

Review

The ecological and evolutionary consequences of tropicalisation

Karolina M. Zarzycny ^{1,2,*} Marc Rius,^{3,4} Suzanne T. Williams,² and Phillip B. Fenberg^{1,2}

Tropicalisation is a marine phenomenon arising from contemporary climate change, and is characterised by the range expansion of tropical/subtropical species and the retraction of temperate species. Tropicalisation occurs globally and can be detected in both tropical/temperate transition zones and temperate regions. The ecological consequences of tropicalisation range from single-species impacts (e.g., altered behaviour) to whole ecosystem changes (e.g., phase shifts in intertidal and subtidal habitats). Our understanding of the evolutionary consequences of tropicalisation is limited, but emerging evidence suggests that tropicalisation could induce phenotypic change as well as shifts in the genotypic composition of both expanding and retracting species. Given the rapid rate of contemporary climate change, research on tropicalisation focusing on shifts in ecosystem functioning, biodiversity change, and socioeconomic impacts is urgently needed.

Introducing tropicalisation

Tropicalisation (see [Glossary](#)) is a recent, global phenomenon characterised by poleward range expansions of marine tropical (or subtropical) species and range retractions or a decreased abundance of temperate species in biogeographic transition regions and temperate areas ([Figure 1](#)) [1,2]. Such range shifts are caused by contemporary climate change and lead to altered species interactions that have knock-on effects on **ecosystem functioning** and stability [3,4]. The term 'tropicalisation' was initially coined to describe an increase in tropical species in the Mediterranean Sea [5]. Since then it has been widely used to denote the increase in the ratio of tropical to temperate species in resident marine temperate communities [2]. Tropicalisation is marine-specific ([6] for a rare terrestrial example) and encompasses poleward shifts of whole communities. Tropicalisation can alter community assemblages over decadal timescales [1,2] and lead to long-term ecological and evolutionary consequences (discussed in following sections). Similar phenomena include **borealisation** and **desertification** ([Box 1](#)) that, together with tropicalisation, contribute to the global redistribution of biota and rearrangement of ecological communities [7].

In general, marine range shifts occur at a much faster rate than those in terrestrial ecosystems [8,9], mainly because marine species often live closer to their **thermal thresholds** and experience fewer barriers to dispersal than terrestrial species [8,9]. In a region undergoing tropicalisation, range retractions occur at a slower rate than range expansions [10]. Tropicalisation is often first detected by the periodic arrival of new tropical species into biogeographic transition regions or temperate regions [11], as well as by reduced ecological performance (e.g., reduced growth rates, fecundity, or resilience to stressors) of temperate species [12]. As a result, range-retracting species often persist and co-occur with range-expanding species but may occur at lower abundances [13]. Consequently, tropicalisation quickly creates novel communities containing a mix of tropical, subtropical, and temperate species [1,6,14]. Ultimately, tropicalisation alters eco-evolutionary dynamics more rapidly than range shifts in biogeographic regions where species have had a longer history of interaction [4,15].

Highlights

Contemporary climate change is causing poleward range shifts of species globally.

In the ocean, tropical species are expanding into temperate regions as they warm, whereas temperate species' ranges are receding, leading to changes in community composition in a phenomenon known as tropicalisation.

Tropicalisation has a multitude of ecological and evolutionary consequences for species, communities, and whole ecosystems, and is altering global biodiversity patterns.

Tropicalisation research has primarily focused on ecological impacts, but our understanding of its evolutionary consequences remains limited.

A comprehensive strategy that integrates genetic and ecological research is essential to better understand the drivers and consequences of tropicalisation. Such a holistic approach is pivotal for predicting changes in ecosystem functioning and consequent biodiversity and socioeconomic impacts.

