

Community theory: Testing environmental stress models

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Abstract

Intensifying climate change and an increasing need for understanding its impacts on ecological communities places new emphasis on testing environmental stress models (ESMs). Using a prior literature search plus references from a more recent search, I evaluated empirical support for ESMs, focusing on whether consumer pressure on prey decreased (consumer stress model; CSM) or increased (prey stress model; PSM) with increasing environmental stress. Applying the criterion that testing ESMs requires conducting research at multiple sites along environmental stress gradients, the analysis found that CSMs were most frequent, with 'No Effect' and PSMs occurring at low but similar frequencies. This result contrasts to a prior survey in which 'No Effect' studies were most frequent, thus suggesting that consumers are generally more suppressed by stress than prey. Thus, increased climate change-induced environmental stress seems likely to reduce, not increase impacts of consumers on prey more often than the reverse

KEYWORDS

consumer stress models, consumer–resource interactions, environmental stress gradients, environmental stress models, herbivory, predation, prey stress models

INTRODUCTION

Climate change, arguably the most existential threat to humankind in history (IPCC, 2021; Myers, 2014; Singh et al., 2021), has elevated several ecological issues from being primarily of academic interest to topics of great societal importance. For example, stability of ecosystems, communities and populations is challenged as never before (Bernhardt & Leslie, 2013; Oliver et al., 2015), and the sustainability and persistence of the globe's biota is at stake. A primary factor undermining stability is increased environmental stress brought about by warming and other factors. Specifically, climate change has negatively altered organismal stress regimes, moving tolerances towards and often exceeding extremes of (e.g.) temperature, acidification, salinity and water availability with potentially drastic consequences travelling up levels of organisation, from individuals, to populations, food webs, communities and ecosystems (Bernhardt & Leslie, 2013). Earth's biota includes taxa varying in mobility, trophic status, size, whether primary or secondary producers and thermal physiology. All experience many types of perturbations, but biotic responses likely vary across taxonomic and functional categories. Thus, understanding effects of increasing environmental stress on organisms in different

categories, and their interactions is critical to understanding the future of humankind's life support system, and to adjusting policy and management practices to meet, and hopefully mitigate, challenges to this system.

THEORETICAL BACKGROUND: CONCEPTUAL MODELS IN ECOLOGY

In 1976, John Sutherland and I published the first of several papers addressing how community structure varied with environmental stress (Menge & Sutherland, 1976). Inspired by experiments in marine ecosystems, we proposed an alternative dynamic to Hairston et al. (1960). We suggested that in some systems, omnivory could generate inverse relationships between predation and competition in moving down the food web as opposed to the alternating control proposed by HSS (Figure S1). Among communities separated in space along a gradient of decreasing environmental stress, we hypothesised that importance of predation (competition) would increase (decrease) with increasing trophic level and food web complexity. Later (Menge & Sutherland, 1987) we added recruitment rate as a second environmental gradient. We

proposed that with increasing environmental stress, dominant structuring forces for the basal trophic level were predation, then competition, followed by direct mortality from disturbance or stress (Figure S2). We modelled increasing recruitment gradients as orthogonal to the environmental stress gradient and suggested competition's importance covaried positively with recruitment (Menge & Sutherland, 1987).

Empirical rocky intertidal examples were cited in Menge and Sutherland (1976) as consistent with their hypothesis (e.g. Connell, 1970; Dayton, 1971; Menge, 1972; Paine, 1974). A later review of freshwater, terrestrial and other marine literature showed that as predicted, predation effect frequency decreased with increasing trophic level (Sih et al., 1985). Additionally, field experiments (Lubchenco, 1986) indicated that frequency of control of algal communities by herbivory, competition and disturbance along a wave stress gradient was consistent with the basal-level model of Menge and Sutherland (1987). Evidence from Gaines and Roughgarden (1985) suggested that the importance of competition increased with increasing prey recruitment.

At intermediate trophic levels, predictions of the relative importance of interactions and disturbance were like those for basal species, except for a key assumption: consumers were relatively more susceptible to stress than were sessile (basal) species (Figure S2). This assumption was based on: (1) mobility was likely more energetically expensive than was a sessile habitus, but (2) mobility enabled consumers to retreat to lower-stress microhabitats when stress was severe while sessile species had to adapt to a wider range of stresses or die and (3) hypothesised energy budget differences and resulting stress-related adaptations suggested that mobile species were more susceptible to severe environmental stress than sessile species. Because they could move to less stressful microhabitats, predators could still co-occur with prey, but stress avoidance would reduce foraging time, thereby reducing consumer pressure with increasing environmental stress. Thus, at the intermediate trophic level, predation importance was reduced compared to the basal level, competition importance was shifted towards lower stress and direct stress mortality was more important at lower environmental stress (Figure S2). Finally, by definition, at the top trophic level, predation was unimportant, and structure was driven by competition at lower, and by direct mortality or suppression of foraging at higher environmental stress (Figure S2).

