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Review

Towards Integrating Evolution, Metabolism, and Climate Change Studies of Marine Ecosystems

Federico Baltar,^{1,*} Barbara Bayer,¹ Nina Bednarsek,² Stacy Deppeler,³ Ruben Escibano,⁴ Carolina E. Gonzalez,⁴ Roberta L. Hansman,⁵ Rajani Kanta Mishra,⁶ Mary Ann Moran,⁷ Daniel J. Repeta,⁸ Carol Robinson,⁹ Eva Sintés,^{1,10} Christian Tamburini,¹¹ Luis E. Valentin,⁸ and Gerhard J. Herndl^{1,12,*}

Global environmental changes are challenging the structure and functioning of ecosystems. However, a mechanistic understanding of how global environmental changes will affect ecosystems is still lacking. The complex and interacting biological and physical processes spanning vast temporal and spatial scales that constitute an ecosystem make this a formidable problem. A unifying framework based on ecological theory, that considers fundamental and realized niches, combined with metabolic, evolutionary, and climate change studies, is needed to provide the mechanistic understanding required to evaluate and forecast the future of marine communities, ecosystems, and their services.

The Future of Marine Ecosystems

The ocean absorbs most (~93%) of the heat generated by greenhouse gas emissions, resulting in a predicted increase in the sea surface temperature of 1–10°C over the next 100 years [1]. The ocean also absorbs CO₂ released to the atmosphere from anthropogenic sources (currently ~1/3 of this CO₂), resulting in a profound change in the carbonate chemistry and predicted increased acidity of seawater [1] to 100–150% above pre-industrial era values [1]. In addition to ocean warming and acidification, anthropogenic stressors are decreasing the concentration of dissolved oxygen and consequently expanding oxygen minimum zones [2] as well as potentially modifying large-scale oceanic circulation patterns [3]. These environmental changes might also impact fundamental community-structuring processes (i.e., selection, dispersal, drift, and speciation) [4], changing the relative importance of ecological processes for structuring of communities. Collectively, these changes will alter the structure and functioning of marine organisms and ecosystems and, consequently, the biogeochemical cycles of the ocean [5–8].

Generally recognized predictions regarding climate-induced changes on the composition and distribution of the marine biota include shifts in the species distribution from lower to higher latitudes, shifts from near-surface to deeper waters, shifts in annual phenology, declines in calcifying species, and increases in the abundance of warm-water species [1,9]. However, most models of the response of biological communities to climate change assume a fixed, genetically determined environmental niche for each species, and the migration of intact (i.e., nonadapting or nonevolving) populations, so that their distribution on our future planet is basically governed by the environmental conditions [10–12]. Yet, local populations may evolve, acclimate, and adapt to environmental changes. In fact, local adaptation is a recognized phenomenon in ecological studies on terrestrial systems [13,14]. In contrast to terrestrial systems where most (≈96%) of the living biomass are plants, most of the biomass of the ocean (≈70%) is microbial [15]. Since microbes have short generation times and large population sizes, it is possible that these engines of the Earth's biogeochemical cycles might be particularly capable of adapting to global environmental changes [16–18]. Indeed, recent laboratory experiments and field studies present evidence of evolution and local adaptation of marine microbial strains and populations in response to environmental factors [11,19–23]. Thus, we need to consider how externally imposed physical and chemical drivers interact with evolving metabolisms, community structure, and interactions among populations to predict the future of marine ecosystems and their associated services.

However, understanding and predicting the future of marine ecosystems is a challenging issue, requiring a multidisciplinary approach combining different fields across biological, chemical, and physical sciences that integrate vast and different temporal and spatial scales. We advocate the

Highlights

Marine ecosystems are changing and the services they provide are threatened by global environmental changes.

Environmental changes can provoke evolution of species, affecting both the realized and fundamental niches of species.

Environmental change can drive evolution, but evolution can also affect environmental conditions.

There is a need for a unifying framework that combines studies of evolution, metabolism, and climate change.

That framework should be based on ecological theory, on the study of the realized and fundamental niche dynamics, their spatial and temporal dynamics, and their potential response to environmental changes.

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need to combine the study of evolution, together with metabolism and climate change, since a more realistic representation of the future of marine ecosystems and biogeochemical cycles can only be obtained at the intersection of these three fields. To study these interactions, a framework based on theoretical ecology that considers fundamental and realized niches, including their spatial dynamics and potential alterations in response to environmental changes, appears to be a promising approach. In the following sections we will first consider the intersection between evolution and climate change, then how microbial metabolism might interact with climate change, before commenting on the interaction of all three processes.

Evolution of Ecological Niches and Responses to Environmental Changes

The ecological niche concept considers how abiotic and biotic factors constrain the distribution of species and, consequently, is more informative than just focusing on geographic distribution patterns of populations [24]. The fundamental niche is the multidimensional environmental space under which a species can potentially persist in the absence of biotic interactions and dispersal barriers [25]. In contrast to the fundamental niche, the realized niche is the environmental space that a species occupies resulting from the tolerances of a species to environmental conditions, inter- and intraspecific biotic interactions, and dispersal barriers. Thus, the realized niche varies in space and time in response to biotic and abiotic factors. The fundamental niche is genetically determined but can change via evolution, horizontal gene transfer, or the acquisition of symbionts [24,26,27]. Theoretical ecologists (mostly terrestrial) have long studied the potential response of ecological niches to changing biotic and abiotic factors. Populations can respond to rapidly changing environmental conditions either by migrating to stay within the boundary conditions determining the ecological niches, or persisting locally in novel or changing environments via both phenotypic plasticity and adaptive evolution [29].

