measures of survival are complementary to each other, as survival at an extreme temperature doesn't automatically mean normal physiological performance. Research on the thermal tolerance of fishes and crustaceans associated with mangroves shows great interspecific variability. Juvenile ribbontail stingrays (*Taeniura lymma*) from hyperthermic nursery areas show physiological traits that are compatible with a survival strategy in an unusually warm nursery environment (Dabruzzi et al., 2012). Likewise, the juvenile spotted rose snapper (*Lutjanus guttatus*), exhibits temperature-related changes in respiratory metabolism and expression of stress related genes, where increased temperature resulted in Hsp70 and Ldh-a expression (Larios-Soriano et al., 2020). There is also intra- and inter-specific variation in UTL in fiddler crabs due to differences in thermal specialization and local adaptation (Fusi et al., 2014). Predicting warming vulnerability has to take into account such physiological diversity. But physiological tolerances are not enough to assess ecological resilience, as organisms may be subjected to temperatures "above their optimal range" before they reach lethal limits. Therefore, physiological responses need to be viewed in conjunction with behaviour, habitat structure and environmental variability to determine responses to climate change in mangrove nurseries.

4.1 Thermal performance curves

The physiological and ecological performance tends to be nonlinear, with the greatest responses to temperature occurring to an optimum level before decreasing at the highest temperatures. This connection makes a difference between temperature limits that are tolerable and temperature ranges that are optimal for the function of organisms. The critical thermal maximum is the highest temperature found by experiment, at which normal function ceases while the thermal safety margin is the difference between the organism's upper thermal limit and the environmental temperature it experiences. These two concepts are of value in assessing warming vulnerability, but should not be used without considering ecological context. The frequency and duration of exposure to thermal extremes are important factors in determining biological consequences because there may be a significant difference between routine temperature and short-lived thermal extremes in mangrove organisms. Upper critical limits of 40–42°C have been observed in fiddler crabs living in disturbed mangroves, suggesting that they are not thermally safe under extreme conditions (Capparelli et al., 2024). However, in fishes, acclimation may alter thermal performance and physiological parameters, suggesting that observed thermal limits can be influenced, at least in part, by the thermal history of recent events (Larios-Soriano et al., 2020). The thermal safety margins can thus vary between populations depending on the habitat structure, local climate, and behavioural thermoregulation. Selection pressures on upper thermal limits may be greater in cooler environments, while in warmer environments, populations that have secure thermal refugia may have weaker

selection pressures on upper thermal limits. The combination of CT_{max}, field temperature and behavior yields a more realistic estimate of climate vulnerability.

5. Physiological Plasticity and Acclimation in Mangrove-Associated Fishes

The ability of the mangrove-associated organisms to alter their thermal performance with changes in environment may lessen the immediate impact of warming. While acclimation may affect metabolism, the performance of respiration, limits to heat tolerance, and responses to cellular stress, the extent and direction of any changes will vary among species and populations. Acclimation temperature affected thermoregulatory behavior, thermal tolerance and respiratory metabolism in juvenile spotted rose snapper (*Lutjanus guttatus*), and the increased temperatures led to higher expression of heat-shock protein 70 (HSP70) and lactate dehydrogenase-related responses (LDRP) (Larios-Soriano et al., 2020). These responses are all signs of the ability to engage physiological responses to sustain cell function during thermal stress. Local adaptation may interact with plasticity because of the population-level variation. There are also reports of variability in metabolic response and thermal sensitivity among populations of Atlantic killifish (*Fundulus heteroclitus*) (Fangue et al., 2006), suggesting that thermal environments can influence physiological phenotypes. But acclimation is not to be confused with evolutionary adaptation. Plastic response happens within her lifetime and can initially be of benefit, but adaptation involves heritable changes that affect the distribution of traits across generations. Furthermore, energetic costs incurred by physiological plasticity can decrease growth, reproduction, and/or other aspects of fitness. The ability to acclimate is thus an important element in thermal resilience, however, this is only useful to the extent that changes in the environment are large in magnitude, prolonged in duration and generally unpredictable, and that there are limits to physiological acclimation.