Menge and Olson (1990) proposed the prey stress model (PSM) alternative to these ideas, where consumers could be less, not more susceptible to environmental stress than are prey communities. While environmental stress should still suppress consumer pressure, because of relatively greater sensitivity of prey than consumers (e.g. reduced anti-predator defences in higher, relative to lower, environmental stress habitats), negative consumer effects may be greater with high than with low

environmental stress. Note that consumer effects on prey were negative in both CSM and PSM scenarios; possible relative importance of positive interactions were later added to ESMs by Bruno et al. (2003). Examples of PSMs were few then, but in one experiment bittercress was more susceptible to insect herbivory under high stress than under low stress (Louda & Collinge, 1992). Whether this population effect was community-wide, however, was not addressed.

Prior assessment

In a literature review assessing the sensitivity of consumer–resource interactions to environmental stress, Silliman and He (2018) found that the majority of studies (111 of 7109 screened; see their supplementary information for details) were ‘additive’, that is, consumer–resource interactions did not vary with different stress levels. Further, proportions of ‘antagonistic’ (i.e. dampened consumer control or CSM) and ‘synergistic’ (i.e. intensified consumer control or PSM) studies were similar.

Here I re-examine this analysis. My primary reason for this reassessment was surprise at the high frequencies of ‘additive’ (‘No Effect’) results. This conclusion was inconsistent with my qualitative impression that literature frequencies of significant environmental stress effects on consumer control, whether CSM or PSM, was higher. However, their literature survey included many terrestrial examples, and my impression perhaps was biased by my less extensive familiarity with terrestrial than aquatic literature. Thus, I collected the papers cited in their report and added additional papers from a search for publications that addressed ‘environmental stress models’.

METHODS

Protocol for testing environmental stress models.

Menge and Sutherland (1987) and Menge and Olson (1990) were expressly proposed as landscape or meta-community models and briefly laid out protocols enabling tests of ESMs. Here I make those criteria more explicit. Thus, criteria for evaluating the consistency of literature studies with ESMs include:

1. CSM/PSM models apply at community, assemblage or subweb levels, not population levels. That is, like Hairston et al. (1960), they assume that species within a trophic level respond similarly to environmental stress and interactions, and that measures of how abiotic and biotic factors affect community structure are ‘relative’, that is, that proportionally, impacts are zero-sum, totalling to 1.0.
2. The models consider only negative consumer–prey interactions. The difference between CSMs and PSMs is

that negative effects are either weaker or stronger with high environmental stress respectively.

3. Experiments must be done at least at two (ideally more) different points along environmental stress gradients. Environmental stress gradients can occur across short (e.g. metres as in high to low intertidal) or long distances (e.g. 10–100s of km as from xeric to mesic terrestrial habitats). Here, ‘sites’ indicate specific locations along most of the range of an environmental stress gradient. For example, high and low intertidal locations can each be a site because they occur at the end points of a steep vertical thermal/desiccation environmental stress gradient. In streams, pools and rapids are separate sites because they have different flow velocities. On land, alpine and lowland areas are separate sites because thermal conditions differ.
4. As implied in (3), models focus on spatial, not temporal differences. Temporal responses to perturbations test community resilience and thus relate to stability, while ESMs were proposed to reflect temporally averaged conditions that characterise sites as differing in overall environmental stress. Thus, while wave-exposed intertidal sites might have calmer periods, on average they will have much stronger wave forces than more wave-protected sites. However, certain temporal studies may test ESMs, for example, in cases where studies were done over several years/seasons differing in environmental stress levels.
5. Ideally, focal environmental stress gradients capture most of the full range of conditions across which the system occurs. This is most easily done in habitats with steep environmental stress gradients, such as intertidal height, wave-beaten shores versus sheltered coves or bays, salinity or sedimentation estuarine gradients, streams differing in flow rate and periodicity of flooding events, frequency of ice scour or fires, and pH stress in oceans or lakes, to name a few. Terrestrial environments with small changes in environmental conditions across large distances are far more challenging because of the great distances involved, but mountainous temperature and moisture environmental stress gradients, while still logistically difficult, are more feasible.
6. Studies should provide evidence that environmental stress affects both consumers and prey. Lack of such information makes assessment of consistency with an ESM subjective.
7. Studies should examine community-level responses to environmental stress, including at least demonstrably strongly interacting consumers and the most abundant prey (*sensu* Power et al., 1996).
8. Studies should be conducted in the field. This criterion excludes strictly laboratory-based experiments, whose relevance to field conditions is problematic. Similarly, mesocosm experiments (e.g. flow channels, outdoor tanks or seawater tables) qualify only if they incorporate a wide range of environmental stress (e.g. fast or slow flow rates, hot or cold, high or low salinity, wet or dry).