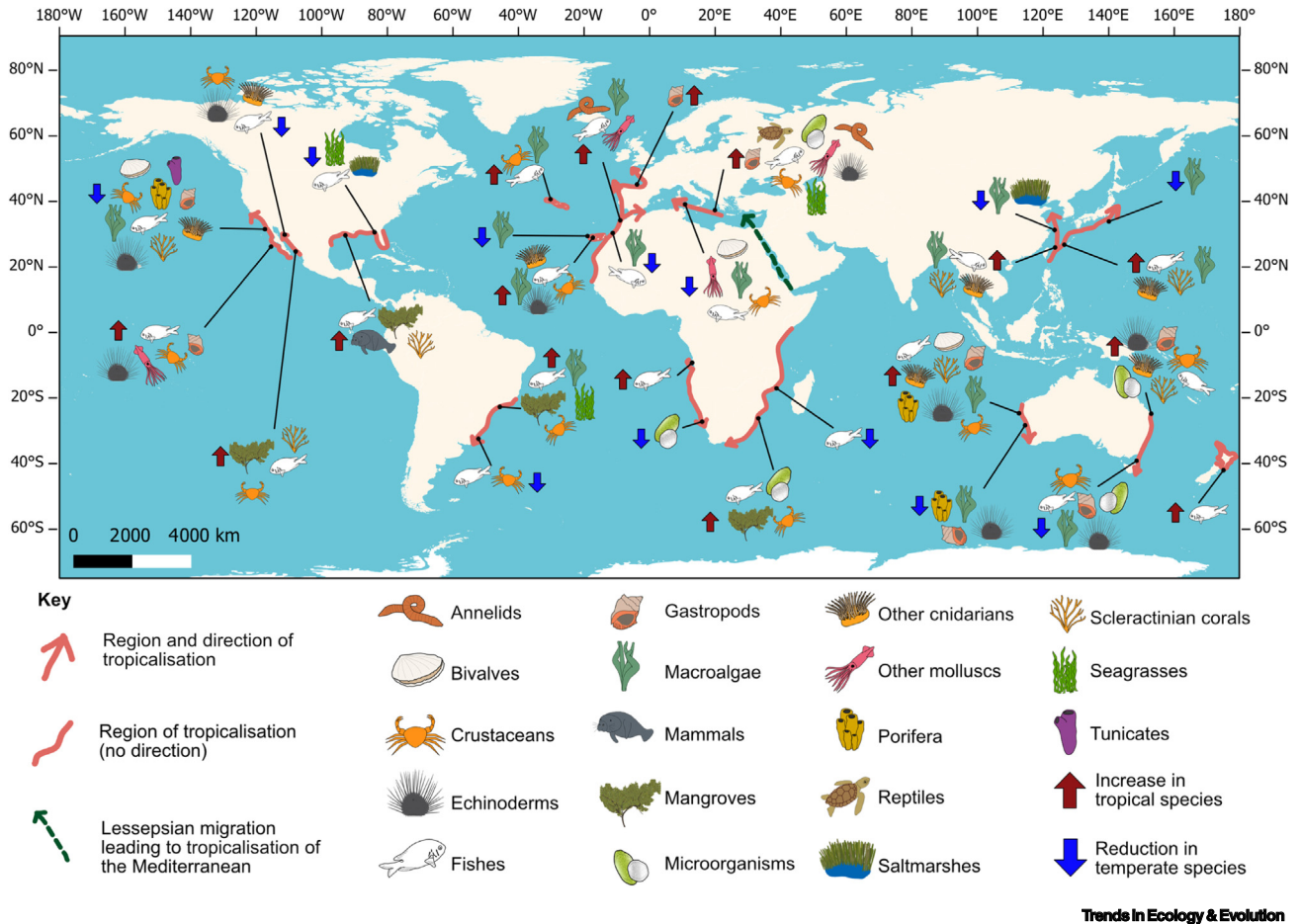
¹School of Ocean and Earth Science, National Oceanography Centre, University of Southampton, Southampton SO14 3ZH, UK

²Natural History Museum, Cromwell Road, London SW7 5BD, UK

³Centre for Advanced Studies of Blanes (CEAB), Consejo Superior de Investigaciones Científicas (CSIC), Accés a la Cala Sant Francesc 14, Blanes 17300, Spain

⁴Department of Zoology, Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Auckland Park, 2006 Johannesburg, South Africa

*Correspondence: k.m.zarzycny@soton.ac.uk (K.M. Zarzycny).



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Figure 1. The range of taxa and geographic areas where tropicalisation has been detected. An increase in tropical species (red 'up' arrow) indicates that studies show range expansions and an increase in the abundances of tropical species. Reduction in temperate species (blue 'down' arrow) indicates that studies have shown a reduction in temperate species abundance, local extinctions, and range retractions. Lessepsian migration (i.e., species movement through an artificial canal) is marked (green broken arrow) because it facilitates tropicalisation of the Mediterranean Sea via the Suez Canal and poses a unique challenge in detangling human-facilitated range expansions and climate-induced expansions of tropical species within this region (Box 3). Data for this figure were extracted from 138 peer-reviewed papers published between 2004 and 2023. Studies include those documenting tropicalisation specifically, as well as independent records of increases in tropical species and reduction in temperate species which collectively contribute to regional tropicalisation (Table S1 in the supplemental information online). Illustration created using QGIS 3.24.1 and Affinity Designer 1.10.5.

Documenting tropicalisation and gaining a holistic understanding of its consequences relies on a range of scientific methods (Box 2) and disciplines. By reviewing scientific works spanning community and functional ecology, biogeography, and molecular and evolutionary biology we identify global patterns of tropicalisation, explore tropicalisation drivers, and evaluate the role of ecosystem functioning in shaping tropicalisation patterns. We then describe the observed and predicted ecological and evolutionary consequences of tropicalisation and emphasise pressing knowledge gaps. Finally, we highlight the socioeconomic implications of tropicalisation and outline urgent research areas for future work.

Global patterns of tropicalisation

Tropicalisation occurs along most of the nearshore tropical–temperate transition regions of the globe (Figure 1 and see Table S1 in the supplemental information online). This phenomenon is particularly well documented in Australia and the Mediterranean Sea where studies span a

Box 1. Navigating the nomenclature of climate-induced shifts of whole communities

The global redistribution of biota as a result of climate-induced range shifts follows temperature gradients, typically latitudinally (but sometimes longitudinally) [117], altitudinally [118], or with depth [119]. Tropicalisation is a marine-specific example of a poleward shift of tropical communities that occurs because of climate-induced range shifts at mid to low latitudes where tropical and temperate biogeographic regions coincide. However, biota redistribution is a global phenomenon that spans all latitudes and has occurred repeatedly throughout Earth's history. We discuss similar nomenclature for two other climate-induced shifts of whole communities.

The expansion of temperate species into Arctic polar regions has been coined 'borealisation' [30,120]. Similar to tropicalisation, borealisation leads to the breakdown of biogeographic barriers [121]. In contrast to tropicalisation, borealisation applies to both marine [120] and terrestrial [122] ecosystems, although reference to marine ecosystems appears to be more common. The redistribution of temperate and polar communities is also apparent in the Southern Hemisphere [123], although it has been less studied than in the Northern Hemisphere. However, to our knowledge a term equivalent to 'borealisation' does not exist for the Southern Hemisphere.