Although range shifts via migration are commonly assumed as the main response of species following climate change [30], it is becoming evident that migration alone frequently fails to explain the response of species to environmental change [31]. Early models have aimed at quantitatively predicting the adaptation capability of species in response to changing environmental conditions. The Lynch and Lande model [32] suggests that populations are able to persist by keeping a steady rate of adaptation. This rate of adaptation, however, has to keep up with the rate of change in optimum ecological conditions. The rate of adaptation is determined by the genetic variation, individual fecundity, effective population size, environmental stochasticity, and strength of selection. If that threshold is surpassed, the rate of adaptation cannot compensate for the rate of environmental change, causing a decrease in fitness, adaptational lag, and, potentially, extirpation [32]. In the Bürger and Lynch model, a stronger fitness loss (or greater extinction risk) in response to a changing trait has been related to small effective population sizes [33]. Bürger and Lynch concluded that a small population size is more prone to fitness losses due to the combined effects of genetic drift and demographic stochasticity. These models are tremendously informative, yet they are based only on a single trait. In reality, local adaptation and fitness are affected by multiple traits and the interactions among these traits might ultimately affect the rates of evolution [34]. Although the above-mentioned models have intrinsic limitations, overall they suggest that the species tolerating environmental changes better (i.e., able to adapt) will be those with large population sizes, large fecundity, large genetic variance, and short generation times [32,33]. All of those are common features of most pelagic microbes [35] although not necessarily of other marine microbial communities, like those in subsurface sediments with their extremely long generation times [36].

Contemporary evolutionary adaptation is recognized as a significant process at ecologically relevant time scales, with many examples of species, from microbes to fish, showing phenotypic evolution over just a few generations [13,37,38]. Early stages of contemporary speciation have been observed among populations within species subjected to strong selection [39–41]. This suggests that evolution takes place rapidly enough to impact ecological interactions and thereby ecosystem structure and function [42,43]. According to theoretical predictions, the effects of evolution on ecology are most relevant when there is substantial variation in the traits under selection and when these traits strongly influence ecological interactions [44]. The growth rate of a population can occasionally be more

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influenced by evolutionary changes than by changes in environmental factors [44], highlighting the potentially strong impact of evolutionary change on ecosystems. Thus, ecological processes affect adaptive evolution and evolutionary changes affect demographic and community processes. These observations stress the need to consider the mutual back-and-forth relationship between ecology and evolution to better understand and predict the present and future of ecosystems and their processes, particularly in the light of environmental and climate change.

Metabolism and Responses to Environmental Changes

An organism's metabolism is defined as the sum of all enzyme-driven chemical reactions within a cell [45]. The metabolism of marine organisms and communities is tightly linked with the ecosystem services they provide. Despite extensive evidence suggesting impacts on the metabolism and physiology of marine species by factors such as changing oxygen concentrations, stratification, and ocean acidification, most studies on the impact of climate change are based on the effect of changing temperature [9]. The main reason for the focus on temperature as a key variable in metabolism is the acceleration of all chemical reactions, including cellular biochemical reactions, with increasing temperature [46]. The universal temperature dependency (UTD) ecological theory created a common framework for physiology and ecology based on theoretical biochemistry and biophysics [47]. UTD theory asserts that the metabolism of organisms is a function of the body size and temperature and that this dependence on temperature is a universal thermodynamically driven phenomenon. Building upon UTD, the metabolic theory of ecology (MTE) was developed based on the dependence of respiratory processes on temperature and body size [48]. This theory placed metabolism as a cornerstone component within global elemental cycling, with the power to shape communities, ecosystems, and their services. MTE provides a mechanistic, quantitative, synthetic framework to determine the effect of individual organisms on the pools and flow of energy and matter in populations, communities, and ecosystems [48].

The MTE predicts that photosynthesis and respiration, two of the most important metabolic processes, respond very differently to temperature [48–50], due to their dissimilar activation energies (i.e., activation energy of respiration of ~ 0.6 – 0.7 eV set by the ATP synthesis and activation energy of photosynthesis of ~ 0.32 eV, determined by Rubisco carboxylation) [49,50]. The MTE posits that heterotrophic metabolism increases more than gross primary production in the ocean in response to warming. This MTE prediction on the differential response of respiration and photosynthesis to temperature is conserved among heterotrophic and autotrophic taxa and scales to community levels [48,49,51]. Based on that, the MTE predicts that ocean warming will impact the efficiency of the ocean to act as a carbon sink by changing the balance between autotrophic and heterotrophic metabolism, which might have a critical feedback on marine community and ecosystem structure and global climate [52]. Growth in heterotrophic organisms also seems to respond differently to temperature when compared with metabolic rates in fish, which could affect both the efficiency of energy transfer as well as the shape of trophic pyramids [53]. This seems to be also manifested in how fisheries' catches respond to changes in temperature [54].

In laboratory experiments, however, phytoplankton cultures have been shown to increase their carbon use efficiency within ≈ 100 generations in response to elevated temperatures [55], which might dampen the decrease in C sequestration predicted by the MTE in response to warming [49,50]. Also, a rather stable biomass-normalized gross primary production over a 20°C temperature gradient was recently reported from a geothermally heated stream, providing *in situ* evidence of a strong temperature-driven selection on photosynthetic traits in a natural community [56]. This implies that temperature-driven selection on metabolic traits within and among taxa controls how metabolic rates scale from populations to ecosystems, questioning ecosystem level predictions based on the effect of temperature on single enzyme kinetics. These responses to temperature in carbon use efficiency and photosynthetic traits also serve as examples of how adaptation in marine microbes (in this case thermal adaptation) might impact biogeochemical cycles and ecosystem structure and function in response to climate change. Although experiments indicate the potential for evolutionary change to mitigate effects of warming on carbon-use efficiency, we still lack evidence on whether this

evolutionary change also happens within a food web where multiple intra- and interspecific interactions (not yet accounted for experimentally) are in play.

Combining Evolution, Metabolism, and Climate Change to Predict the Future of Marine Ecosystems

The application of ecological theory to the response of populations and ecosystems to environmental changes can shed light on the response of marine ecosystems to global climate change. Below, we describe some specific outcomes that can be derived from the application of theoretical ecology to marine ecosystems (Figures 1–5).