Assembling the datasets

The 111 papers assessed by Silliman and He (2018) included 174 tests which they felt enabled testing if studies were consistent with either antagonistic/CSM, synergistic/PSM models or additive/no effect (the effect of consumers on prey along environmental stress gradients was statistically insignificant or neutral). Papers were sorted by habitat (marine, freshwater and terrestrial), consumer–resource interaction type (predation and herbivory), plant prey type (algae, herbaceous and woody), predator thermal strategy (ectothermic or endothermic), performance measure (biomass, density and survival), stress factor (fire, thermal and desiccation, drought, salinity and others) and stress type (temporal, spatial and experimental).

In reassessing the Silliman and He (2018) dataset, I read all abstracts, and in most papers, methods, relevant results and discussion, and in some cases, the whole paper. To these, I added papers from Google Scholar and Web of Science searches for papers citing ESMs. These searches found earlier papers not included in Silliman and He (2018) and scanned papers published since 2015 when Silliman and He (2018) ended their search. I summarised each paper, listing each by its environmental stress gradient, the specific environmental stress examined, the biotic factor (predation or herbivory), the habitat, whether the study was in the field, mesocosm or laboratory, trophic level number, specific consumers, specific resource (food or prey) and a summary of results. I then determined if the paper tested if all interactors were affected by environmental stress, if environmental stress affected consumer or prey abundance, and assessed if results were CSM, PSM, or No Effect. Spreadsheets with this information, that is, the ‘Included’ versus the ‘Excluded’ sets are in [Tables S1](#) and [S2](#) respectively. The original citations used by Silliman and He (2018) are in Document [S1](#) and the ones I added are in [Table S1](#) with Silliman and He (2018) references in the Included dataset.

Data analysis followed the same protocol as in Silliman and He (2018), that is, assessment of significance of consumer and stress effects was based on analyses in each paper. I used the same categories as Silliman and He (2018) in data summaries and presented results as the percentage of each result in each category. I used the SigmaStat module of Sigmaplot (v. 13.0) to conduct χ^2 tests to determine if frequencies in each category differed from the null case of equality ([Table S3](#)). Expected numbers were rounded to the nearest whole number to meet Chi-square assumptions.

RESULTS: LITERATURE EVALUATION OF ESMs

In all, I used 87 papers with 113 tests done at two or more levels of environmental stress including 52 papers from

Silliman and He (2018) and 35 additional papers from the literature (Table S1). Fifty-nine papers and 85 tests from Silliman & He (2018)'s survey were excluded (Table S2). The primary reason for exclusion was that studies were conducted once at a single site instead of at two or more sites along environmental stress gradients or in multiple years/seasons differing in environmental stress (Criterion 3 above). For example, many cases had fire or drought as the environmental stress, but rather than have a fire or drought gradient (i.e. sites with frequent vs. infrequent disturbance), the fire or drought occurred once at one location, after which succession/recovery was followed in presence/absence of consumers, usually in comparison to nearby control sites having the same environmental conditions. While single-site experiments manipulating consumers and environmental stress are a perfectly reasonable approach to understanding stress $\times$ consumer–resource interactions, such experiments commonly do not reflect the full spatial range of environmental stress across which the system occurs. For example, based on observations of limpet mortality during unusually warm conditions in 2004, in 2005 Morelissen and Harley (2007) manipulated temperature in a limpet-alga system using shading treatments and found no effect of temperature on herbivory. This result was attributed to persistent fog in 2005, so unshaded treatments were not exposed to severe heat as was observed in 2004. In a stream mesocosm study, Ludlam and Magoulick (2010) found no effect of disturbance stress (simulated flood spate) on primary production, leaf decomposition, or chironomid abundance, a result attributed to a limited range of disturbance frequency and intensity.