'Desertification' predominantly applies to terrestrial areas, typically situated near the equator, but can also include non-equatorial regions surrounding barren habitats (e.g., South Africa) [124]. In contrast to tropicalisation and borealisation, desertification refers primarily to biodiversity loss associated with both contemporary climate change and human activities (in particular improper agricultural practices) which lead to degradation and reduced productivity of land (i.e., global expansion of deserts) [124]. Interestingly, the term 'desertification' has occasionally been used to describe mass losses of macroalgal forests that result in a drastic reduction of primary productivity and the formation of barren habitats [125]. The term 'marine desertification' may also be applicable to the loss of biota in tropical regions, which is particularly relevant to loss in equatorial regions where it is already thought to be too hot for some taxa [104].

wide range of taxa and spatial scales. There are also several tropicalisation studies from Japan [16], but the taxonomic coverage is limited to cnidarians, fishes, and macroalgae (Figure 1 and see Tables S1 and S2 the supplemental information online).

Several regions where one could expect tropicalisation (e.g., [1,16,17]) remain understudied. For example, the eastern coast of South America and southeastern Africa are expected to be tropicalisation hotspots [1] because they are heavily influenced by **warm-water boundary currents** (discussed in following sections), but only a handful of studies on tropicalisation have been conducted in these regions (see Tables S1–3 the supplemental information online). Conversely, regions without warm boundary currents such as southwestern Africa are experiencing tropicalisation, albeit research in this region is limited (Figure 1 and see Tables S1–3 the supplemental information online). This raises the question whether the scarcity of studies in these and other regions (e.g., the Pacific coast of South America) is indicative of an absence of tropicalisation or is a result of insufficient exploration. Further investigation into these understudied regions will be imperative to gain a general framework of the physical drivers and dynamics of tropicalisation.

Physical drivers of tropicalisation

Biogeographic transition zones that separate tropical/subtropical and temperate regions are often marked by large gradients in physical conditions that prevent dispersal, such as abrupt changes in sea-surface temperature or oceanographic currents [18]. Contemporary climate change is rapidly altering these gradients, facilitating the poleward movement of tropical species, and reinforcing the retraction of temperate species [1,7,19].

Warm-water boundary currents are currently heating faster than the global seawater average, and consequently their surrounding regions are expected to be tropicalisation hotspots [1]. For example, the Eastern Australian current has aided microbial tropicalisation [20] and the Kuroshio Current has contributed to the tropicalisation of southwestern Japan by facilitating the poleward dispersal of corals [16], tropical fishes [16,17], and tropical macroalgae [21]. Another example comes from anomalous poleward currents associated with El Niño that have facilitated the tropicalisation of copepod communities in Baja California [22]. Conversely, the increasing

Glossary

Borealisation: expansion of boreal regions driven by the expansion of northern temperate communities into Arctic areas, and the retraction of Arctic communities.

Desertification: expansion of deserts and barren bioregions as a result of climate warming, and anthropogenic activities (particularly poor farming practices) leading to degradation and reduced productivity of land.

DNA barcoding: the use of sequence data from a 'barcoding gene' (often a section of the mitochondrial cytochrome oxidase subunit I gene for animals) that is sufficiently variable to distinguish species using molecular species delimitation methods.

Ecosystem functioning: processes and interactions occurring within an ecosystem which enable it to maintain its structure, dynamics, and productivity. Ecosystem functioning includes trophic interactions and the provision of ecosystem services which maintain ecosystem stability.

Ecosystem phase shift: a significant and often irreversible change in the structure, function, and composition of an ecosystem.

Environmental DNA: DNA found in the environment that can be isolated and sequenced to detect living and recently dead species.

Founder effects: a phenomenon in population genetics where a loss of genetic diversity is observed in a population newly established from a subset of individuals of the original population.

Functional niche: the specific function and interactions of a species within its ecosystem, including its unique adaptations, behaviour, and resource utilisation strategies that allow it to fulfil its ecological niche.

Genotype: the genetic make-up of an organism which determines its traits and characteristics.

Marine heatwave: an extreme climatic event where the sea-surface temperature increases to abnormally high levels for a prolonged period of time.

Microevolution: an evolutionary change within a species.

Phenotype: an observable trait of an organism that is shaped by its genetic makeup (genotype) and the environment.

Box 2. Documenting tropicalisation

Documenting tropicalisation and its consequences relies on knowledge of spatiotemporal biodiversity patterns. The identification of range expansions and retractions often requires different data sources and documenting approaches (Figure 1). The range of methodologies that can be applied to the study of tropicalisation include field, laboratory, and *in silico* approaches. The choice of approach will depend on the specific study region and objectives.

Field-based sampling approaches typically require taxonomic expertise, extensive funding, multiple sampling events over extended periods of time, and access to reliable historical species distribution data (e.g., [46]).

Laboratory-based methods can remove the need for taxonomic expertise by using DNA sequence differences to identify species (**DNA barcoding**) but require specialist laboratory skills (e.g., [82]); in the absence of taxonomic expertise, access to accurate reference databases for species identifications is required. Although not yet used in the context of tropicalisation, **environmental DNA** metabarcoding could be an effective method for documenting whole-community changes [126].