Looking Deep: Niches Will Change Not Only Latitudinally but Also with Depth

Increased temperature together with higher respiration rates (as predicted by the MTE) will decrease dissolved oxygen levels, and thereby expand oxygen minimum zones, towards deeper layers, with consequences on biogeochemical cycles due to the disproportional importance of these zones in the C, N, and S cycles [57]. This might lead to a decrease in the diversity and population size of zooplankton, provoking a niche reduction by forcing mesopelagic zooplankton to move up in the water column (Figure 1) [58,59], decreasing their relative contribution to organic matter cycling in the deep ocean [60]. However, it is noteworthy that not only decreased activities and niches are to be expected, since the decrease in oxygen concentration will cause an expansion of activity/niches of suboxic or anoxic metabolisms and associated ecosystem services such as sulfide oxidation, sulfur-based organic carbon respiration, metal-based redox reactions, methane production, and consumption, etc. This example highlights the importance of studying the niche breadth of relevant marine species not only latitudinally (which is usually the case), but also over depth, since many important ecological and biogeochemical processes take place in the dark ocean [61].

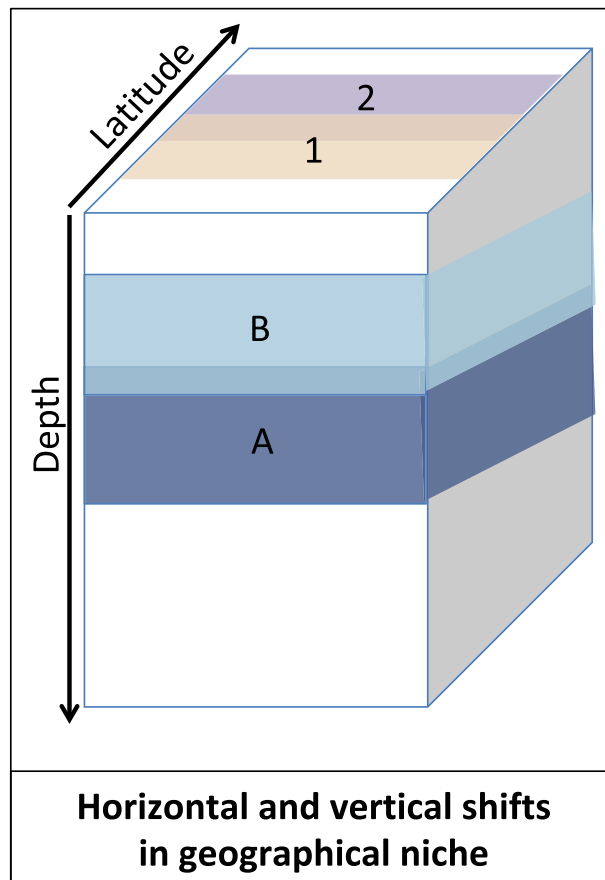
Climate-Related and Extreme Weather-Related Events

Climate models predict an increase in the occurrence of extreme weather events and increased fluctuations in weather conditions [1]. According to theoretical ecology models, an increase in the amplitude of environmental fluctuations might reduce the mean fitness of populations because of the increase in the average deviation from the optimum or realized niche (Figure 2). There is substantial evidence indicating that thresholds in individual species and ecosystem responses to weather extremes are linked to altered ecosystem structure and function [62]. For instance, a marine 'heat-wave' event caused a strong decline in habitat-forming macroalgae and a tropicalization of fish communities in Australian waters [63]. However, we need to distinguish between weather- and climate-related events. The example mentioned above is related to a sudden shift in the weather conditions (e.g., heat-wave), which triggered a sudden change in key organisms (e.g., kelp), referred to as 'ecosystem engineers', and subsequently, a new succession process. This gave rise to dominating species different from the species composition prior to this particular event (e.g., turf-forming algae dominating), drastically and rapidly changing the ecosystem structure.

Climate-related events, however, take place on longer time scales than weather events and are generally associated with poleward-flowing currents creating warming hotspots in the ocean. Poleward-flowing current systems facilitate the expansion of tropical corals and herbivorous fishes into existing temperate macroalgae communities, which are contracting faster than they are expanding, causing a community shift from macroalgae to corals [64]. At the same time, coral reefs are drastically declining in areas previously harboring extensive coral biomass and diversity [65]. While considerable attention is paid to climate-related tropicalization phenomena, theoretical ecology predicts that extreme weather events might play a key role in the evolutionary response of marine ecosystems to global environmental changes.

Importance of Peripheral Populations in the Ecology and Evolution of Marine Ecosystems

Populations living at the periphery of their realized niches are often under greater environmental stress or interspecific competition than those in the center of their realized niches [66]. Generally,



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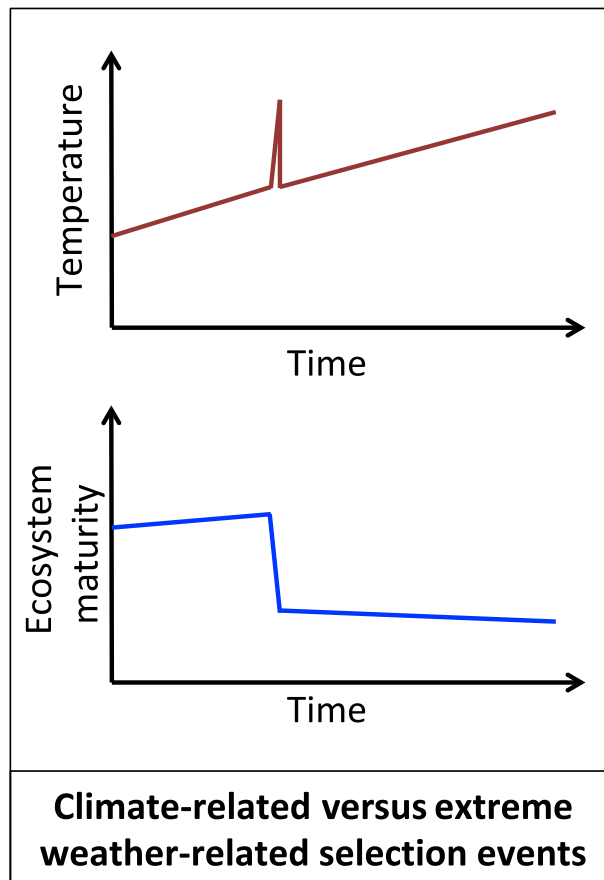
Figure 1. Example 1 of Specific Relevant Points/Outcomes That Can Be Derived from the Application of Theoretical Ecology to Marine Ecosystems: Horizontal and Vertical Shifts in Geographical Niches.

