



Net effect of environmental fluctuations in multiple global-change drivers across the tree of life

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Jensen's inequality predicts that the response of any given system to average constant conditions is different from its average response to varying ones. Environmental fluctuations in abiotic conditions are pervasive on Earth; yet until recently, most ecological research has addressed the effects of multiple environmental drivers by assuming constant conditions. One could thus expect to find significant deviations in the magnitude of their effects on ecosystems when environmental fluctuations are considered. Drawing on experimental studies published during the last 30 years reporting more than 950 response ratios ($n = 5,700$), we present a comprehensive analysis of the role that environmental fluctuations play across the tree of life. In contrast to the predominance of interactive effects of global-change drivers reported in the literature, our results show that their cumulative effects were additive (58%), synergistic (26%), and antagonistic (16%) when environmental fluctuations were present. However, the dominant type of interaction varied by trophic level (autotrophs: interactive; heterotrophs: additive) and phylogenetic group (additive in Animalia; additive and positive antagonism in Chromista; negative antagonism and synergism in Plantae). In addition, we identify the need to tackle how complex communities respond to fluctuating environments, widening the phylogenetic and biogeographic ranges considered, and to consider other drivers beyond warming and acidification as well as longer timescales. Environmental fluctuations must be taken into account in experimental and modeling studies as well as conservation plans to better predict the nature, magnitude, and direction of the impacts of global change on organisms and ecosystems.

additive effects | interacting drivers | Jensen's inequality | manipulative experiments | variable environments

Historically, ecologists have focused on average environmental conditions to understand the responses of organisms and ecosystems. However, more than a century ago, Jensen (1) demonstrated, with his famous inequality, that the response of a system to constant, average conditions is different from the system's average response to variable conditions. The reason is that the relationship between a given environmental driver and the response of an organism or ecosystem is often nonlinear. Nonlinearity is a response pattern commonly found in nature, and it affects different trophic groups (i.e., autotrophs, herbivores, or carnivores) and biological properties of populations (i.e., abundance, growth rates) and communities (i.e., biodiversity, plant biomass, primary productivity, species richness) from marine (2, 3), freshwater (4, 5), and terrestrial (6, 7) ecosystems. This response pattern means that variations in a hypothetical environmental driver will increase (or decrease) an organism's performance when the mean value of such a driver is in the concave (or convex) segments of the response curve. Although Jensen's inequality (also known as the fallacy of the average) provides a foundational framework for understanding and predicting the ecological consequences of environmental fluctuations, it remains underappreciated in the growing field of global-change biology (8). In fact, the concept of environmental fluctuation (or variability) was virtually absent from the scientific literature until the 1990s (9).

More recently, ecologists have become increasingly aware that the variance (not just the average) is essential to explain many of the ecological processes and phenomena occurring in nature (10–13). Moreover, natural fluctuations in many abiotic properties exceed the mean change predicted by the end of the 21st century due to climate change, such as surface temperature in the ocean (14) and in soils (15), dissolved oxygen concentration in coral reefs (16) and salt marshes (17), or pH in upwelled coastal waters (18), among others.

Natural fluctuations in environmental drivers are ubiquitous, pervasive, diverse in the variables involved (e.g., temperature, light, pH, resources), timescale (e.g., seconds, days, seasons), spatial scale (e.g., micrometers, kilometers) and form (i.e., gradual, drastic) and can affect the behavior, ecology, and evolution of organisms across multiple

Significance

Recent advances in ecology show evidence that multiple environmental drivers interact and that their impact on community and ecosystem functioning cannot be predicted from single-driver studies. However, ecologists still largely disregard the role that fluctuations in these drivers (i.e., changes above/below mean trends) play in modulating the magnitude and direction of global-change impacts. Through a 30-year quantitative review, we show that contrary to the established paradigm, additive effects are more frequent when environmental fluctuations are considered in multiple-driver (i.e., acidification, hyperoxia and hypoxia, light, resource supply, or temperature) scenarios, although such effects are strongly dependent on trophic strategy and phylogeny. Our findings stress the need to consider environmental variability in ecological studies and conservation plans to better predict the impacts of global climate change.

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trophic levels. In particular, and because life span is directly affected by organism size, it is plausible that organisms with a very small size (i.e., those experiencing the largest spatial environmental gradients) and those with a very large size (i.e., those with the greatest travel speeds) have perhaps the highest potential to encounter environmental variation in their lifetimes (19). Environmental fluctuations may accelerate molecular evolution by promoting major genomic and phenotypic changes (20) and a greater genetic trait variation (21) in communities than found in those evolved under constant conditions, thus leading to different evolutionary strategies (22). Organisms exploit these fluctuations in environmental drivers to survive and persist; hence the ways in which they anticipate, respond, and adapt to environmental drivers determine the patterns of biodiversity (23). In particular, fluctuations may contribute to maintain high population diversity when conditions change faster than species lifetimes by favoring some species over others, but not so fast that the communities essentially experience it as one stable condition (24, 25). In addition, more diverse communities can maintain ecosystem functioning under increasing fluctuations because they harbor more species with the capacity to resist such environments compared to communities with low specific richness (26). These species-rich communities produce more temporally stable ecosystem services due to the complementarity among species to perform similar ecosystem functions (i.e., the portfolio effect [27, 28]).