6. Metabolic Responses to Temperature

When temperature influences the long-term survival and reproductive success of individuals, warming may shift physiological plasticity from a plastic response to a possible target for natural selection. To have evolutionary changes, there needs to be genetic variation in thermal traits that is associated with differences in fitness. Mangrove associated crabs are evidence of the possibility of geographical variation in the species' thermal specialization. For instance, *Uca urvillei* had a wider thermal tolerance, indicative of higher thermal generalism, than populations from cooler areas while *Perisesarma guttatum* populations from warmer equatorial regions were more tolerant to heat stress and had partial thermoregulatory capacity than those from cooler regions (Fusi et al., 2014). This geographic variation can be reconciled with local adaptation, but it is difficult to separate genetic adaptation from developmental plasticity using reciprocal-transplant or common-garden designs. Warming is thus likely to create a different set of selective pressures depending on the structure of habitats. Behavioral thermoregulation can lead to a decrease in mortality and a decrease in the intensity of selection on ULs where cool refugia are constantly available. If refugia are rare or unavailable, repeated thermal stress can lead to higher differential survival and reproductive success of more tolerant individuals. This establishes a potential pathway for eco-evolutionary change from environmental warming to changes in population-level thermoregulatory traits. But evolutionary solutions could be limited by trade-offs, lack of genetic variation, dispersal, generation time and the rate of change. Therefore, physiological plasticity and/or geographic variation does not necessarily represent evidence for evolutionary adaptation in the recent past.

7. Cellular Stress Responses

The structure of the habitat can greatly influence whether mangrove organisms are able to behaviorally avoid thermal stress. Organisms can choose conditions with less heat exposure as the thermal environment of channels, pools and burrows may also be spatially heterogeneous due to dense vegetation and complex root systems. These buffering effects could markedly modify the environmental warming/physiological stress link. For instance, in the context of increasing temperatures, mosquitofish shifted from exposed water towards mangrove shade, showing the availability of accessible thermal refugia, which is provided by the vegetation (Hendy et al., 2020). Similar principles have been observed in other ectothermic systems, where habitat structure can affect the ability to make behavioral adjustments, and therefore can affect sensitivity to climate warming (Neel et al., 2021). Consequences of habitat degradation in mangroves might thus go beyond loss of biodiversity. The removal of canopy, modification of the hydrology, degradation of the root systems, and fragmentation can lead to a decrease in available cooler microhabitats or in the connectivity of cooler microhabitats, which can cause organisms to be exposed to increasingly stressful temperatures. In this case, behavioral buffering can reduce, and even remove, its effectiveness, which can drive up mortality and intensify the selection for physiological tolerance. In certain cases, however, there are habitat structure trade-offs; cooler refugia may offer fewer food resources, more predators or competitors. Therefore, the complexity of mangrove cover and thus thermal value is dependent on the spatial distribution of refuges and their ecological accessibility. Conservation of structural complexity can then help to maintain not only habitat, but also behavioural options by which organisms can cope with warming.

8. Warming in Combination with Other Environmental Stressors

Thermal stress in mangrove nursery is seldom used in isolation of other environmental stresses. Hypoxia and salinity, acidification, pollution, changed hydrology and habitat degradation may interact with elevated temperature, and may produce physiological effects that are additive or greater than the effects of temperature alone. Under heat wave conditions, shallow mangrove ecosystems can simultaneously experience high temperatures and low dissolved oxygen (DO) levels, especially if water exchange is limited. These conditions may cause some increase in metabolic demands and decrease in oxygen provision, thus adding to aerobic limitations. When mangroves are disturbed, they could potentially be particularly vulnerable, because habitat degradation could lead to loss of thermal refugia and changes to water quality and environmental stability. During the heatwave period the responses of the fiddler crabs are a good example of this vulnerability; disturbed populations exhibited behavioral responses, but limited thermal safety under extreme heat conditions (Capparelli et al., 2024). Physiological stress can also be identified via biomarkers during marine heatwaves and is known to occur when the temperature is not lethal, yet impacts the condition of the organisms (Capparelli et al., 2025). These interactions make it difficult to predict using only CT_{max} or ambient temperature. A relatively high thermal limit organism can still be limited in growth or survival in situations where heat is imposed in combination with hypoxia or other stress factors. Similarly, eco-evolutionary responses might be dependent on a combination of selective environment and not just temperature. Multiple environmental stressors should therefore be considered in future climate vulnerability assessment of mangroves, and the effectiveness of the combination of behavior and response in the face of realistic combinations of changes.