Ecosystem-relevant shifts in geographic niche will not only occur horizontally (from 1 to 2) (e.g., latitudinal tropicalization observed in marine communities), but also vertically in the water column (from A to B) (e.g., expanding oxygen minimum zones will impact the vertical geographical niche of zooplankton, ultimately affecting the 'active carbon flux' and the sequestration of carbon in the deep ocean).

the population density decreases from the center towards the periphery of a species' realized niche, and variations in abundance are known to impact evolution at the metapopulation level, affecting the way populations adapt to changes in the environment [67] (Figure 3). For example, changes in abundance can provoke migration asymmetries, resulting in the reduction or inhibition of local adaptation and fitness reduction in the periphery [68], ultimately impacting the geographic limits of species. These lower fitness and genetic variations imply that peripheral populations will be more susceptible to environmental changes, particularly if their migratory abilities within their fundamental niche are limited due to competition with others. Therefore, the evolutionary responses to climate change are expected to be more pronounced in peripheral populations of realized niches [69]. Thus, peripheral populations appear disproportionately critical for the survival and evolution of a given species [70] and will play a major role in the interplay between migration and adaptation processes [14].

Contemporary Adaptive Evolution and the Role of the Rare Biosphere

Adaptive evolution is controlled by the interplay between natural selection and genetic variability, where beneficial alleles favored by selection are predicted to increase in frequency, independent of



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Figure 2. Example 2 of Specific Relevant Points/Outcomes That Can Be Derived from the Application of Theoretical Ecology to Marine Ecosystems: Selection Events Caused by Extreme Weather Events.

Climate-related events (e.g., ocean warming or de-oxygenation) take place over long temporal scales and in addition extreme weather-related events can occur and cause sudden drastic changes in key communities or ecosystem engineers, decreasing ecosystem maturity and causing a resetting of ecological succession that, on the way to resuming higher ecosystem maturity, might give rise to a different ecosystem structure and different temporal response to long-scale climate-related processes.

whether they are new mutations or pre-existing, segregating genetic variants [71]. Adaptation from existing genetic variation has been suggested as the main process occurring when selection pressure shifts rapidly in response to fast environmental changes or colonization of a new habitat [72], even for slowly evolving (sessile and/or long generation time) organisms such as trees [14]. A phenomenon used to explain the contribution of genetic variation to adaptation is 'conditional neutrality'. This term refers to an allele being neutral in one particular environment but displaying a fitness advantage in another [73]. Neutral alleles drift randomly until a shift in selection pressures makes them advantageous. This process favors fast, adaptive evolution to increase fitness in newly emerging conditions since these beneficial alleles are instantly accessible and at higher occurrences than *de novo* mutations [71,72]. The idea of pre-existing variants within a natural population becoming beneficial under environmental changes during different times ('temporal conditional neutrality') has been recently put forward to address the interplay of demographic and adaptive evolutionary responses to Quaternary climate dynamics [14]. In the same way as a higher genetic variation within a species allows better response to selection, a higher genetic/functional diversity across species of the same communities might allow these communities to better respond to

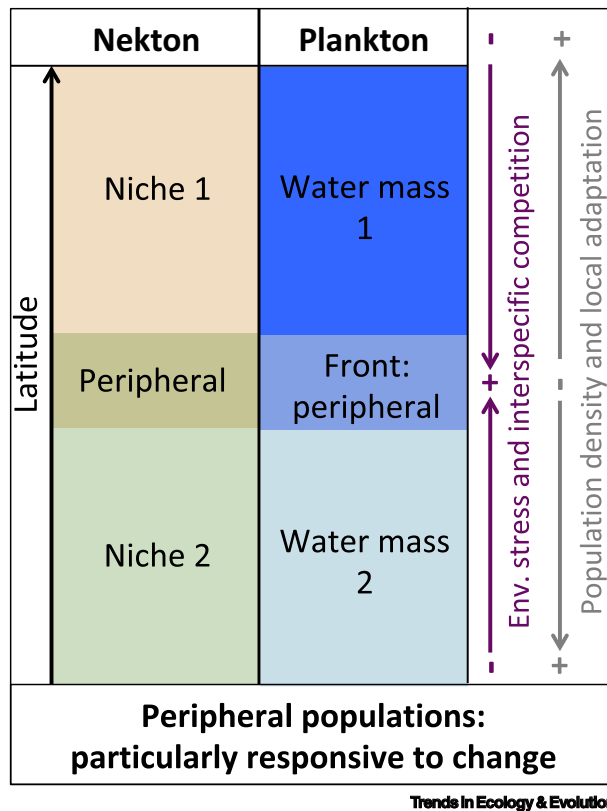
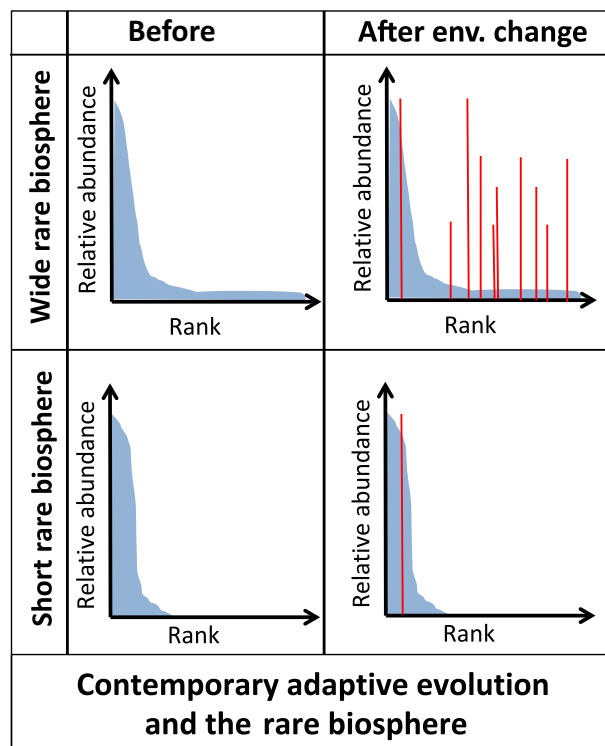


Figure 3. Example 3 of Specific Relevant Points/Outcomes That Can Be Derived from the Application of Theoretical Ecology to Marine Ecosystems: Peripheral Populations as Sentinels of Change of Evolutionary, Metabolic, and Ecological Changes of Niches and Ecosystems.