In silico methods are particularly useful for documenting tropicalisation over large spatial scales (e.g., [112]) and modelling studies can predict future tropicalisation dynamics [17]. They are, however, constrained by the availability of data over both spatial and temporal scales. We recommend that tropicalisation studies combine complementary methodologies to effectively and reliably study tropicalisation.

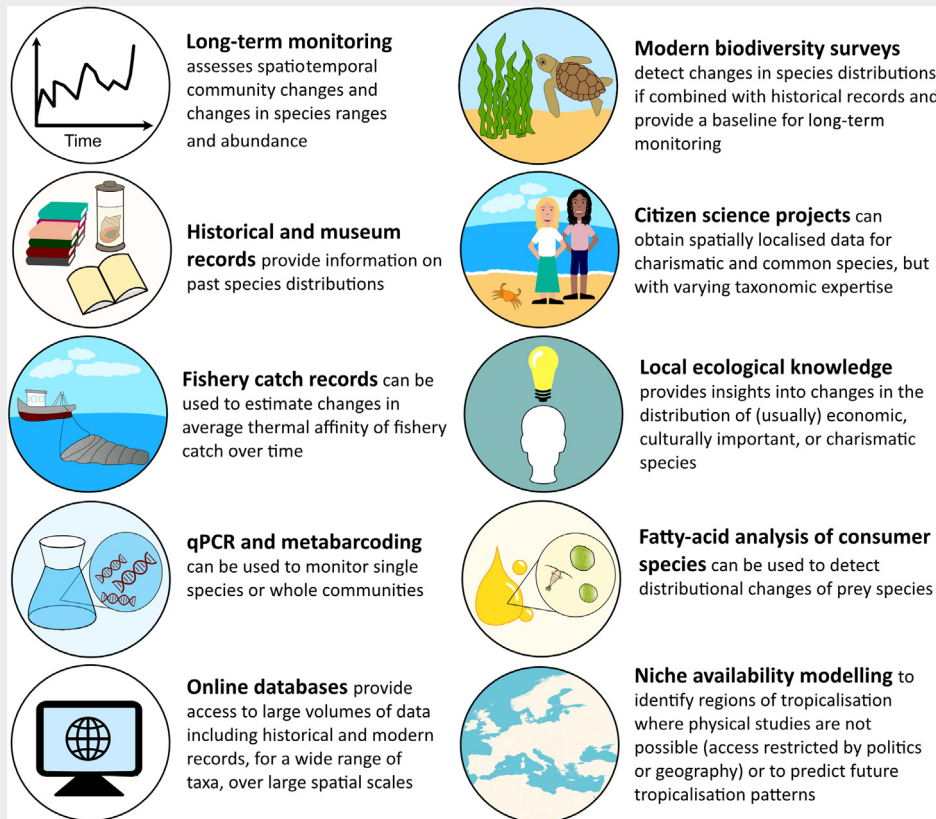
Phenotypic plasticity: the ability of an organism to change its observable characteristics (phenotype) in response to an external stimulus.

Thermal threshold: the temperature limit (either lower or upper) beyond which the physiological processes of an organism are inhibited.

Tropicalisation: a product of multiple climate-induced range shifts, including the expansion of tropical species towards the poles and concomitant loss of temperate species from warming areas, which alters and is reinforced by changes in species interactions and may lead to changes in marine biogeographic structure.

Warm-water boundary currents:

narrow, deep, and fast-flowing ocean currents on the western side of ocean basins which carry warm water polewards from the equator.



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Figure 1. Summary of different approaches and methods that can be used to study tropicalisation. Study examples and the metadata underpinning this graphical summary are available in Table S1 in the supplemental information online. Illustration created using Affinity Designer 1.10.5.

frequency and magnitude of **marine heatwaves** has resulted in direct loss of temperate species such as seaweeds [23] and seagrasses [24]. Establishment of tropical species in temperate regions is often restricted by winter temperatures [25–27]. For example, freezing temperatures currently limit poleward range expansion of the black mangrove, *Avicennia germinans*, in North America [28,29] which limits the survival of tropical vagrant reef fishes [26].

The role of species traits and niches in tropicalisation

Although tropicalisation is largely driven by changing environmental conditions [1,7,30], taxon-specific traits influence range shifts [31]. Thermal tolerance [29,32], acclimation ability [33], dispersal capabilities [34], behavioural changes [35], and niche specialisation [34,36] all influence tropicalisation dynamics. Moreover, **functional niche** availability [36] and habitat availability [11,37] in temperate regions influence the expansion dynamics of tropical species. Niche specialisation further influences tropicalisation dynamics. Generalists are more likely to find a suitable niche at the new range edge than specialist species [38,39], and consequently undergo range expansions faster than specialists [38,39]. Generalist species are also able to modify their behaviour to allow coexistence in tropicalised communities [36,40]. For example, in southeastern Australia range-expanding tropical fishes and resident temperate species that are capable of foraging on the same species modify their food choice to allow coexistence without increasing competition for food [40]. In that same region, range-expanding tropical fish and temperate residents have been observed to modify feeding and shoaling behaviours to allow resource partitioning and coexistence [35]. This suggests that generalist fish species may be able to persist in regions undergoing tropicalisation due to niche segregation. Whether this tropicalisation pattern exists in other taxa remains unknown.