Another issue is that ideally environmental stress should be a 'press' (Bender et al., 1984). That is, environmental stress should be continuous or, if variable (e.g. 'pulse'), average to differing intensities. Single environmental stress events (e.g. a fire) therefore cannot reflect an environmental stress gradient. For example, fire was a single pulse disturbance in most surveyed cases of fire (31 of 33). Examples of environmental stresses that vary in frequency are wave-force severity varying through time but differing in average severity in space, periodic desiccation or drought events that are on average more severe at some locations and less at others, or storm-driven spates or flood events in some rivers and streams but not others. Examples of continuous stresses are UV radiation, acidification in lakes or hypoxia with ocean depth.

Types of abiotic stress in these studies were diverse (Figure 1). Desiccation/drought and temperature were the most common gradients in Included studies, while fire was by far the most frequent abiotic stress in Excluded studies (Figure 1a). Rocky intertidal, forest/woodland, salt marsh and grasslands/fields were the most common habitats in Included studies and were joined by lab/mesocosm studies in Excluded studies (Figure 1b). Eight types of herbivores were common in the Included set while five were most frequent in Excluded studies, led by herbivorous insects and

livestock (Figure 1c). For predators, marine species were most common in Included studies, while fish and 'other' categories were most frequent in Excluded experiments (Figure 1d). Relatively few categories of plant resources occurred in both Included and Excluded sets, with algae, herbaceous vegetation, marsh grass and shrubs most common (Figure 1e). Finally, mobile prey were most common in the Excluded studies while Included studies had both sessile and mobile prey, with mussels, barnacles and herbivorous insects most frequent (Figure 1f).

Multi-site studies along an environmental stress gradient

I used mostly the same categories as in Silliman and He (2018) for both Included and Excluded studies. Exceptions were that I calculated proportions of Consumer rather than Predator Thermal Strategy to include herbivores and combined desiccation with drought rather than thermal stress since desiccation can occur independently of thermal stress. The Included dataset (Figure 2, Table S3) indicates that the CSM (antagonistic) model was overall most frequent with PSM (synergistic) and No Effects of stress (additive) about equally but less frequent (Figure 2, upper left bar; $\chi^2 = 17.2$, $p < 0.001$). By ecosystem, No Effect was least frequent in marine and most frequent in terrestrial systems. By interaction types, No Effect was least frequent in predator–prey interactions, and similar in frequency to PSM studies in herbivore–plant interactions. CSM was more frequent than PSM models in plant prey types, and PSM was more frequent than No Effect only for woody plant resources. Similar patterns occurred for consumer thermal strategy (ecto- vs. endothermic), performance measure, and environmental stress factor and source. That is, contrary to the analyses of Silliman and He (2018), No Effect results were usually much less frequent than CSM, but often similar in frequency to PSM interpretations (Figure 2). Note that few (6) studies that did experiments along a fire gradient were available, and five of these were in the No Effect category. Low sample size also compromised χ^2 tests of freshwater, woody, salinity, endothermic, other performance measures, temporal and experimental categories (Table S3).

Single site studies

In analysis of Excluded studies, No Effect was by far the most frequent of the three possible outcomes (Figure 3, Tables S2, S3). For example, 86 of 88 cases were 'experimental', that is, manipulations of environmental stress and consumers were conducted at a single site, not along an environmental stress gradient. All 'single site' lab and mesocosm studies were also included in the 'experimental' category. As in the Included dataset, χ^2 analysis of several categories was limited by small sample size (Table S3).