Peripheral populations located at the edges of niches are predicted to present higher interspecific competition and environmental stress and lower population densities and local adaptability. We made a distinction between peripheral populations of nekton (i.e., organisms that can swim) and plankton (i.e., organisms that cannot swim faster than currents), because the inability of plankton to swim suggests that frequently fronts (where the edges of different water masses meet) will delimit the location of planktonic peripheral populations, and frontal zones can result in nutritional alleviation of limiting resources, which might counteract the predicted lower fitness and adaptability of peripheral populations of plankton. In contrast, the ability of nekton to swim allows them to more easily respond to different environmental factors via migration, but, being peripheral populations, they are probably more affected (unless they are also in fronts, where higher primary production will also potentially increase their fitness) than the planktonic counterparts.

environmental change. This suggests that complex microbial communities forming hyper-connected metabolic networks might exhibit more plasticity, ultimately implying a primacy of functional diversity over genetic variability in controlling ecosystem services. Alternatively, instead of plasticity, taxa replacement might occur, which may lead to different community states and ecosystem functioning [74,75]. Considering that the vast majority of genetic diversity in marine environments is present in the 'rare biosphere' [76] (i.e., the microbes persisting at extremely low abundances in a given community), it is possible that most genetic diversity follows the temporal conditional neutrality framework, implying a potentially fast evolutionary adaptability of marine ecosystems to environmental changes (Figure 4). This also implies that, from an evolutionary perspective, the study of the rare biosphere linked to environmental change and ecosystem processes deserves more attention, not only in marine systems but also in other environments harboring a rare biosphere with a high richness.



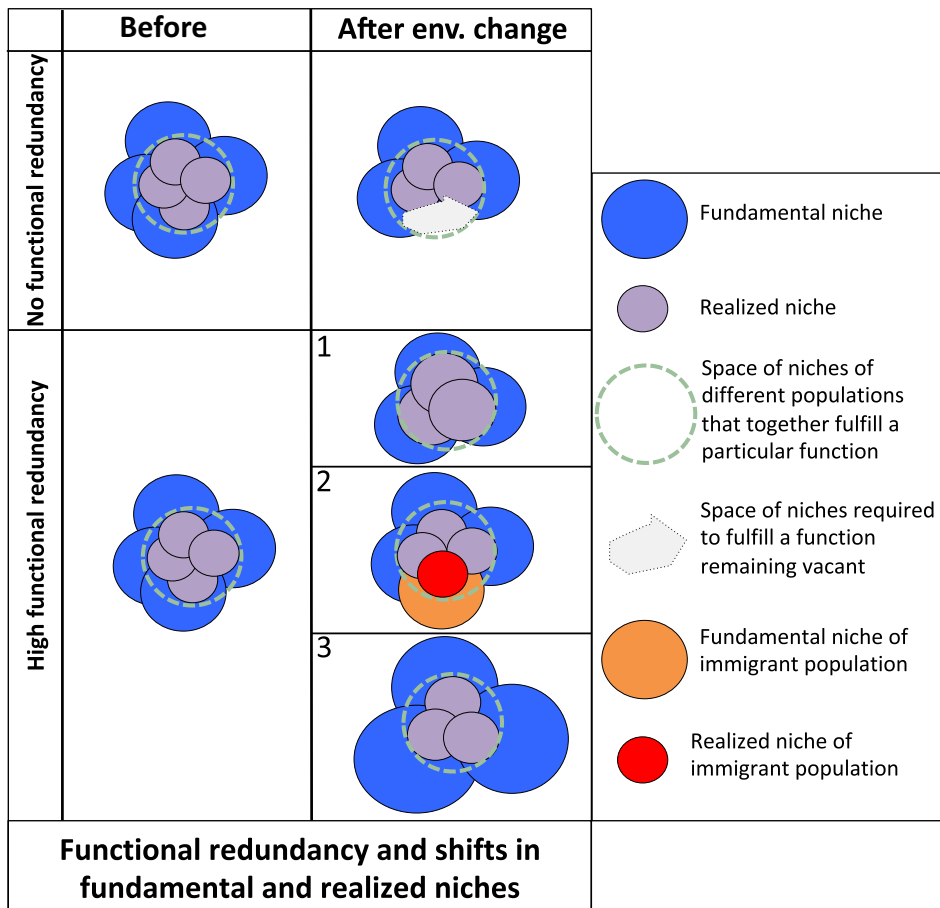
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Figure 4. Example 4 of Specific Relevant Points/Outcomes That Can Be Derived from the Application of Theoretical Ecology to Marine Ecosystems: Key Role of the ‘Rare Biosphere’ in Contemporary Adaptive Evolution.

Rank-abundance distribution of the species of two different populations (i.e., with and without rare biosphere) at the initial time (in blue) and abundance of these same species in response to the environmental change (in red). A community with a wider rare biosphere will generally have a higher adaptability to environmental changes because the higher genetic reservoir of the rare biosphere allows for higher probability of having the right genes/taxa/functions to adequately respond to the environmental change.