When attempts are made to predict ecological change by conducting manipulative experiments, running simulation-based ecosystem models, or synthesizing literature data, the drivers under study are often represented by average, constant environmental conditions in order to decrease noise and detect responses of organisms in inherently noisy biological systems (12). These efforts have generated either excessively optimistic projections or overly catastrophic ones and have stressed the predominance of synergistic and antagonistic interactions, in which the effect of two drivers acting together is larger or smaller than their additive effect (the sum of the effects of each separate driver) (29–32). The conclusions of the few available studies that have incorporated the role of environmental fluctuations remain unclear: Accentuation, attenuation, or even reversion of the effect (i.e., positive or negative) of a particular driver has been found when natural variability was incorporated into the experimental design (pH [33], light [34], nutrients [35], temperature [36]). Together with the natural variations in the environmental conditions mentioned, the second major type of stochasticity occurring in ecological systems is the internal population fluctuations. These can promote the onset of transient dynamics, leading the ecosystem away from an asymptotic state for extended periods of time (37) and ultimately altering its potential capacity to cope with global change. Finally, modeling simulations project that the frequency and intensity of extreme events will increase in the coming decades under a global-change scenario (38). Therefore, there is a pressing need to determine the direction and magnitude of the effects of multiple interacting global-change drivers on communities and ecosystems when natural environmental fluctuations are considered.

Here we conduct a literature meta-analysis to test quantitatively 1) the nature (i.e., interactive vs. additive effects), direction (i.e., positive vs. negative), and distribution frequency of interactions between global-change drivers and environmental fluctuations affecting different properties of terrestrial and aquatic organisms and communities, and 2) how these interactions vary among response traits and interacting driver pairs. Our analysis also serves to identify gaps in knowledge regarding

the ecological impacts of environmental fluctuations and thus to guide future research priorities and needs.

Results

Evidence and gaps in knowledge in environmental fluctuations research. The number of publications, assessed as a publication ratio, testing the biological impacts of environmental fluctuations has increased exponentially since 2005 ($R^2 = 0.80$, $F_{22} = 34.03$, $P < 0.00001$; *SI Appendix, Fig. S1A*). These studies investigated the effects of environmental fluctuations in combination with other global-change drivers, mostly using partial factorial experimental designs (i.e., not all potential combinations of drivers were considered; ~60% of studies;). The majority of studies considered 1) short-term scales of exposure (i.e., < 1 mo, ~65% of studies; *SI Appendix, Fig. S1B*), 2) Animalia ($> 70\%$ of studies, particularly Insecta; *SI Appendix, Fig. S1C–E*), and 3) temperate species ($> 70\%$ of studies; *SI Appendix, Fig. S1F*) from marine or terrestrial ecosystems (*SI Appendix, Fig. S1G*). Experimental studies quantifying the effect of environmental fluctuations on other groups or species and on natural communities (i.e., mixed-species assemblages) from freshwater ecosystems or considering intermediate (several months) or long-term (> 1 y) scales are comparatively scarce. In addition, there are almost no studies considering polar organisms (*SI Appendix, Fig. S1F*).

We identified five major global-change drivers addressed in the scientific literature: temperature, pH, dissolved oxygen concentration (i.e., hypoxia and hyperoxia), light, and nutrients (*SI Appendix, Fig. S2*). We found that ~77% percent of the total species used to evaluate the individual and interactive effect of these drivers under environmental fluctuations were Animalia. Chromista represented ~24% of total species tested in all the studies together and 100% of total species in the case of studies addressing the effect of light. Bacteria, Fungi, Plantae, and mixed species (Mixed) were investigated in a small number of studies focused on specific drivers and interactions.

Biological responses to environmental fluctuations under global-change conditions. Fluctuations in light (F_{light}) and resource availability ($F_{\text{resources}}$) had a significant inhibitory effect, whereas those in pH (F_{pH}) and hypoxia (F_{hypoxia}) were stimulatory. By contrast, fluctuations in temperature (F_{temp}), and hyperoxia ($F_{\text{hyperoxia}}$) and interactions between fluctuating temperature and warming ($F_{\text{temp}} \times W$) or fluctuating pH and acidification ($F_{\text{pH}} \times A$) did not have any significant effect (Fig. 1 *A* and *B*). The natural logarithm of response ratios (LRR) exhibited highly significant heterogeneity among studies ($I^2 =$ between 96.46 and 99.98%; Cochrane's $Q_{\text{test}} =$ between 309.87 and 57,818.46; $P < 0.001$; *SI Appendix, Table S1*), with no evidence of publication bias (Rosenthal fail-safe, $n =$ between 324 and 83,692, $P < 0.001$; *SI Appendix, Table S2*). When we classified the LRR by biological trait (Fig. 1 *B–F*), we observed that nonsignificant LRRs dominated over significant ones. Within the significant LRRs, F_{pH} had a contrasting effect on different traits—i.e., it inhibited behavior traits (e.g., jump number and total jump distance in fishes; Fig. 1*B*) but stimulated metabolism (Fig. 1*D*). Other interactions exhibited a consistent and inhibitory effect regardless of the category considered (i.e., $F_{\text{resources}}$ on metabolism and physiology, Fig. 1*D* and *F*; $F_{\text{temp}} \times W$ on fitness, Fig. 1*C*). The individual and interacting effects of the drivers considered here were not tested for all traits. For instance, studies evaluating, under constant and fluctuating conditions, the individual effects of hypoxia or

