

Editorial: Fluctuating Habitats: Ecological Relevance of Environmental Variability and Predictability on Species, Communities, and Ecosystems

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Editorial on the Research Topic

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THE IMPORTANCE OF THE SPATIAL AND TEMPORAL VARIABILITY IN ECOLOGY AND PHYSIOLOGY

Temporal and spatial environmental variability are wide spread and life evolved adapting to constantly ever changing conditions (Desmond, 2021). In marine and freshwater productive ecosystems water temperature and light availability dictate diel change in oxygen, pH and CO₂ by controlling the photosynthetic activity of the aquatic primary producers (Bitter et al., 2021a). Landward, intertidal environments are governed by the alternation of emerged and submerged periods that determine a temporal and spatial heterogeneity in salt stress and water availability to which species need to adapt. These diel changes are also observed in terrestrial ecosystems. For instance, in the desert, seasonal humidity and temperature fluctuation control the water availability create the conditions for life to thrive (Makhalanyane et al., 2015 and reference within). Although most of the models of species adaptation consider the biological response to one or few relevant environmental factors, such as temperature in climate change models, there are growing evidences that the cumulative effect of the variability of abiotic factors has to be considered. For instance, fluctuating conditions can mitigate the net impact of the corresponding stressor, increasing physiological tolerance and promoting adaptation to novel environmental conditions at all biological levels (Booth et al., 2021; Fusi et al., 2021). For microorganisms, in addition to spatial patterns, environmental fluctuations can determine localized spatial jackpot events that ensure persistence of strains across environmental dynamic conditions (Ciccarese et al., 2022). At the holobiont level, desert plants stabilize the associated bacterial community (e.g., stable composition) by modulating the release of exopolysaccharides therefore insulating the bacterial community around the rhizosphere, attaining the effect of daily and seasonal fluctuations. This process mediated by the plant holobiont ensures the persistence of important plant promoting bacteria that can support plant growth and homeostasis in such harsh environment (Marasco et al., 2022).

In coastal areas, marine ectotherms experience such a high magnitude of environmental variability that significantly shapes their physiological response to climate change and stresses (Baldanzi et al., 2015; Giomi et al., 2019). Increasing number of studies highlight the importance of environmental fluctuations as main driver of all the eco-evolutionary processes of life on earth. However, when it comes to investigate the effect of the environmental change on physiological and ecological processes through both, laboratory and theoretical approaches, the "mean conditions paradigm" still prevail (Kroeker et al., 2020). This Research Topic brought together contributions that re-shape our understanding of how environmental heterogeneity and fluctuations drive population and community assembly across diverse habitats.

CONSIDERING THE TEMPORAL AND SPATIAL ENVIRONMENTAL VARIABILITY

Environmental fluctuations exert an impact on organism physiology which has been recognized either as a threat (*e.g.*, marine heatwaves) or a benefit (Huey and Bennett, 1990; Bernhardt et al., 2020). Manríquez et al. studied the acclimatization to upwelling conditions (variable *vs.* stable) of the marine ectotherm *Achanthopleura echinata* of two Chilean populations and demonstrated that a fluctuating environment increases the thermal tolerance of *A. echinata*, however carrying a high energetic cost. Eaton et al. using thermal fluctuations

to investigate the effect of heatwaves on pinfish, found that thermal stress induced metabolic plasticity as a response to thermal anomalies. As a results, the pinfish increased their resilience to heatwaves. Similarly, individual plastic response was investigated by El Moussaoui et al.. The authors find that American wisteria, a perennial climbing plant, responded to increasing stressing condition by modifying its morphology such that it could withstand aridity ad increasing temperatures. Likewise, a terrestrial orchid shows a degree of variability in growth, flowering and mortality over time as a respond to changing harvesting strategies and climate fluctuations occurring over the years (Timsina et al.).