9. Ontogeny: Life-Stage Variation in Thermal Responses

Thermal responses vary significantly across life stages and are a critical factor in the ecological and evolutionary impacts of warming, particularly given that development is a crucial process to consider. Early life stages of fishes, crustaceans and elasmobranchs often use mangrove habitats and can therefore be subject to different thermal conditions than in later life stages. Juveniles can be significantly different from adults in terms of metabolic requirements, thermoregulatory tolerances, behavioral abilities, or energy needs. For instance, juvenile ribbontail stingrays (*Taeniura lymma*) live in warm coastal nursery habitats and have physiological traits associated with hyperthermic persistence (Dabruzzi et al., 2012). This specialization can be beneficial in warm nursery temperature but limiting when temperatures are above historic ranges. The influence of ontogenetic differences in selection can also be mediated by selection because the mortality in the young stages of life may lead to disproportionate recruitment effects and subsequent population size. Selective removal of juvenile fish with lower thermal tolerance by warming may change the phenotypic composition of recruits in subsequent generations if this condition is repeated over many years. However, behavioral refugia can create less of this filtering if individuals that are vulnerable to extreme temperatures can avoid them. The ontogeny-habitat structure-thermal physiology interface is thus an important facet of mangrove resilience. Research which looks at adults alone can underestimate the effect of climate change on population dynamics as recruitment failure may not be detectable until after changes in adult abundance have been observed. Life-stage specific behaviors and physiological tolerance and survival will be combined, leading to more accurate predictions for long-term persistence of mangrove nursery populations with warming.

10. Population Differentiation and Potential Local Adaptation

Individual performance, population dynamics, species interactions and thermal traits distribution can all be modified by warming the habitats, creating eco-evolutionary feedback. Organisms can react at the individual level by behavioral thermoregulation, or by physiological plasticity. Thermal stress may cause differential survival and reproduction at the population level and alter the distribution of phenotypes at the population level. These changes could then affect the composition of the community and the function of the nursery. The power of this pathway depends on the ability of organisms to avoid extreme temperatures, as well as the heritable variation in thermal traits that may allow them to respond to selection. These processes can be exacerbated by habitat warming and fragmentation, as the latter can cause a decrease in the availability of suitable habitat which can decrease opportunities for behavioral buffering and increase exposure to stressful conditions (Faillace et al., 2021). Climate warming may restructure community interior species composition at the community level by changing the growth and development of species with different thermal niches and life history strategies. Under warming, marine fish nurseries may experience functional changes, such as on predator-prey interactions and recruitment, for instance (McLean et al., 2018). These ecological modifications can in turn influence selective environments, through modifications in competition, predation and resource availability. So, warming is not just a pressure on a single organism or species. Rather, it is possible for thermal change to trigger interconnections of ecological and evolutionary changes at the individual, population and community levels, and impact mangrove nursery ecosystem persistence and function.

11. Plasticity Versus Adaptation

Feedback loops between behavioural thermoregulation and physiological tolerance may drive mangrove responses to ongoing warming. In the presence of suitable thermal refugia, organisms may minimize their exposure by moving or selecting habitats, which could limit the initial mortality and lower the intensity of

selection for physiological tolerance. This mechanism is similar to the Bogert effect, which occurs when behavioural thermoregulation can decrease the environmental exposure that would otherwise cause evolutionary adjustments to the physiological limits (Huey et al., 2003). But habitat degradation can turn this around. Without shade, root complexity or hydrological connectivity, behavioral choice can be limited, which can lead to greater exposure to the thermal extremes and enhance the selection for physiological traits. Physiological tolerance may then affect habitat use by changing thermal capacity and allowing them to hold on to resources in hot microhabitats, which in turn will affect competition. Behavioral and physiological are then used in a way that they can interact rather than work separately as strategies. Importantly, such feedbacks are largely conceptual in mangrove systems because very few studies have measured changes in the frequency of thermal traits over generations in mangrove systems and quantified the use of the habitat. Population differentiation in thermal tolerance for mangrove crabs is an indicator of evolutionary divergence in thermal traits, but does not, by itself, explain the mechanism (Fusi et al., 2014). Future studies of this should involve not only longitudinal studies in the field but also common-garden experimental studies, genomic studies, and direct body temperature measures, to clarify when behavioral buffering leads to resilience and when environmental warming results in measurable evolutionary changes. Figure 2 summarizes the proposed eco-evolutionary pathway linking habitat warming and loss of thermal refugia with behavioral thermoregulation, physiological stress, natural selection, and potential evolutionary change.