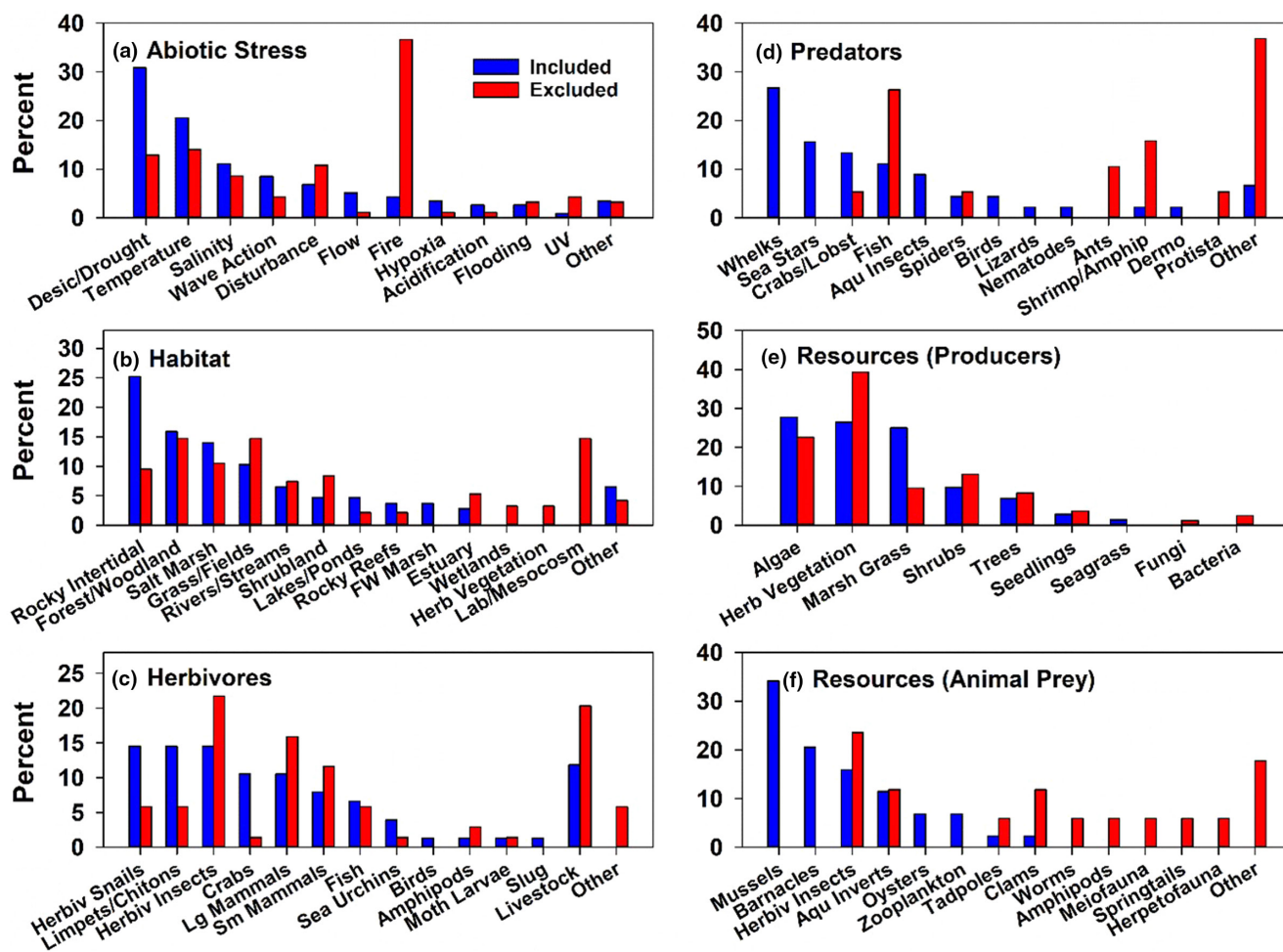


FIGURE 1 Per cent of categories of studies included in the analysis of Silliman & He, 2018 among (a) types of abiotic stress (n included = 117, n excluded = 93), (b) habitats (n = 107 and 95), (c) herbivores (n = 76 and 69), (d) predators (n = 45 and 19), (e) plant and related resources (n = 72 and 84) and (f) animal resources (n = 44 and 17) in the studies included (blue) and excluded (red) from the analyses.

I then queried the data on several issues: (1) Were both interactors affected by environmental stress (Figure 4a, Table S3)? In the Included dataset, most 'Yes' studies were CSMs while in the Excluded set each result occurred at similar frequencies in the 'No' category. In the Excluded dataset, CSM and 'No Effect' results occurred in similar frequencies in the 'Yes' category (but only 15 studies sorted into this group), while 'No Effect' was by far the most frequent category in the 'No' category.

(2) What was the effect of environmental stress on consumers? On resources (Figure 4b)? In both data sets for effects on consumer abundance, 'not tested' (NT in Figure 4; Table S4) was relatively frequent, about 40% of the total number. But of those tested CSM was most frequent in the Included set and 'No Effect' was most frequent in the Excluded set (Figure 4b). In contrast, for resources, CSM was most frequent while No Effect and PSM frequencies were similar in both datasets, but 'not tested' occurred in ~30% of the Included set and only ~10% in the Excluded set.

(3) What was the effect of consumers on prey with high and low environmental stress (Figure 4c, Table S4)?