Functional Redundancy and Changes in Marine Ecosystems

Several studies suggest that different, coexisting microbes can perform the same function, indicating a high degree of functional redundancy in the marine environment [77–79]. In a recent global ocean analysis, combining phylogenetic and functional profiling, the distribution of functional groups in marine communities was found to be controlled by environmental conditions shaping metabolic niches [79]. A high level of oceanic functional redundancy has been suggested to be a consequence of diverse evolutionary processes such as adaptive loss of function and metabolic convergence accelerated by frequent horizontal gene transfer [79]. Similarly, model simulations suggest that function rather than phylogeny dictates biogeochemical gradients [80]. In contrast to this, evidence for low functional redundancy has also been reported [81,82]. Clearly, the methodology used to define functional redundancy affects the data interpretation and ultimately the conclusion drawn in studies. Yet, the degree of functional redundancy of an ecosystem might not be a constant feature but might change in the future in response to climate change [83]. In any case, if high functional redundancy is a characteristic feature of marine ecosystems (as most studies presently suggest), changes in the phylogenetic composition in response to climate change might not necessarily translate into relevant shifts in function. This also suggests that a trait-based framework would be the best avenue to predict shifts in realized and fundamental niche dynamics (expansion, contraction) and in the resulting ecosystem services in response to climate change [84] (Figure 5). In this respect, the ‘trait driver theory’, which integrates trait, metabolic/allometric, and



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Figure 5. Example 5 of Specific Relevant Points/Outcomes That Can Be Derived from the Application of Theoretical Ecology to Marine Ecosystems: Influence of Fundamental and Realized Niche Changes on Functional Redundancy and Ecosystem Response to Environmental Changes.

Each pair of blue and purple circles represents the fundamental and realized niche of a given population. A particular function will generally be performed by a group of populations whose realized niches overlap to perform that particular function. The extinction of one particular population due to environmental changes will cause different responses depending on whether a community has or has not functional redundancy. In the case of a high-functional redundancy community, three potential responses might occur: (1) the remaining population might expand their realized niche (within the limits of their fundamental niche) and occupy the niche left by the extinguished population, a process that will be greatly controlled by competition; (2) there is recruitment (immigration) of a new population (either from the rare biosphere or external communities) that occupies the same niche left by the extinguished population; or (3) there is an expansion of the fundamental niche of some of the remaining populations via adaptive evolution that allows fulfillment of the niche left by the extirpated population. In contrast, in the case of a community with no functional redundancy, the niche left by the extinguished population will not be covered, which will ultimately affect the community and ecosystem structure and that particular function/service.

species-richness-based approaches, is a novel framework to predict functional biogeography and the response of species/populations to climate change [85].

Taken together, the response of marine ecosystems to climate change will be linked to reductions or expansions in the realized and/or fundamental niche breadth of key species. For instance, the common denominator among the above-mentioned outcomes derived from the application of theoretical

ecology to marine ecosystems is the change in niche breadths of populations. Thus, we suggest that a framework based on ecological theory focusing on fundamental and realized niches, their spatial dynamics, and their potential responses to environmental changes has the potential to provide insights into the composition of communities in the future ocean and the pace of biogeochemical cycles mediated by these communities. This framework will develop and benefit from empirical and theoretical studies on present and past shifts in fundamental and realized niche breadth in response to marine environmental changes. Studies linking our understanding of the metabolic potential (taking advantage of the development of multi-omic data) with rates of biogeochemical cycling and community composition and function in the marine environment in the light of evolutionary forces will also be of particular relevance. A better integration among these different fields of research will be important. Systems biology is a promising avenue to integrate genetic and functional information from communities to assess their role in biogeochemical processes, by determining ecological properties using metabolic networks and resolving ecological niches from multi-omic data [28].

Concluding Remarks

The climate is changing and marine communities and ecosystems are responding to those changes. Environmental shifts can cause evolution of species, affecting both realized and fundamental niches [86]. Local adaptation to environmental conditions is also occurring [87]. Since local adaptation is related to genetic diversity [88], the loss of realized niche breadth might be linked to a loss of adaptive genetic diversity [89]. This will impact the evolutionary responses to climate change and the ability of a species to change both its fundamental and realized niche [90]. In turn, not only can environmental changes drive evolution, evolution can also impact environmental conditions. A dramatic example of such an interplay is the impact of the evolution of oxygenic photosynthesis on the evolution of Earth's systems. Simultaneously, these environmental changes are affecting the metabolism of marine organisms and their ecosystem services. Understanding how climate changes affect the metabolism of marine species is a major focus of marine ecological and biogeochemical studies. Still, the integration of the evolutionary niche dynamics and the study of the metabolic changes of marine organisms in the light of climate and environmental changes have received limited attention. We argue that the response of marine ecosystems and their services (e.g., elemental fluxes) will be a function of the response of key species to climate change, which will be linked to reductions or expansions in their realized and/or fundamental niche breadth. These modifications of the niches will, in turn, be controlled by differences in the environmental stressors and by the response of the organisms to tolerate or react to them. Environmental changes might presently occur faster than species with long generation times are able to adapt, while organisms with short generation times, such as microbes, are better suited to keep pace with environmental changes. Thus, we propose that a framework based on ecological theory that considers fundamental and realized niches, their spatial dynamics, and their potential responses to environmental changes, combining metabolic, evolutionary, and climate change studies, will provide the mechanistic understanding of how environmental changes affect the marine biota from genes to ecosystem services and from past times to the future to come (see Outstanding Questions).

Author Contributions

F.B. and G.J.H. wrote the initial draft and coordinated the drafting of the paper. All authors contributed to the discussion of ideas and the writing of the paper.

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Outstanding Questions

How will the interaction and/or combination of local adaptation and migration affect marine ecosystem services in response to current and future environmental changes?

Is it possible to simplify the response of marine ecosystems and their services to climate change to just the response of a few key marine species (linked to reductions or expansions in their realized and/or fundamental niche breadth)? If so, which should those key species be? What should be the parameters needed to define/select those key species?

How will these modifications of the niches of marine organisms be affected by differences in the environmental stressors and by the response of the organisms to tolerate or react to these stressors?

What can empirical and theoretical studies on past and present shifts in fundamental and realized niche breadth in response to marine environmental changes tell us about the future of marine ecosystems and their services?