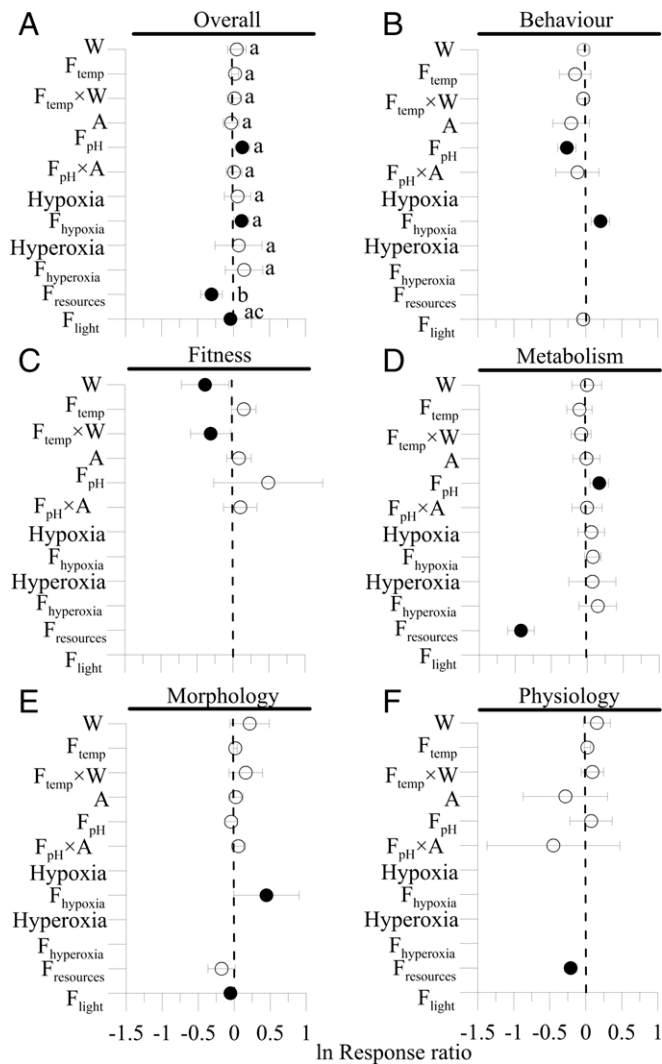


Fig. 1. Overall (A) mean effect categorized by biological traits (B, behavior; C, fitness; D, metabolism; E, morphology; and F, physiology) of warming (W), fluctuating temperature (F_{temp}), acidification (A) and fluctuating pH (F_{pH}) and their interactions, and hypoxia, fluctuating hypoxia ($F_{hypoxia}$), hyperoxia, fluctuating hyperoxia ($F_{hyperoxia}$), fluctuating resources ($F_{resources}$), and fluctuating light (F_{light}). Natural LRR < 0 or > 0 indicates a negative (i.e., inhibitory) or a positive (i.e., stimulatory) effect, respectively. Significant effect (black circles only) when the LRR 95% confidence interval does not overlap zero. Different letters (a–c) indicate significant differences by Tukey’s honest significance tests. Ln, natural logarithm.

hyperoxia on fitness and physiology were not found (SI Appendix, Fig. S1 C and F). By contrast, studies quantifying the effect of warming and acidification under constant and fluctuating conditions have considered all traits addressed here.

Finally, after separating the LRR values by trait and taxon to obtain a fine-scale view, we found that the magnitude of the individual and interacting effect of the drivers tested was medium (LRR < 0.5; see Materials and Methods; Fig. 2), with some exceptions. In these cases, the individual (e.g., F_{temp} on Bacteria fitness; Fig. 2A) or interacting effect was of large magnitude (LRR, > 0.8; $F_{temp} \times W$ on Mixed_{morphology} [Fig. 2A]; $F_{pH} \times A$ on Plantae_{physiology} [Fig. 2B]; $F_{resources}$ on Chromista_{metabolism} [Fig. 2C]). In addition to the magnitude, the effect of the drivers studied was highly variable between groups. On the one hand, warming, F_{temp} , or their interaction had a negative (and significantly distinct; Tukey’s posthoc test, $P < 0.01$) effect in Animalia and Fungi (and Plantae; only F_{temp}) but a positive effect in Chromista (and Bacteria; only F_{temp}). Acidification, F_{pH} , and both drivers

together positively affected morphology and physiology in Animalia and fitness in Chromista and negatively affected physiology and metabolism in Plantae (i.e., highest LRR values, > -4). On the other hand, F_{light} and $F_{resources}$ had a mostly negative effect on Animalia and Chromista, particularly on the metabolism of the latter (i.e., temporal variability of net primary productivity; Tukey’s posthoc test, $P < 0.001$), whereas hyperoxia and hypoxia did not exert any significant effect (except $F_{hypoxia}$ on Animalia_{behavior}; Fig. 2C).