12. Evidence Hierarchy for Eco-Evolutionary Responses

Evidence for eco-evolutionary responses to warming can be arranged along a hierarchy from short-term (behavioral) to longer-term (evolutionary) responses (Table 1). The first level is behavioral thermoregulation, which involves moving from one microhabitat to another, or to some other location to reduce thermal exposure, and is a rapid indicator that the organisms have the capacity to change their thermal exposure (e.g., moving to a shaded microhabitat or to some other location that is cooler) (Hendy et al., 2020). The second level is physiological plasticity, such as changes in metabolic performance, heat-shock response or thermal limits after exposure or acclimation to different temperatures (Larios-Soriano et al., 2020). The third level refers to the variation in thermal traits at the population level, including local adaptation (genetic evidence is needed), such as geographic variations in heat tolerance between populations of mangrove crabs (Fusi et al., 2014). Evolutionary change at the highest level is shown by heritable shifts in the distribution of traits across generations that are linked to differential fitness of what is being changed under different thermal conditions. These are important because they are frequently confused in climate-change research. Flexibility in behaviour does not necessarily reflect physiological acclimation, and physiological acclimation does not imply evolutionary change. Also, geographic variation may be due to environmental plasticity without genetic divergence. The application of an evidence hierarchy can then make for a better distinction between observed responses and inferred evolutionary mechanisms. Current evidence is strongest for behavioral and physiological responses, moderate for population-level thermal differentiation, and is comparatively weak for directly demonstrated contemporary evolution for mangrove nurseries. This awareness helps to avoid over-interpretation and to identify experiments needed to ensure real eco-evolutionary change.

Table 1
Evidence for behavioral, physiological, and potential evolutionary thermal responses among mangrove-associated taxa under warming conditions.

Taxon	Species	Thermal challenge	Behavioral response	Physiological response	Evidence for adaptation
Fish	<i>Gambusia</i> spp.	Extreme warming	Movement to mangrove shade	Reduced thermal exposure	Not demonstrated
Elasmobranch	<i>Taeniura lymma</i>	Hyperthermic nursery	Thermal habitat use	Specialized physiological tolerance	Not demonstrated
Teleost	<i>Lutjanus guttatus</i>	Elevated temperature	Thermoregulatory response	Hsp70/Ldh-a responses	Not demonstrated
Crab	<i>Perisesarma guttatum</i>	Geographic thermal variation	Partial thermoregulation	Population-level tolerance differences	Possible local adaptation
Crab	<i>Uca urvillei</i>	High environmental temperature	Limited thermoregulation	High thermal tolerance	Consistent with generalism
Fiddler crabs	Various species	Marine heatwave	Aggregation/movement	Biomarker responses	Not demonstrated

13. Knowledge Gaps and Research Priorities

Although the evidence for thermal responses among mangrove-associated organisms continues to ramp up, there is still a lot that is not understood about whether there are measurable evolutionary changes that follow warming. While there is a large number of studies available quantifying physiological limits, short-term acclimation, or behavioural responses, the number of studies quantifying heritable variation in thermal traits across generations is relatively small. Repeated exposure to heat should be studied in a longitudinal fashion to see if population-level thermal phenotypes are modified. Field measurements of body temperature should also be incorporated into research, as ambient temperature may not reflect the thermal exposure to the organism(s). Replicated common-garden and reciprocal-transplant experiments would help identify genetic differentiation from thermal (developmental) plasticity among populations assigned to different thermal regimes. Genomic methods can also be used to determine alleles or regulatory mechanisms that are related to thermal tolerance but genetic associations should be correlated with fitness assessments before any evolutionary inferences can be made. A second priority is to understand the effects of habitat degradation on selection through its dual action of both decreasing thermal refugia and increasing the stress exposure to the individual from several stress factors. Greater attention must be paid to differences in life stage as well, since some life-stage effects on thermal selection may have a larger impact on recruitment than adult effects. Lastly, research needs to assess the ecological costs of behavioral thermoregulation, such as changes in feeding, predation risk, competition, and reproductive success. These gaps would take the field from measuring thermal tolerance to examining how habitat warming changes behavior, how it affects physiological variation, how it filters natural selection, and how thermal tolerance impacts long-term population persistence in mangrove nursery habitats.