How important is the link between metabolic potential and actual rates of biogeochemical cycling and community composition and function in the marine environment in the light of evolutionary forces?

References

- IPCC. (2013) *Climate Change 2013: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press
- Bopp, L. et al. (2002) Climate-induced oceanic oxygen fluxes: implications for the contemporary carbon budget. *Global Biogeochemical Cy.* 16, 6-1-6-13
- Wu, L. et al. (2012) Enhanced warming over the global subtropical western boundary currents. *Nat. Clim. Chang.* 2, 161-166
- Vellend, M. (2010) Conceptual synthesis in community ecology. *Q. Rev. Biol.* 85, 183-206
- Poloczanska, E.S. et al. (2013) Global imprint of climate change on marine life. *Nat. Clim. Chang.* 3, 919-925
- Gattuso, J.-P. et al. (2015) Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science* 349, aac4722
- Nagelkerken, I. and Connell, S.D. (2015) Global alteration of ocean ecosystem functioning due to increasing human CO₂ emissions. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13272-13277
- Moran, M.A. et al. (2016) Deciphering ocean carbon in a changing world. *Proc. Natl. Acad. Sci. U. S. A.* 113, 3143-3151
- Poloczanska, E.S. et al. (2016) Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* 3, 62
- Tagliabue, A. et al. (2011) The response of marine carbon and nutrient cycles to ocean acidification: large uncertainties related to phytoplankton physiological assumptions. *Global Biogeochemical Cy.* 25, GB3017
- Thomas, M.K. et al. (2012) A global pattern of thermal adaptation in marine phytoplankton. *Science* 338, 1085-1088
- Flombaum, P. et al. (2013) Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. *Proc. Natl. Acad. Sci. U. S. A.* 110, 9824-9829
- Carroll, S.P. et al. (2007) Evolution on ecological time-scales. *Funct. Ecol.* 21, 387-393
- de Lafontaine, G. et al. (2018) Invoking adaptation to decipher the genetic legacy of past climate change. *Ecology* 99, 1530-1546
- Bar-On, Y.M. et al. (2018) The biomass distribution on Earth. *Proc. Natl. Acad. Sci. U. S. A.* 115, 6506-6511
- Collins, S. et al. (2014) Evolutionary potential of marine phytoplankton under ocean acidification. *Evol. Appl.* 7, 140-155
- Hellweger, F.L. et al. (2014) Biogeographic patterns in ocean microbes emerge in a neutral agent-based model. *Science* 345, 1346-1349
- Cavan, E.L. et al. (2019) The sensitivity of subsurface microbes to ocean warming accentuates future declines in particulate carbon export. *Front. Ecol. Evol.* 6, 1-10
- Collins, S. and Bell, G. (2004) Phenotypic consequences of 1,000 generations of selection at elevated CO₂ in a green alga. *Nature* 431, 566-569
- Lohbeck, K.T. et al. (2012) Adaptive evolution of a key phytoplankton species to ocean acidification. *Nat. Geosci.* 5, 346-351
- Irwin, A.J. et al. (2015) Phytoplankton adapt to changing ocean environments. *Proc. Natl. Acad. Sci. U. S. A.* 112, 5762-5766
- Logares, R. et al. (2018) Contrasting prevalence of selection and drift in the community structuring of bacteria and microbial eukaryotes. *Environ. Microbiol.* 20, 2231-2240
- Rengefors, K. et al. (2015) Evidence of concurrent local adaptation and high phenotypic plasticity in a polar microeukaryote. *Environ. Microbiol.* 17, 1510-1519
- Scheele, B.C. et al. (2017) Niche contractions in declining species: mechanisms and consequences. *Trends Ecol. Evol.* 32, 346-355
- Hutchinson, G. (1957) *Concluding Remarks: Population Studies, Animal Ecology and Demography*, Cold Spring Harbor Symposium of Quantitative Biology
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecol. Lett.* 3, 349-361
- Colwell, R.K. and Rangel, T.F. (2009) Hutchinson's duality: the once and future niche. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19651-19658
- Muller, E.E. et al. (2018) Using metabolic networks to resolve ecological properties of microbiomes. *Curr. Opin. Syst. Biol.* 8, 73-80
- Anderson, J.T. et al. (2012) Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proc. R. Soc. Lond. B Biol. Sci.* 279, 3843-3852
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637-669
- Catullo, R.A. et al. (2015) Extending spatial modelling of climate change responses beyond the realized niche: estimating, and accommodating, physiological limits and adaptive evolution. *Glob. Ecol. Biogeogr.* 24, 1192-1202
- Lynch, M. and Lande, R. (1993) Evolution and extinction in response to environmental change. In *Biotic Interactions and Global Change* (Kareiva, P.K. et al. eds), pp. 234-250, Sinauer Associates
- Bürger, R. and Lynch, M. (1995) Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution* 49, 151-163
- Etterson, J.R. and Shaw, R.G. (2001) Constraint to adaptive evolution in response to global warming. *Science* 294, 151-154
- Bennett, A.F. and Hughes, B.S. (2009) Microbial experimental evolution. *Am. J. Phys. Regul. Integr. Comp. Phys.* 297, R17-R25
- Braun, S. et al. (2017) Microbial turnover times in the deep seabed studied by amino acid racemization modelling. *Sci. Rep.* 7, 5680
- Garant, D. et al. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature* 433, 60-65
- Phillips, B.L. et al. (2006) Invasion and the evolution of speed in toads. *Nature* 439, 803
- Hendry, A.P. et al. (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290, 516-518
- Filchak, K.E. et al. (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* 407, 739
- Schwarz, D. et al. (2005) Host shift to an invasive plant triggers rapid animal hybrid speciation. *Nature* 436, 546-549
- Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13, 329-332
- Fussmann, G.F. et al. (2007) Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* 21, 465-477
- Hairton, N.G., Jr. et al. (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8, 1114-1127
- Moyes, C.D. and Schulte, P.M. (2005) *Animal Physiology*, Benjamin Cummings
- Johnston, I.A. and Bennett, A.F. (2008) *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, Cambridge University Press
- Gillooly, J.F. et al. (2001) Effects of size and temperature on metabolic rate. *Science* 293, 2248-2251