Recall that CSMs predict that consumer effects will be weakly negative to nonexistent with high, and consistently negative with low environmental stress, while PSMs predict more strongly negative effects with high, and weakly negative or No Effect with low environmental stress. In the Included dataset, effect frequencies were more consistent with the consumer stress model, that is, CSM and No Effect were similar in frequency with high environmental stress but CSMs were ~4x more frequent than No Effect with low environmental stress. In the Excluded dataset, frequencies of CSMs and No Effects were similar with high and low environmental stress. In all cases, however, the frequency of PSMs was low (Figure 4c).

DISCUSSION

In the Included survey, more strongly negative effects in less stressful locations (CSMs) were most frequent while many fewer cases of No Effect and PSMs were tabulated (Figure 2, Table S1). Notable patterns were: (1) frequencies of No Effect of consumers increased from marine to

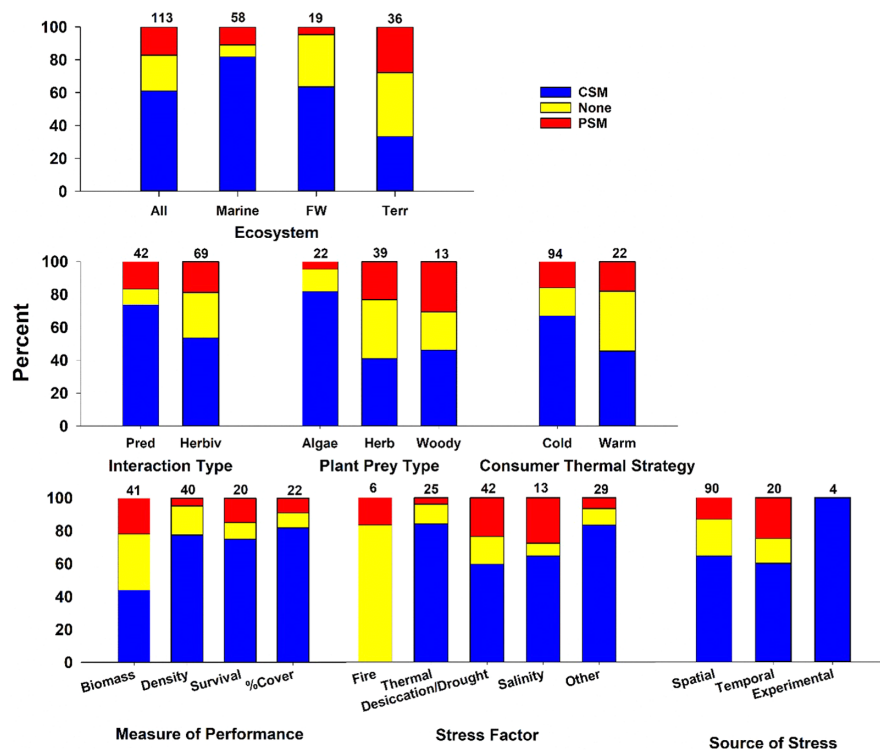


FIGURE 2 Included studies: Per cent of CSM ('antagonistic'), PSM ('synergistic') and no effect (None or 'additive') tests arranged by ecosystem, interaction type, plant prey type, consumer thermal strategy, measure of performance, stress factor and source of stress. The number of studies in each category is shown above each bar. Numbers do not always total to the same number because some studies fell into more than one category (e.g. Spatial and Temporal sources of stress) or did not fall into any category (e.g. the modelling study of Vasseur & McCann, 2005).