Ecological consequences of tropicalisation

Herbivory and competition underpin ecosystem stability

The role of herbivory and competition in shaping tropicalisation patterns has been studied predominantly in fishes and foundation species such as macroalgae and coral [1,4]. Herbivory pressure and species richness of herbivorous fish communities are noticeably higher in tropical regions compared to temperate regions [41,42]. Tropicalisation therefore leads to an increase in the intensity and spatial extent of herbivory [16,43,44] and facilitates **ecosystem phase shifts** away from macroalgal communities [1,4,45]. However, emerging evidence suggests that elevated herbivory pressure is not the only factor maintaining algae-free states on tropicalised reefs, and the filling of previously unoccupied functional niches by expanding tropical herbivores also contributes [46]. Although temperate herbivores can exert significant herbivory pressure on adult macroalgae [44], tropical herbivores often feed upon algal turf containing macroalgal recruits, thus preventing recruitment and recovery [47,48].

Temperate seagrass meadows and associated communities are also rapidly changing with ongoing tropicalisation [27]. Although temperate seagrasses are declining in some regions undergoing tropicalisation (e.g., *Posidonia oceanica* in the Mediterranean Sea [49]), tropical species are proliferating in others (e.g., *Halophila decipiens* in southeast Brazil [50]). Globally, seagrasses are predicted to undergo significant range reductions, leading to higher levels of endemism or reduced species diversity in some regions [51]. Communities hosted by these foundation species are also undergoing changes. For example, seagrass meadows of the northern Gulf of Mexico have experienced a significant increase in tropical fishes [52], but little is known about how such changes will alter interspecific interactions in these ecosystems. In the Mediterranean Sea, the herbivorous fishes *Sarpa salpa*, *Siganus rivulatus*, and *Siganus luridus* shift their feeding preferences from seagrasses to seaweeds with increasing levels of tropicalisation [53]. This suggests that in some regions tropicalisation may release seagrass meadows from herbivory pressure while placing temperate macroalgae under further stress [53]. However, to better understand the impacts of

herbivory on seagrass meadows in the context of tropicalisation, more research is needed on a wider range of herbivorous taxa and across larger spatial scales. For example, in Western Australia, dugongs (*Dugong dugong*) and green turtles (*Chelonia mydas*) consume significant volumes of seagrasses [27]. With ongoing ocean warming, dugongs are expected to undergo substantial range expansions and green sea turtle abundances are expected to increase, leading to elevated herbivory pressure on Australia's seagrasses [27]. Although less studied in the context of tropicalisation, sea urchins can also exert significant top-down control on both seagrass [27,54] and algal communities [42,55,56], and ultimately facilitate tropicalisation.

Changes to trophic interactions as a consequence of tropicalisation can have cascading effects on ecosystems. For instance, increased herbivory pressure leading to loss of macroalgae allows coral settlement by reducing competition for space, leading to algae–coral phase shifts [16,57]. Where corals do not settle, turf habitats can persist [48,58] and maintain greater diversity of fishes than some non-tropicalised macroalgal systems [58]. Such increase in species diversity is likely to lead to new competitive interactions. For example, resource competition can lead to resident temperate and range-expanding tropical territorial fishes occupying suboptimal microhabitats in transition regions [26]. Furthermore, changes in interspecific competition caused by tropicalisation can also lead to reduced fitness of resident temperate species (e.g., reductions in body size [59]), ultimately affecting their potential for population growth.

Tropicalisation is also causing phase shifts away from salt marshes to more mangrove-dominated ecosystems [29,60]. Mangroves outcompete salt marshes by suppressing the biomass of salt marsh plants [61]. The replacement of salt marshes by mangroves has cascading ecological consequences. First, because the two ecosystems have structural and functional differences, phase shifts from salt marsh to mangrove habitats will inevitably lead to changes in community assemblages and impact on species interactions [62–64]. For instance, mangrove plants are lower-quality food sources than salt marshes, and this negatively impacts on energy storage by some herbivorous invertebrates [63]. Furthermore, given that salt marshes and mangroves are a transition region between the terrestrial and marine ecosystems, phase shifts also impact on terrestrial fauna [64]. For example, the replacement of salt marsh plants by the black mangrove *A. germinans* in the Gulf of Mexico is associated with reduced insect diversity and biomass [64]. In addition, salt marsh to mangrove shifts alter the sediment properties and local microclimate, which can in turn influence the seasonal dynamics of nearby seagrass systems [60,65]. Nevertheless, both salt marshes and mangroves provide crucial ecosystem services (see Socioeconomic consequences of tropicalisation section) [60,62,63]. However, whether the net effect of mangrove expansion is seen as positive or negative will depend on local factors and perceptions [60,62].

Predator–prey interactions

Altered predator–prey interactions are an inevitable consequence of tropicalisation. We know from the extensive literature on predator–prey interactions in marine ecosystems that single predator species can have strong top-down impacts on the structure and diversity of local marine communities (i.e., 'keystone' predators [66]). However, whether top-down impacts arising from range-expanding tropical predators into temperate regions will have similarly strong ecological consequences is unknown. Nevertheless, predation pressure and consumption rates often increase towards lower- and mid-latitude regions [67,68], and recent studies of marine fish and invertebrates support this hypothesis [69–71]. These biogeographic shifts in predation are thought to be due to a combination of turnover in predator species composition and their functional traits, which can include body size, prey selectivity, dispersal capabilities, and rates and/or modes of feeding [71–73]. For example, some eastern Pacific tropical gastropod predators are expanding into temperate regions, and they tend to be large-bodied generalists with higher dispersal potential than

their cool-water counterparts [72]. Thus, we can not only expect tropical predators to expand into temperate regions but they will also likely have different functional traits, modes of feeding, and consumption rates than resident, temperate predators. Although understudied to date, we expect that these differences could result in enhanced and novel predation pressure on temperate prey, which may lead to top-down impacts on local communities undergoing tropicalisation.