Interactive effects between environmental fluctuations and global-change drivers. Overall, we found that the negative effects of environmental fluctuations and global-change drivers were more frequent than the positive ones (ranging between 20 and 75%; Fig. 3), although the neutral effect was the dominant response (ranging between 30 and 100%). In addition, negative effects were more frequent than positive ones when the drivers only fluctuated (e.g., F_{temp}) than when they were individually (e.g., warming) or interactively altered (e.g., $F_{temp} \times W$, excepting $F_{hypoxia}$; Fig. 3D). From the data presented above (Figs. 2 and 3), we found a dominance of additive over interactive effects (Fig. 4A). Within the interactive effects, we found that synergisms were slightly more frequent than antagonisms. By contrast, when we investigated major groups of organisms, we found that antagonisms were more frequent than synergisms for primary producers, i.e., Plantae (—antagonism and synergism, and + synergism of $F_{pH} \times A$ on metabolism, physiology, and morphology, respectively) and Chromista (i.e., + antagonism of $F_{temp} \times W$ on morphology and physiology, and + synergism of $F_{pH} \times A$ on morphology). Synergism, either negative or positive, was the only interaction detected on Animalia ($F_{temp} \times W$ on morphology and fitness) and Mixed communities (i.e., $F_{temp} \times W$ on morphology), respectively (Fig. 4B).

Discussion

Overall effect of environmental fluctuations under multiple global-change drivers. Our study shows that the cumulative impacts of multiple global-change drivers are generally additive when Jensen’s inequality (i.e., environmental fluctuations above or below mean values) are considered. These results contrast with previous meta-analyses synthesizing the results of manipulative experiments, which found predominantly interactive responses (marine—synergism, 31; terrestrial—antagonism; freshwater—antagonism, 32). A potential explanation for these contrasting results is that experimental studies addressing the impact of multiple drivers have traditionally assumed that they operate in a constant way (i.e., no variations above or below mean values occur). Using constant extreme stress conditions, as simulated under experimental global-change scenarios, ignores reprieves from stress that allow organisms to cope with these conditions, or at least reduce their impact (39). For instance, we found a positive antagonistic effect of warming under thermally varying conditions on Chromista morphology and physiology. Recent results have shown that thermal fluctuations promote transient “benign” conditions for organisms during cooling periods (40) and allow rapid phenotypic changes in metabolic traits and elemental composition (20) that accelerate the adaptation to warming stress. In addition, it is likely that studies testing the effect of global-change drivers under a constant regime tend to consider shorter experimental periods than those in which environmental fluctuations are also evaluated, thus overestimating the frequency of the interactive responses detected. The development of acclimation, adaptation, or recovery mechanisms, which