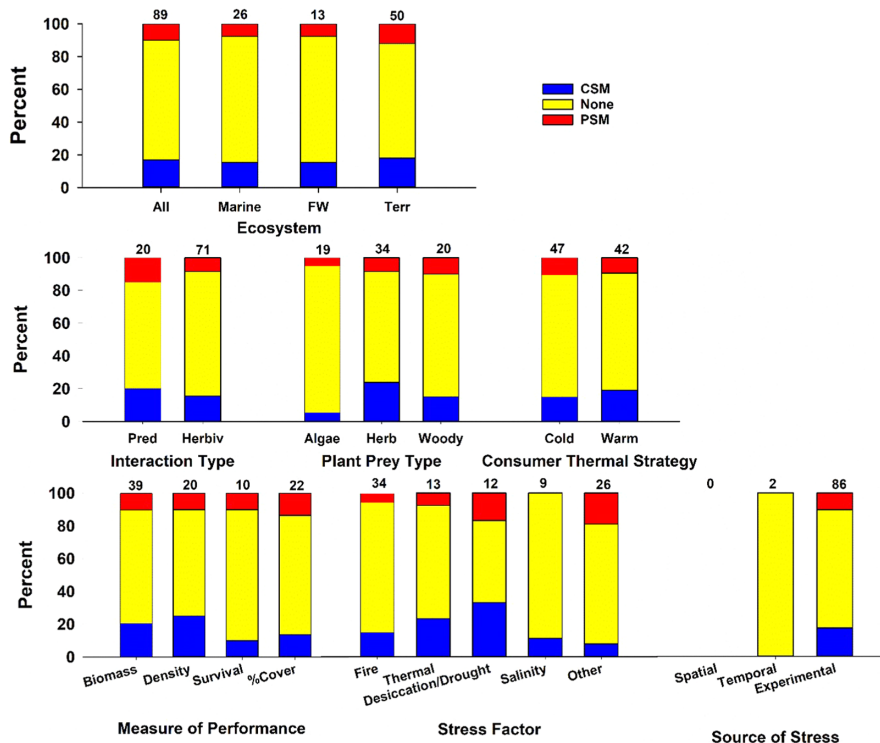


FIGURE 3 Excluded studies: Percent of CSM ('antagonistic'), PSM ('synergistic') and No Effect ('additive') tests arranged by ecosystem, interaction type, plant prey type, consumer thermal strategy, measure of performance, stress factor and source of stress.

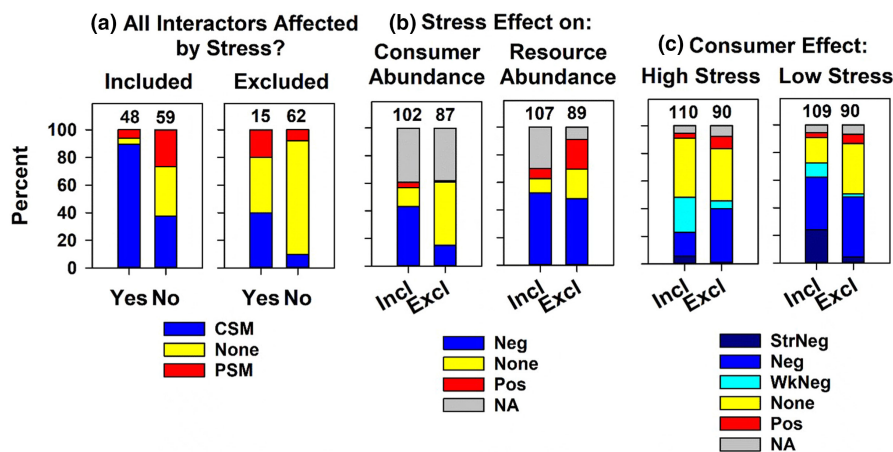


FIGURE 4 Frequencies of CSM, 'No Effect' and PSM results that (a) did ('Yes') or did not ('No') find that both consumer and resource were affected by stress in included and excluded data sets, (b) found negative, positive or no effects of stress on consumer and resources in included versus excluded datasets and (c) found strongly, weakly or moderately (Neg) negative effects, positive, or no effects of consumers on prey under high or low stress in each dataset. In included data in (a), five cases were categorised as 'not tested' while in the excluded set 22 cases were so categorised. NA (not tested) frequencies are shown in (b) and (c).

freshwater to terrestrial studies, from predator–prey to herbivore–plant studies, and from ectothermic to endothermic species. (2) The frequency of CSMs among prey plant types decreased from algal to herbaceous to woody plants, which is logical because woody plants are typically more resistant to environmental stress. (3) Among stress factors, fire was the only category with no CSMs. In this case, however, the dominance of No Effect followed by PSMs likely were artefacts of small sample size ($n=6$). (4) Except for biomass, which had relatively high frequencies of No Effect, no obvious trends were evident for measures of performance (density, survival and per cent cover) in the Included dataset. (5) For source of environmental stress, few 'experimental' studies (i.e. lab, mesocosms and greenhouse) qualified for the Included set ($n=4$) and all were categorised as CSM. The excluded non-field examples consisted of all three possible ESM interpretations ($n=10$ CSM, 3 PSM, 22 No Effect cases), so their removal from the Included dataset should have minimally biased the analysis regarding frequency of CSMs and PSMs.