Invasion science can also provide invaluable insights into the potential ecological impacts of range-shifting tropical predators [74]. For example, invading predators can increase interspecific competition among resident prey species through elevated predator avoidance [75]. Native prey may also be naïve to the cues from newly introduced predators [76], leading to reduced antipredator behaviours [77,78]. As such, invasive predators often have greater detrimental impacts on lower trophic-level species than native predators [78].

Evolutionary consequences of tropicalisation

Shifts in genetic composition

Recently range-expanding species are often characterised by **founder effects** and low genetic diversity in leading-edge populations [79–82]. However, growing evidence suggests that tropical range-expanding species do not necessarily experience reduced genetic diversity at the new range margins [82,83]. In turn, temperate species may have had a longer history of occupying temperate–tropical transition regions than the recently expanding tropical species, allowing more mutations to accumulate in temperate species. Consequently, in a region undergoing tropicalisation, resident temperate species are more likely to have experienced past vicariant events and exhibit population structure than expanding tropical species. In this context, range retractions of temperate species may lead to genetic erosion by loss of genetically divergent populations [82,84]. In addition, marine heatwaves can create selection pressures that cause the loss of **genotypes** unable to withstand the thermal stress [3,85]. This loss of genetic diversity in temperate species can have **microevolutionary consequences** and may be subsequently followed by the proliferation of more thermally resistant individuals [3,85]. Although some species may therefore not experience a range retraction, they may display a loss of genetic diversity, leading to reduced adaptive potential to other climatic or anthropogenic perturbations [86].

Understanding how genetic diversity may change in response to tropicalisation is crucial for effective biodiversity management. High intraspecific genetic diversity is associated with enhanced ecosystem functioning [87] and increased adaptive potential of species [88]. In fact, including intraspecific genetic diversity in predictions of climate change vulnerability is likely to lead to more accurate species distribution modelling [89]. Incorporating genetic diversity into conservation planning for tropicalisation is therefore becoming increasingly important [90,91].

Hybridisation

Hybridisation arising from tropicalisation has been observed in congeneric coastal fishes where the tropical, range-expanding *Argyrosomus coronus* has crossed with the subtropical *A. inodorus* [92]. Moreover, the crossing between subspecies of acorn barnacles *Tetraclita japonica japonica* and *T. japonica formosana* may be a result of a recent poleward range expansion of *T. japonica formosana* [93]. Although a growing number of studies show evidence for a causal role of hybridisation in successful colonisations, and more generally in driving population range expansion [94], the fitness consequences of hybridisation arising from tropicalisation remain unknown. We know that hybridisation with resident congeners may enhance the establishment success of invasive species by improving offspring adaptation through genetic rescue, or by enhancing the probability of finding a mate in the new range where population densities