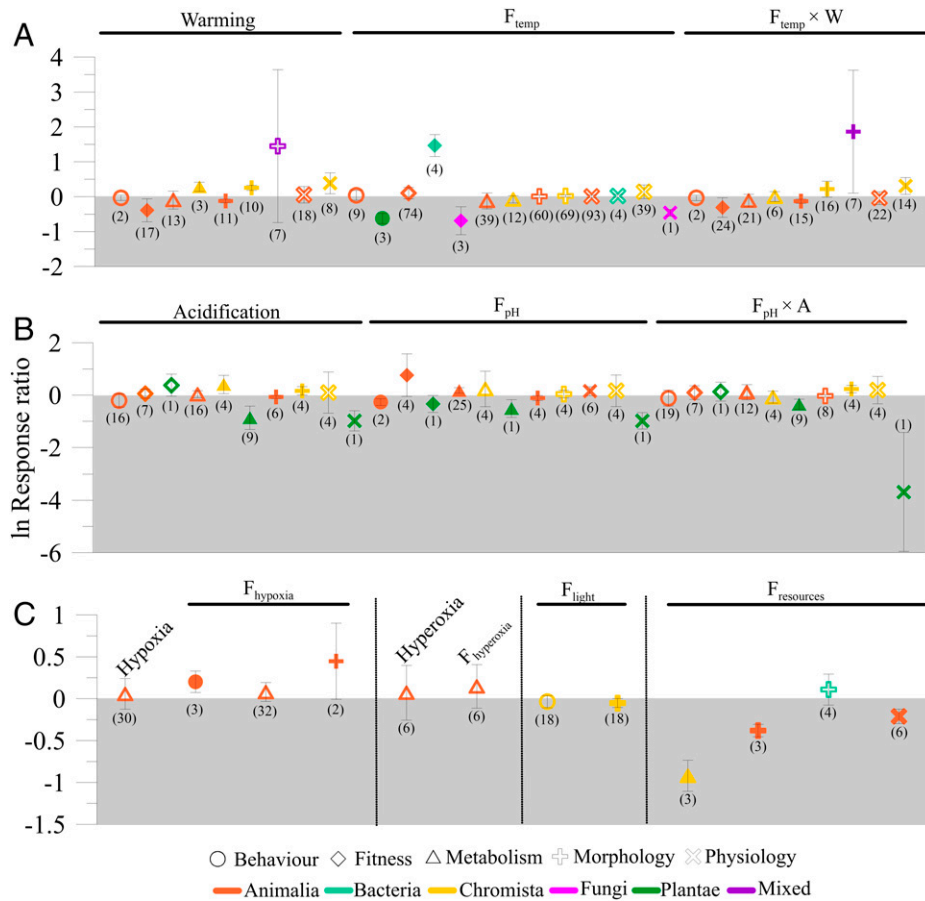


Fig. 2. Comparison of individual and interactive effects of temperature, acidification, hyperoxia and hypoxia, resources, and light under environmental fluctuations across the tree of life. Mean effect of warming and fluctuating temperature (A), acidification and fluctuating pH and their interactions (B), and hypoxia, fluctuating hypoxia, hyperoxia, fluctuating hypoxia, fluctuating light, and fluctuating resources (C) on Animalia, Bacteria, Chromista, Fungi, Plantae, and Mixed community behavior, fitness, metabolism, morphology, and physiology. Natural LRR < 0 (gray rectangle) or > 0 indicates a negative (i.e., inhibitory) or a positive (i.e., stimulatory) effect, respectively. Significant effect when the LRR 95% confidence interval does not overlap zero. Values in parentheses indicate the sample size (as number of LRR). Ln, natural logarithm.

can alter the frequency of interacting vs. additive effects, to cope with the stress imposed on organisms and communities requires longer periods of time to operate than often considered in experimental studies (41, 42).

Responses of different trophic groups: autotrophs vs. heterotrophs. Together with the abiotic environment experienced by organisms and communities, the trophic strategy (autotrophy vs. heterotrophy) and the biological organization level (population vs. community) are key variables influencing the proportion of interactive and additive effects detected. We found that additive effects were dominant in heterotrophs (e.g., Animalia) whereas interactive ones dominated or codominated in autotrophs (e.g., Chromista and Plantae). Thus, our findings indicate that changes in behavioral, fitness, metabolic, morphological, and physiological traits of heterotrophs could be underestimated or overestimated if only antagonistic or synergistic effects are assumed to be common under fluctuating and future global-change scenarios. The predominance of interactive effects in autotrophs contrasts with the results of other studies, where additive responses were more frequent in autotrophs than heterotrophs in both aquatic (43) and terrestrial environments (44, 45). Why autotrophs and heterotrophs are differentially impacted by global-change drivers may lie in that both groups acquire energy and resources through different strategies, or that heterotrophs may have intrinsically higher metabolic rates and energy expenditure than autotrophs because they are more active “foragers”

(46). Furthermore, we found that the interaction between environmental fluctuations and drivers had a positive effect on Chromista and a negative one on Plantae. These opposite effects could be attributed to the different generation times of the two groups. Generation time sets the characteristic timescale at which organisms experience and respond to environmental drivers and ultimately determines their ecological memory (47). Short-lived species, such as Chromista, may experience a stress for the same absolute time as any Plantae; however, the number of generations elapsed will be much higher. A higher number of generations allows organisms to counteract, or even adapt faster to, the stressful environment experienced.

Responses of different biological organization levels: populations vs. communities. The contrasting response patterns in the proportion of additive and interactive effects between previous studies and our analysis could result not only from the fact that we considered the role of environmental fluctuations but also because the articles reviewed here were mostly focused on the population level. A recent review by Gutiérrez-Cánovas et al. (48) in inland waters showed that additive effects were prevalent when the responses to multiple drivers were tested on a population compared to a community level (61 vs. 46%, respectively). These differences in the frequency of additive effects between populations and communities may be explained by the role of interspecific trophic interactions. Beauchesne et al. (49) and P. L. Thompson et al. (50) found that the presence