Environmental variability results also in the variation of diel cycles along seasonal fluctuations. During summer the low pressure in the Indian ocean determined by the El Niño–Southern Oscillation reclaims water from the Red Sea basin and decreases its sea level and consequently its tidal range. Red Sea mangroves inhabiting landward zone experience almost 6 months of high salinity due to the absence of tide. The bacterial community of mangrove sediment in this area differs dramatically from area continuously inundated, significantly changing their ecosystem function (Thomson et al.). The importance of the variability of temperature fluctuation also has a significant impact on the algal biofilm formation. Cotiyane-Pondo and Bornman demonstrate that different localized fluctuations of nutrients, and temperature, at centimeter/millimeter scale, resulted in a differential colonization



FIGURE 1 | This figure aims to represent connections between the different scales of spatial and temporal variability (and predictability) that different levels of biological organization experience. Thus, showing the importance of integrating across different environmental scales that connect organisms/communities/ecosystems to climate and changes due to the anthropogenic impact. Spatial and temporal variability across different levels of biological organization vary in magnitude and scale. At micro/millimeters scales, environmental variables can display random variations across time (rather than a regular, e.g., cyclical, pattern) which make that variability difficult to predict. For example, cyanobacterial biofilms are characterized by a high variability of oxygen and pH fluctuations over time as a result of different micro-conditions (i.e., irradiance, photosynthetic performance). At larger scales, holobionts and communities experience more predictable patterns of variation. For example, hot desert organisms live in a predictable pattern of daily temperature variation; likewise, benthic communities in marine productive ecosystems experience regular daily fluctuations of dissolved oxygen driven by photosynthesis and community respiration. At the ecosystem level, the predictability of environmental variables further increases because of the seasonal pattern corresponding to the latitude where the ecosystem is located.

of diatoms, highlighting the importance of the local variability over large-scale patterns.

Spatial variability in environmental conditions can generate important consequences at species and community levels depending on the scale at which these variations is considered. Pérez-Matus et al. investigated the pattern of fish assemblages and their functional diversity across almost 150 degrees of longitude in eastern and western South Pacific Ocean. They found that, while at large scale, from west-to-east a decline in species diversity was evident, the patterns of variation in functional diversity depend on the environmental domains found at smaller scales. On a similar topic, Pattrick et al. investigated the effects of marine fronts on larval fish assemblages by jointly collecting environmental and biological data in the nearshore waters of the south coast of South Africa. They show that, the onshore retention of fish larvae is highly correlated with offshore larval mixing and the degree of environmental variability at local scales (current velocity and mixing).

INTEGRATING ENVIRONMENTAL TEMPORAL AND SPATIAL VARIABILITY IN NEW FRAMEWORK OF RESEARCH

Temporal and spatial variability are central in many ecological processes driving the biological community assembly, from micro-scale with microorganisms (bacteria, archaea, fungi, viruses, and protists) to macro-scale at individual, community and ecosystem levels (**Figure 1**). Most importantly, the understanding of the predictability of the environmental variability plays a unique and fundamental role in shaping the phenotypic variation observed across natural populations and their organization (Bitter et al., 2021b). *In-situ* high frequency environmental logging, measured at ecological relevant spatial scale, can capture ecological patterns that models based on large spatial resolution often fail to detect (Lima and Wethey,

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2012; Vargas et al., 2022). Environmental fluctuations have been proved to play a fundamental role in ecosystem resistance to climate change (Giomi et al., 2019). Overall, there is a general consensus that in future studies and models, multiple dimensions will need to be integrated to better describe the environmental complexity (Ciccarese and Johnson, 2019; Kroeker et al., 2020).

Measuring the environment as organisms experience it and respond to its variations within laboratory-based experiments will provide new insights to unveil the role of environmental variability in ecosystem structure and functioning (Tecon et al., 2019). This will help to provide a solid base to build more relevant models to predict the consequences of climate change on biodiversity and ecosystems across the planet and the services they provide.

AUTHOR CONTRIBUTIONS

MF, SB, and RM led the article structure and the conceptual model. All authors contributed to the article and approved the submitted version.

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