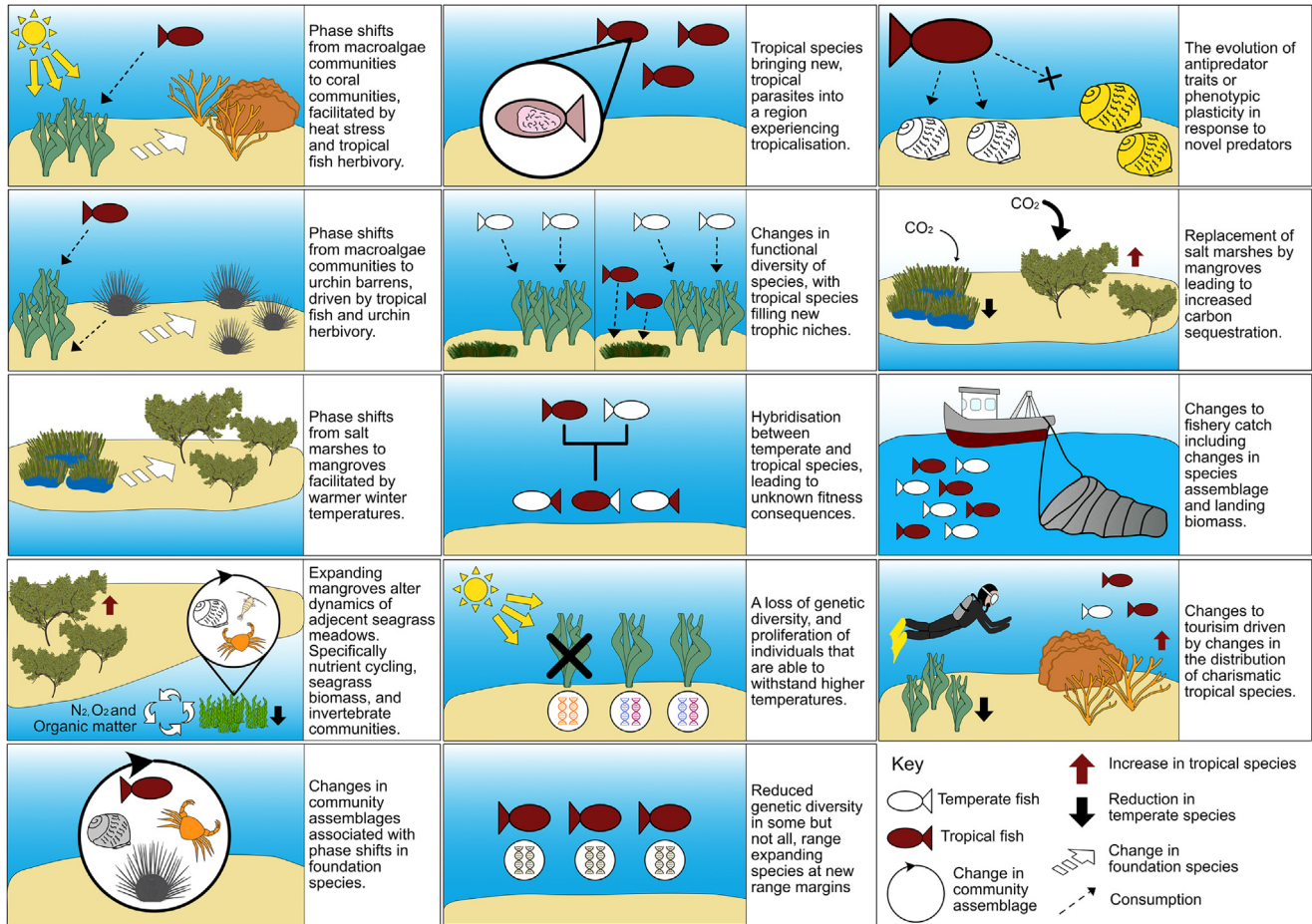


Figure 2. The ecological, evolutionary, and socioeconomic consequences of tropicalisation. The ecosystems and examples illustrated here are hypothetical, but examples of each have been extracted from 102 peer-reviewed studies published between 2015 and 2023 (Table S2 in the supplemental information online). Illustration created using Affinity Designer 1.10.5.

are low [95]. Taken together, the existing evidence (albeit limited) suggests that hybridisation may facilitate tropicalisation [96], but this hypothesis requires further investigation.

Tropicalisation as a driver of phenotypic change

Because ecology and evolution interact reciprocally [97], tropicalisation can be expected to cause **phenotypic** change arising from altered species interactions (Figure 2). Such changes are likely to be species- and community-specific. For example, the more similar the phenotypes of range-expanding tropical species are to the resident temperate species within the same trophic level, the greater the chance that increased competition will have fitness consequences [98] and/or cause character displacement [99,100]. Moreover, increased predation pressure (from range-expanding tropical predators) could enhance the effects of competition on divergent selection, indirectly leading to character displacement in prey species [101].

The influx of tropical predators is likely to exert selection pressure on resident prey species, and this may drive the evolution of antipredator defences [102] or induce a **phenotypically plastic** response. For example, the temperate barnacle species (*Tetraclita rubescens*) only exhibits

Box 3. Human-mediated range expansions (HMREs) and tropicalisation

HMREs can be defined as an increase in range size of non-indigenous species (NIS) as a result of human activities such as shipping, agriculture, and aquaculture. The main difference between HMRE and tropicalisation is that the spread of NIS requires intentional or unintentional artificial transport of species [74]. The spread of NIS can occur across all regions of the globe, whereas tropicalisation specifically occurs around adjacent tropical–temperate regions. Species interactions as a result of HMRE are often truly novel, with no shared evolutionary history between species [19,74]. By contrast, because climate-induced range shifts have also occurred in the deeper past (e.g., over glacial/interglacial cycles) there may be shared evolutionary histories between species in a region undergoing tropicalisation. Therefore, temperate species may be preadapted to range-expanding tropical species (e.g., interactions between temperate prey and tropical predators [72]), which will not necessarily be the case in novel species interactions arising from HMRE. Despite these clear differences between HMRE and tropicalisation, there are situations where disentangling them becomes challenging. This is the case of the massive influx of previously allopatric tropical species into the Mediterranean Sea as a result of the opening of the Suez Canal, known as Lessepsian migration (see Figure 1 in main text) [5]. Tropical species are expanding from the Red Sea into the Mediterranean Sea, but this is only possible due to the artificial removal of a natural land barrier. The matter is further complicated by the heavy maritime traffic passing through the Suez Canal, which leads to HMRE facilitated by ongoing sea warming [127]. The influx of tropical species into the region (as a result of both natural and artificial dispersal) has resulted in tropicalisation of the Mediterranean Sea by NIS [1,5].

predator-induced defences ('bent morphs') in populations that overlap with range-expanding warm-water predators in a region undergoing tropicalisation [72]. Whether this is a phenotypically plastic or microevolutionary response is unknown, but it provides evidence of partial resilience of this temperate species to the indirect impacts of tropicalisation. It also suggests that some temperate species may not be naive towards range-expanding predators, suggesting a shared history of interaction in the deeper past (e.g., over glacial–interglacial cycles [103]), bringing up an important difference when drawing parallels with tropicalisation and invasion science (Box 3).