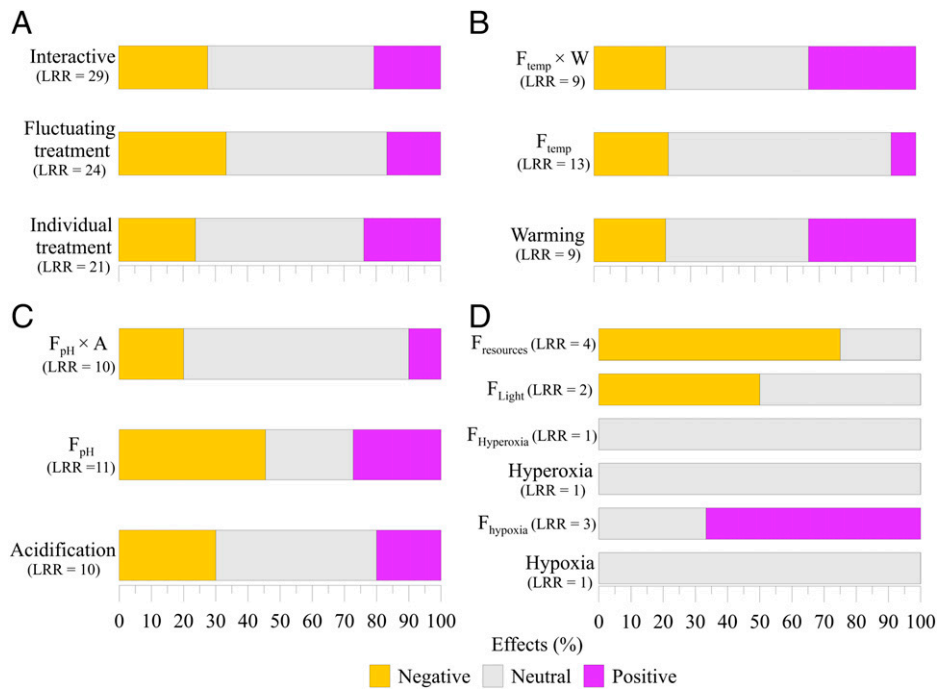


Fig. 3. Comparison of the neutral, negative, and positive effects of multiple global-change drivers and environmental fluctuations across the tree of life. Frequency distribution of negative (yellow), positive (purple), or neutral (gray) effects across the overall individual, fluctuating, and interactive treatments (A) of warming, and fluctuating temperature (B), acidification and fluctuating pH and their interactions (C), and fluctuating resources, light, hyperoxia and hypoxia, and fluctuating hyperoxia and hypoxia (D).

(or absence) of interspecific interactions causes communities to respond interactively (additively) to multiple interacting drivers. In particular, interspecific interactions involving at least one negative interaction (e.g., competition, predation) increase the negative effect of negative drivers and decrease the effect of positive drivers relative to the additive expectation.

Although our study was not specifically devoted to quantify the interactive effects of multiple global-change drivers and environmental fluctuations on populations, through the screened literature we found that 93% of studies published over the last three decades focused on individual species, mainly Insecta (Animalia). While studies at the community level are scarce, the available

evidence (i.e., mixed category) suggests that positive synergisms are dominant. Thus, interspecific interactions within communities can unmask interactive effects of multiple drivers that are not detected when assessed in single species. Therefore, population-level data may have, in some circumstances, limited ability to predict community or ecosystem responses to complex global-change scenarios.

Frequency of synergistic vs. antagonistic effects across the tree of life. Discrepancies between studies, some claiming that multiple global-change drivers promote interactive effects (31, 32, 51) and others suggesting that such interactions are rare or infrequent (44, 52, 53), could arise from different analytical approaches followed to estimate such effects or from differences in experimental design in the original studies. In the present analysis, given that we followed the same standardized procedure to quantify the magnitude, sign, and direction of the multiple interacting drivers addressed and selected studies that followed the same experimental design (i.e., factorial approach), we can rule out that the differences encountered in the frequency of interactive effects among trophic groups results from methodological differences. Although factorial designs are the more common approach used to quantify the effects of global change drivers, it should be noted that they treat continuous variables as discrete (e.g., temperature treated as current vs. future conditions). Likewise, the majority of published studies have used only two levels for each driver considered; hence the specific experimental levels chosen together with the choice of the baseline level (i.e., control conditions) can potentially alter the nature of the inferred interaction (54).

When considering interactive effects, we found that synergisms were slightly more frequent than antagonisms. These results are in line with previous marine meta-analyses (30, 31, 55) and contrast with the higher prevalence of antagonisms found in freshwater (32, 48) and terrestrial (44, 45) ecosystems. A higher occurrence of synergisms could be related, as stated

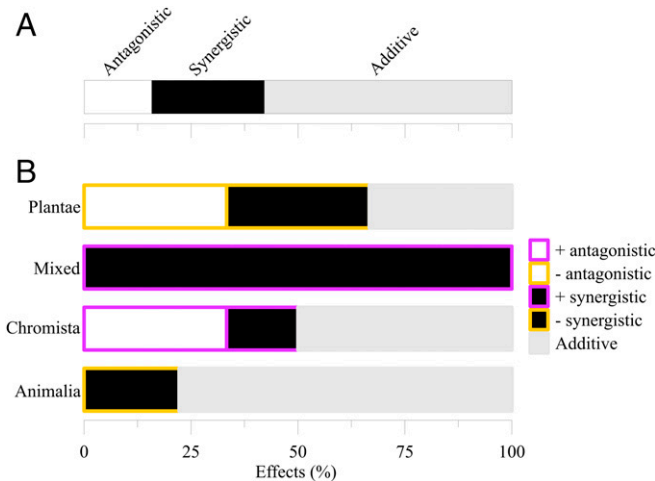


Fig. 4. Comparison of the additive and interactive effects of multiple global-change drivers and environmental fluctuations across the tree of life. Frequency distribution across the overall additive, synergistic, and antagonistic effects (A and B) and the particular positive/negative antagonistic, synergistic, and additive effects on Animalia, Chromista, Mixed, and Plantae (C).