14. Conservation and Management Implications

These implications of the eco-evolutionary approach are relevant to conservation of mangrove nurseries in the face of increasing thermal stress. Preserving mangrove structure may offer behaviour choices that help organisms survive when temperature extremes occur, thus maintaining thermal resilience. Conservation efforts should thus not focus on reducing the amount of mangrove habitat, but also on ensuring canopy cover, root complexity, tidal connectivity, the presence of heterogeneity in shallow water and other features that create accessible thermal refuges. Restoration of habitat could be especially useful in disturbed systems where the cooler microhabitats are depleted because of the warming. However, restoration should not be viewed as a climate mitigation strategy, as local habitat buffering can't be a substitute for rising regional temperatures forever. Species and population variation in thermal specialization also needs to be considered by management. Populations of species with higher tolerance to higher temperatures could have higher tolerance, while thermal specialists could be more sensitive to climate warming rates, and to habitat fragmentation (Fusi et al., 2014). Maintaining connectivity between mangrove habitat may help to enable gene flow between populations and promote migration to appropriate thermal habitats. Monitoring programs should be designed to include more than abundance, such as distribution, behavior, physiological conditions and recruitment as well as temperature. This integrated monitoring could be used to detect populations that were near their thermal limits before significant population declines. Thus, maintaining structural and functional diversity in mangrove ecosystems might maintain immediate functional resilience and ecological conditions for populations to respond evolutionarily to ongoing environmental change.

15. Conclusion

Mangrove nurseries are dynamic thermal environments, where the organisms react to the warming by interacting behavioral, physiological, ecological and possibly evolutionary processes. Exposure to body temperature can be minimized through behavioral thermoregulation, which enables organisms to take advantage of shaded channels, burrows, deeper water, and other thermal refugia; and physiological plasticity and tolerance can determine the ability to function when avoidance is restricted. There is significant variability in these responses, as evidenced by the responses of mangrove associated fishes (Dabruzzi et al., 2012; Fusi et al., 2014), elasmobranchs (Hendy et al., 2020; Larios-Soriano et al., 2020). But the presence of behavioural flexibility or physiological plasticity does not necessarily imply evolutionary adaptation. There is more support in the current literature for behavioral and physiological reactions and less for changes in heritable thermal traits across generations that can be directly demonstrated. The availability of thermal refugia is thus a key mediator of climate vulnerability, as it can prove to be a crucial determinant of the effects of climate warming on physiological stress and natural selection. Otherwise, habitat degradation can lead to elimination of behavioural options and increase the selection pressure on physiological tolerance. The long-term effects will be dependent on species-specific thermal niches, life-history traits, genetic variation, dispersal potential, and environmental change rates. These mechanisms require further testing directly in the field and should be investigated using a combination of the fields of thermal ecology, experimental physiology, field observations of behaviour, population genetics and demographic data. Maintaining structural complexity of mangroves and mitigating overall climate stressors may thus be pivotal for their ability to maintain nursery function and ecological resilience in a future of continued warming.

Declarations

Declaration of Interest Statement

☒ 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.

Author Contribution

M.S. supervision, manuscript-writing and editing ; N.M. manuscript-reviewing and editing.