48. Brown, J.H. *et al.* (2004) Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789
49. Allen, A. *et al.* (2005) Linking the global carbon cycle to individual metabolism. *Funct. Ecol.* 19, 202–213
50. Chen, B. *et al.* (2012) Does warming enhance the effect of microzooplankton grazing on marine phytoplankton in the ocean? *Limnol. Oceanogr.* 57, 519–526
51. López-Urrutia, Á. *et al.* (2006) Scaling the metabolic balance of the oceans. *Proc. Natl. Acad. Sci. U. S. A.* 103, 8739–8744
52. Boscolo-Galazzo, F. *et al.* (2018) Temperature dependency of metabolic rates in the upper ocean: a positive feedback to global climate change? *Glob. Planet. Chang.* 170, 201–212
53. Barneche, D.R. and Allen, A.P. (2018) The energetics of fish growth and how it constrains food-web trophic structure. *Ecol. Lett.* 21, 836–844
54. Carozza, D.A. *et al.* (2019) Metabolic impacts of climate change on marine ecosystems: implications for fish communities and fisheries. *Glob. Ecol. Biogeogr.* 28, 158–169
55. Padfield, D. *et al.* (2016) Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. *Ecol. Lett.* 19, 133–142
56. Padfield, D. *et al.* (2017) Metabolic compensation constrains the temperature dependence of gross primary production. *Ecol. Lett.* 20, 1250–1260
57. Meyer, K. *et al.* (2016) The influence of the biological pump on ocean chemistry: implications for long-term trends in marine redox chemistry, the global carbon cycle, and marine animal ecosystems. *Geobiology* 14, 207–219
58. Stramma, L. *et al.* (2012) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Chang.* 2, 33–37
59. Deutsch, C. *et al.* (2015) Climate change tightens a metabolic constraint on marine habitats. *Science* 348, 1132–1135
60. Pörtner, H.-O. *et al.* (2014) Ocean systems. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 411–484, Cambridge University Press
61. Aristegui, J. *et al.* (2009) Microbial oceanography of the dark ocean's pelagic realm. *Limnol. Oceanogr.* 54, 1501–1529
62. Smith, M.D. (2011) The ecological role of climate extremes: current understanding and future prospects. *J. Ecol.* 99, 651–655
63. Wernberg, T. *et al.* (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Chang.* 3, 78–82
64. Kumagai, N.H. *et al.* (2018) Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proc. Natl. Acad. Sci. U. S. A.* 115, 8990–8995
65. Hoegh-Guldberg, O. *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742
66. Case, T.J. and Taper, M.L. (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* 155, 583–605
67. Aitken, S.N. *et al.* (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1, 95–111
68. García-Ramos, G. and Kirkpatrick, M. (1997) Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51, 21–28
69. Sexton, J.P. *et al.* (2009) Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* 40, 415–436
70. Hampe, A. and Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8, 461–467
71. Barrett, R.D. and Schluter, D. (2008) Adaptation from standing genetic variation. *Trends Ecol. Evol.* 23, 38–44
72. Olson-Manning, C.F. *et al.* (2012) Adaptive evolution: evaluating empirical support for theoretical predictions. *Nat. Rev. Genet.* 13, 867
73. Mitchell-Olds, T. *et al.* (2007) Which evolutionary processes influence natural genetic variation for phenotypic traits? *Nat. Rev. Genet.* 8, 845
74. Graham, E.B. *et al.* (2016) Coupling spatiotemporal community assembly processes to changes in microbial metabolism. *Front. Microbiol.* 7, 1949
75. Graham, E.B. *et al.* (2016) Microbes as engines of ecosystem function: when does community structure enhance predictions of ecosystem processes? *Front. Microbiol.* 7, 214
76. Sogin, M.L. *et al.* (2006) Microbial diversity in the deep sea and the under-explored "rare biosphere". *Proc. Natl. Acad. Sci. U. S. A.* 103, 12115–12120
77. Baltar, F. *et al.* (2012) Prokaryotic community structure and respiration during long-term incubations. *MicrobiologyOpen* 1, 214–224
78. Aylward, F.O. *et al.* (2015) Microbial community transcriptional networks are conserved in three domains at ocean basin scales. *Proc. Natl. Acad. Sci. U. S. A.* 112, 5443–5448
79. Louca, S. *et al.* (2016) Decoupling function and taxonomy in the global ocean microbiome. *Science* 353, 1272–1277
80. Coles, V. *et al.* (2017) Ocean biogeochemistry modeled with emergent trait-based genomics. *Science* 358, 1149–1154
81. Ward, C.S. *et al.* (2017) Annual community patterns are driven by seasonal switching between closely related marine bacteria. *ISME J.* 11, 1412–1422
82. Galand, P.E. *et al.* (2018) A strong link between marine microbial community composition and function challenges the idea of functional redundancy. *ISME J.* 12, 2470–2478
83. García, F.C. *et al.* (2018) Changes in temperature alter the relationship between biodiversity and ecosystem functioning. *Proc. Natl. Acad. Sci. U. S. A.* 115, 10989–10994
84. Amend, A.S. *et al.* (2016) Microbial response to simulated global change is phylogenetically conserved and linked with functional potential. *ISME J.* 10, 109
85. Enquist, B.J. *et al.* (2015) Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. In *Advances in Ecological Research*, pp. 249–318, Elsevier
86. Pearn, P.B. *et al.* (2008) Niche dynamics in space and time. *Trends Ecol. Evol.* 23, 149–158
87. Savolainen, O. *et al.* (2013) Ecological genomics of local adaptation. *Nat. Rev. Genet.* 14, 807–820
88. Jones, F.C. *et al.* (2012) The genomic basis of adaptive evolution in threespine sticklebacks. *Nature* 484, 55
89. Joost, S. *et al.* (2007) A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Mol. Ecol.* 16, 3955–3969
90. Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19659–19665