above, with the key and overlooked consideration that organisms are not directly affected by climate per se (i.e., mean conditions) but are rather more affected by weather (i.e., variance conditions), which ultimately is trained by climate (56). Alternatively, synergism could be attributable to the low degree of asymmetry found in the magnitude of the individual LRRs between the driver pairs studied (57). This low asymmetry subsequently could explain the lower frequency of antagonism reported here when it is compared with previous findings (16% in this study vs. between 41 [32] and 62% [45]). It would be unrealistic to attempt to account for every possible combination of environmental conditions when predicting ecological responses to climate change. However, neglecting the effect of environmental fluctuations can not only bias our understanding and predictions of the impacts of global change on ecosystems but can also limit the effectiveness of conservation and management strategies (56). Currently, the predicted vulnerability of key species and ecosystems to global-change impacts is based on average climatic conditions (58, 59). By assuming constant environmental forcing, we may not be capturing the interacting nature of multiple environmental drivers or the overriding effect of short-term weather and nonclimatic drivers (60, 61).

Conclusions and Future Perspectives

Overall, our quantitative synthesis highlights four main points that require further research. First is the pressing need to include the effects of Jensen's inequality in experimental and modeling studies to predict the vulnerability of populations, organisms, and ecosystems to the impacts of global climate change (10–12, 62). Second, studies should include higher-order interactions; hence efforts must be devoted to incorporate the study of community responses (63). By scaling up predictions obtained at the level of individual system components, we can underestimate (64) or overestimate (65) the magnitude and direction (i.e., positive or negative effects) of the impacts of global change at the ecosystem level. Because organisms and populations in food webs are intimately linked, any change in one trophic level can potentially be propagated toward higher levels, ultimately leading to altered producer–consumer (66) or predator–prey dynamics (67). Third, future research efforts should move forward the understanding of poorly studied ecological drivers (e.g., hyperoxia or hypoxia) and consider longer exposure scales. Adaptive and evolutionary timescales can attenuate and even reverse the effects of global-change drivers observed at short-term scales (68). Finally, upcoming studies should explore the role that environmental fluctuations could play in the response of polar and boreal ecosystems and communities to global change.

Materials and Methods

Primary studies and case studies. We searched for primary research studies that addressed the biological effect of environmental fluctuations (i.e., variations in a given driver above/below its mean constant conditions), either in isolation or in combination with other environmental drivers, and that were published in indexed scientific journals until September 22, 2020. The literature search was done through Scopus and Web of Science (WoS) using the combination of the following search terms: “variability” AND (fluctuations* OR fluctuating* OR changes*), “fluctuations” AND (fluctuating* OR changes*), and “fluctuating” AND “changes.” Through this search we identified a total of 252 and 829 documents from SCOPUS and WoS, respectively, that included such terms in its titles, abstracts, and keywords (*SI Appendix, Fig. S3*). Because we were particularly interested in organism and community response, we conducted a subsequent screening to consider only studies belonging to the subject areas of Scopus: agricultural and biological sciences, environmental sciences, earth and planetary

sciences, biochemistry, genetics and molecular biology, microbiology, and multidisciplinary sciences (medicine, engineering, neurosciences, and mathematics were excluded). For WoS, we redefined the searching by categories and subcategories to include the same areas mentioned above for SCOPUS. After this reanalysis, we obtained a total of 218 and 629 studies from SCOPUS and WoS, respectively (i.e., screening phase). In addition, we screened the references (i.e., 543 references in total) of selected review articles addressing the effects of fluctuations on organisms (11, 12, 69–71), obtaining a total of 41 potentially eligible articles. In a second selection step, we reviewed the titles, abstracts, and full text and supplementary information (when available) of all entries recovered, obtaining a total of 36 (for WoS) and 50 (for SCOPUS) eligible studies together with the 41 mentioned above (*SI Appendix, Fig. S3*). Some articles retrieved (127 in total) were excluded based on the following criteria: 1) no primary data were reported (e.g., reviews, meta-analyses, and modeling studies); 2) they did not individually (or interactively) manipulate the drivers of interest in a factorial design, i.e., control vs. treatment conditions; 3) sample size was not reported; 4) less than three replicates were used; and 5) no measure of variation was reported (SE, SD, or 95% confidence interval). In relation to criterion 2, we chose experimental studies using a factorial approach because the published literature about the topic of interest is mostly dominated by this type of design, whereas other types of approaches (e.g., collapsed [72]; response-surface [54]) are still scarce. In addition, and for comparison purposes, it is more reasonable and appropriate to quantify the effects of environmental fluctuations and global-change drivers from studies that followed a similar experimental design.