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N/A

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Figures

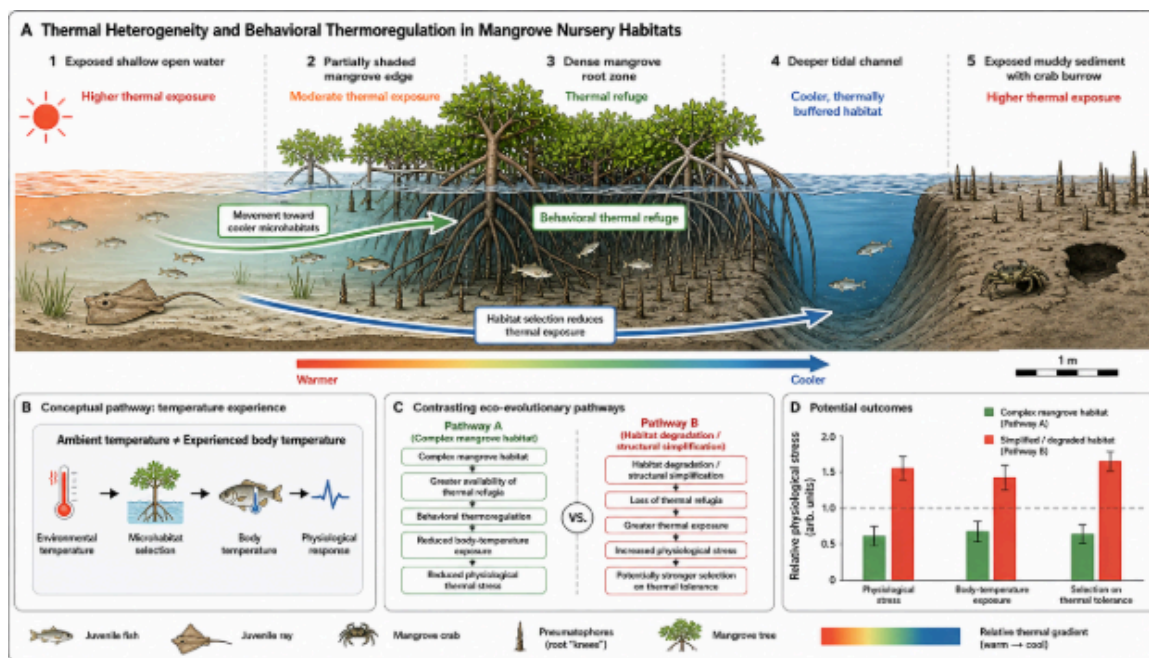


Figure 1

Thermal heterogeneity in mangrove nursery habitats and behavioral thermoregulation through movement toward cooler microhabitats and thermal refugia.

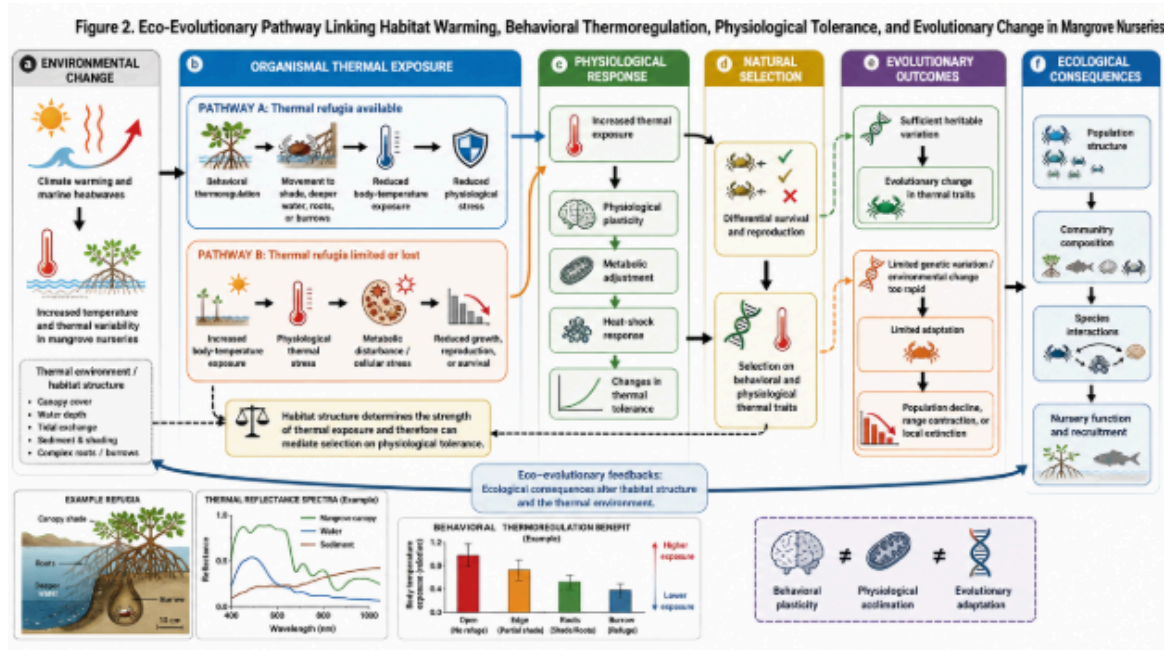


Figure 2

Conceptual eco-evolutionary pathway linking habitat warming, behavioral thermoregulation, physiological tolerance, natural selection, and potential evolutionary change in mangrove nursery organisms.