Macro-eco-evolutionary consequences of tropicalisation

The processes underlying tropicalisation are expected to alter latitudinal patterns of biodiversity [104,105] that have been established for millions of years [106–108]. In general, warm global conditions (greenhouse worlds) have been associated with temperate peaks in species richness whereas cooler climatic regimes (icehouse worlds) were associated with tropical peaks in richness [106]. In fact, greenhouse worlds may even be associated with dips or flat species richness towards the equator [106], presumably due to harsh thermal conditions at low latitudes. These patterns from the deeper past may give clues to how tropicalisation will ultimately impact global biodiversity. For example, we know that range expansions are occurring faster than retractions in the context of tropicalisation [10], and these can lead to an increase in local and regional species richness at tropical–temperate transition zones as a result of increased range overlap [7,58,105]. Meanwhile, higher water temperatures towards the equator may exceed the physiological limits of some tropical species, causing local extinctions and reductions in abundance at low latitudes [7]. If species richness begins to dip towards the equator [7], tropicalisation may lead to a bimodal pattern of latitudinal diversity. Indeed, species distribution modelling based on climate-warming projections predict this pattern [105]. More recently, researchers used a global dataset of pelagic and benthic species over three time periods to provide empirical support, and the most recent period (1995–2005) shows a clear dip at the equator and peaks in richness towards tropical–temperate transition regions [104]. This is reflective of trends associated with greenhouse worlds in the deeper past [106]. Therefore, the past appears to be a good predictor of how tropicalisation will likely impact on global species richness patterns in future scenarios.

The macroevolutionary literature provides insights into how modern tropicalisation may influence diversity dynamics. In recent years macroevolutionary dynamic models have been used to explain the modern latitudinal diversity gradient [109]. One prominent hypothesis, the 'out of the tropics' model, recognises the importance of 'bridge species' [110] which are species of tropical origin that have expanded their thermal ranges to be able to disperse across tropical–temperate

boundaries. Thus, modern tropical species that expand into temperate regions may be thought of as modern analogues of bridge species because they have the thermal flexibility to cope with lower temperatures during winter and the higher seasonality of temperate regions.

Socioeconomic consequences of tropicalisation

Tropicalisation is already having substantial socioeconomic consequences (Figure 2). Tropicalisation of fishery catches is apparent globally [111]; regions undergoing tropicalisation are experiencing increases in overall fishery landings [25,112] associated with increased fish biomass and enhanced nursery habitat [4]. However, despite the increased landings, the same regions may also lose commercially important temperate species [113] and experience an increase in non-target species catches [114]. Range-expanding tropical species can also carry parasites into the new ecosystems [115], but whether these can spread to other species (including commercially important taxa) remains unknown.

Not all socioeconomic consequences of tropicalisation are negative. For example, mangrove ecosystems sequester more carbon than the temperate salt marshes they are replacing [116]. Consequently, tropicalisation involving the growth and spread of mangrove trees may increase overall carbon storage and sequestration in the region [116]. In addition, the expansion of charismatic tropical foundation species, such as coral communities and their associated fauna, is expected to have a positive impact on the local economy through an increase in dive-based tourism [4,17]. However, this pattern is unlikely to happen for regions undergoing kelp loss without the proliferation of charismatic tropical taxa [4].

Concluding remarks

Tropicalisation is a global phenomenon that has significant ecological, evolutionary, and socioeconomic consequences (Figure 2) [4,86]. Most studies to date have concentrated on the ecological consequences of tropicalisation, and range from altered species interactions (namely herbivory and competition) and behaviour to whole ecosystem phase shifts. The evolutionary consequences of tropicalisation remain understudied but include phenotypic and genotypic changes (including hybridisation), as well as broad-scale changes in global diversity dynamics.

Despite the global nature of tropicalisation, some regions of the world have been poorly studied. Investigation into these regions (e.g., tropical–temperate regions of Africa, South America, and Asia) is crucial for gaining a general framework of the physical drivers and the complex dynamics of tropicalisation at a global scale. A more holistic understanding of tropicalisation, its drivers, and its consequences is urgently needed given the emerging socioeconomic consequences of tropicalisation and rapid rate of climate change. By exploring these research frontiers (see Outstanding questions), we can better equip ourselves to mitigate the negative impacts of tropicalisation and preserve ecosystems before irrevocable change occurs.

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Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

Supplemental information associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tree.2023.10.006>

Outstanding questions

How will tropicalisation alter global patterns of biodiversity? As the edges of tropical bioregions shift polewards, potentially causing mid-latitude regions to increase in species richness, will low-latitude equatorial regions experience loss in species richness? Are patterns from the deeper past a good model for how tropicalisation will affect global diversity, now and in the future?

Will tropicalisation induce microevolutionary changes and/or phenotypically plastic responses as a result of altered species interactions (e.g., predator–prey dynamics)?

Tropicalisation is a global phenomenon, but studies from some regions where we could expect tropicalisation (e.g., South America) are limited. Are some regions of the world buffered against tropicalisation, or does this reflect a lack of research in some geographic areas?

Do tropical and temperate taxa modify their behaviour to allow coexistence with tropical range-shifting species in a region undergoing tropicalisation? Although research suggests that fish behaviour can change, studies on other taxa are lacking.

What is the role of functional diversity in shaping the patterns and consequences of tropicalisation? The role of vertebrate herbivores has been studied extensively, but how is tropicalisation reshaping predator–prey dynamics?

What are the long-term impacts of the genetic erosion on temperate species caused by tropicalisation? How will genetic erosion impact future adaptive potential?

Could regions of cold-water upwelling and other cool-water areas within transition zones be targeted as Marine Protected Areas to act as refugia for temperate species?

Can effective ecosystem management allow us to harness the positive socioeconomic impacts of tropicalisation while effectively mitigating its negative impacts?

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