The final literature set consisted of 66 articles: 24 retrieved from Scopus, 10 from WoS, and 32 from references cited in relevant reviews (two more were coincident with SCOPUS and WoS and thus were not considered here) published between 1995 and 2020 (*SI Appendix, Table S3*).

Data extraction. From each study we retrieved authors' names, publication year, biome (i.e., polar, temperate, and tropical, if available) and ecosystem (marine, freshwater, and terrestrial, if available), kingdom, group, species name, and drivers tested (i.e., control and treatments). From the 66 articles, we obtained a total of 5,700 raw measurements in biological traits, corresponding to six environmental drivers (i.e., acidification, hyperoxia and hypoxia, light, resources, and temperature) acting alone or in combination with fluctuations relative to mean constant control or ambient conditions. From these raw data, we calculated the means and SDs, which were subsequently used to calculate the LRR (or cases). Sample sizes were obtained directly from the text or tables. When data were given only as figures, we extracted them using Plot Digitizer v.4.3 (Ankit Rohatgi; <https://automeris.io/WebPlotDigitizer>).

Following previous meta-analysis studies (73), we grouped the biological responses investigated into five main traits for comparison purposes: behavior, fitness, metabolism, morphology, and physiology.

Effect size. The response (effect size) of the behavior, fitness, metabolism, morphology, and physiology of the studied groups to fluctuations in environmental drivers (and their interaction with global-change drivers) was estimated as the natural LRR, given by the ratio of the response variable in the treatment vs. control conditions (74). An LRR = 0 indicated no effect of the treatment considered upon the response variable studied, whereas a negative or a positive LRR indicated a decrease (i.e., an inhibition) or an increase (i.e., a stimulation) in the variable of interest, respectively (75). The variance associated with the effect size, which was needed to weigh each effect size by its precision, was estimated from the sample size and standard deviation (SD) associated with each mean value.

The overall response of the response variable of interest was determined using a random-effects model of meta-analysis. The random-effects model was selected because studies differed from each other in environmental conditions and methodological approaches, and thus an extra variation source (i.e., between studies) had to be taken into account in addition to the within-study variance. This variance was estimated by the restricted maximum likelihood method (76). The effect of fluctuations and their interaction with environmental drivers on the magnitude and direction of the variable of interest was also assessed by group analyses (i.e., by traits and kingdoms). An LRR size was significant if the 95% confidence interval did not include zero. To test significant differences between treatments within random-effects models (overall, for categories, and for traits/kingdoms), we used Tukey's honest significant tests. To ease the interpretation of results, the

magnitude of the effect size was considered small if $|\sim 0.2|$, medium if $\sim |0.5|$, and large if $|\sim 0.8|$ (77). The percentage of total variability due to the between-study variation rather than sampling error (I^2) was also quantified (76; *SI Appendix, Table S1*).

Based on the LRRs, we classified an interactive effect as synergistic or antagonistic when the interacting LRR was higher or lower, respectively, than the sum of the individual LRR of each driver considered in the corresponding interaction (i.e., additive effect size) (32). In addition to being classified as synergistic or antagonistic, the interactions were positive or negative when they increased (i.e., $LRR > 0$) or decreased (i.e., $LRR < 0$) the variable of interest (78). Interaction significance was assessed using the 95% confidence intervals calculated around each LRR, such that any interaction with intervals crossing zero was deemed additive.

Publication bias. Evidence of publication bias in the overall database was assessed by visual inspection of the funnel plot, which plotted effect sizes against precision (i.e., $1/SD$) (79). Evidence of publication bias in the overall database and subsets (i.e., category of response variables) was also assessed by the Rosenthal fail-safe number (Nfs), which provides the number of missing effect sizes showing no significant effect that would be needed to nullify the grand mean effect size. If $Nfs > 5 \times n + 10$, with n being the number of effect sizes, then the results can be considered robust despite the possibility of publication bias (79; *SI Appendix, Table S2*).

Data analysis and calculations. The publication ratio was calculated as the quotient between the number of studies published in the above-mentioned subject areas that tested the effect of environmental fluctuations in a specific year and the mean total number of studies published in Scopus and WoS for the same subject area and year (*SI Appendix, Table S4*). An exponential regression model was fitted to address the relationship between the publication ratio over

time. Assumptions of exponential regression model were checked before analysis. Tukey's honest significance tests were used to test differences among groups and traits inside each single environmental driver tested and its interaction.

The percentage of positive, negative, and neutral effects as well as those of positive and negative synergistic and antagonistic and additive interactions was calculated as the quotient between the total number of records of a specific effect or interaction and the total number of records of effects or interactions, respectively. All data analyses were done using OpenMEE (80) and Rstudio v. 1.4.1717 (81).

Data Availability. Data have been deposited in INVESTIGO (University of Vigo institutional repository) ([10.5281/zenodo.6809820](https://doi.org/10.5281/zenodo.6809820)) (82).

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