Hence, as far as such surveys go, CSMs appear more common in nature than PSMs especially in aquatic systems. In terrestrial systems, CSMs, No Effect, and PSMs were of similar frequency ($\chi^2=0.85$, Table S3), a difference that may be in part driven by the relatively low frequency of CSM effects on herbaceous and woody plants (Figure 2, Table S3). These results contrast with those of Silliman and He (2018), who found that the No Effect category was most frequent (in the Excluded dataset, $n=64$ of 89). The basis for this difference was that many in the Silliman and He (2018) dataset were single-site studies rather than studies with two or more sites arrayed along an environmental stress gradient. As some have noted in their specific studies (e.g. Smit et al., 2009), the contrasts of environmental stress tested in single site experiments often did not reflect the full range of environmental stress, but simply had different levels of (e.g.) temperature, desiccation or drought

(e.g. were watered more or less), salinity (salt added or not) or flow rates (freshwater mesocosms with high flow and low flow channels). In other words, some studies were explicit in incorporating only a small portion of the potential range of environmental stress.

To clarify this point, I redrew Menge and Sutherland (1987) model predictions for the relative importance of consumer–prey, competition and disturbance/stress effects on basal species communities along a gradient of environmental stress under either high (Figure 5a,c) or low recruitment (Figure 5b,d). In the top row, the arrow denotes the environmental stress level of a potential single site experiment and a likely narrow range of stress included in the experiment (pink shade). This range includes high consumer pressure levels (green line intersection with left edge of pink band) and low consumer pressure levels (green intersection with right edge). If recruitment is low (Figure 5b), these relative effects might differ more greatly and may thus help explain the cases of CSM or PSM detected in the Excluded set (but unfortunately, recruitment was rarely quantified in these datasets so its effect could not be tested). In contrast, conducting experiments at two or more sites along a wider environmental stress gradient should encompass more strongly different magnitudes of interactions and disturbance, and better represent how a system responds to more extreme levels of environmental stress (Figure 5c,d).

To explore possible reasons why high frequencies of No Effect might occur in single site studies, I envisioned CSM and PSM scenarios with single- and multi-site designs (Figure 6). Assuming that the testable range of abiotic and biotic conditions in a single-site study is relatively narrow, and that experiment results provide typical levels of temporal variability (as suggested by the box and whisker diagrams), CSM results seem more likely to detect consumer effects ($-C$ vs. $+C$ in Figure 6a) than stress effects ($-S$ vs. $+S$ in Figure 6a). This is because prey are assumed to

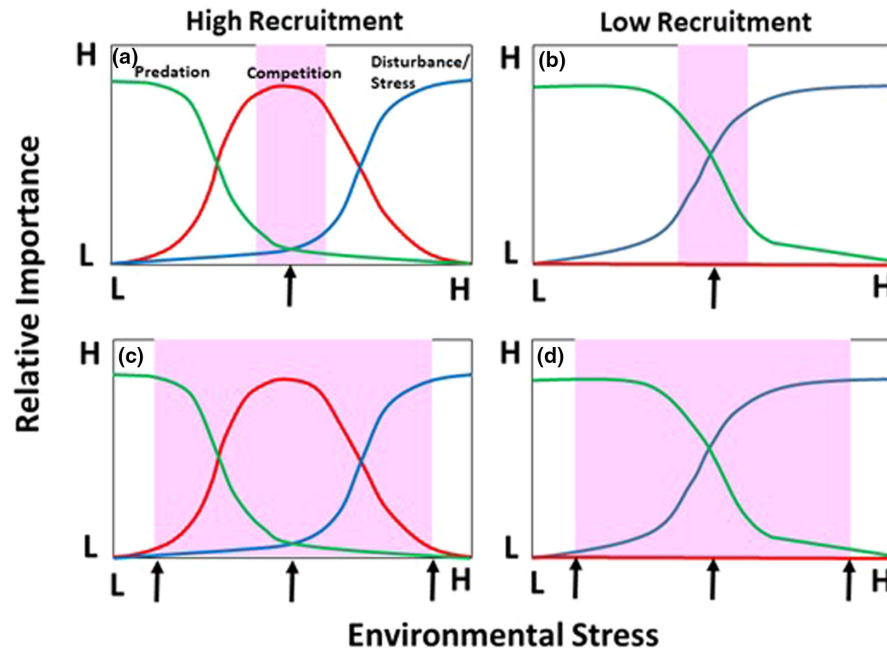


FIGURE 5 Menge-Sutherland (1987) model predictions for relative importance of consumer, competition, and disturbance/stress effects in structuring communities under conditions of high recruitment (a, c) and low recruitment (b, d). The pink shading in a and b illustrates how single-site experimental manipulations (e.g. at the site represented by the arrow) can fail to represent a broad enough spatial range of environmental stress to provide clear results—that is, the possible reason why so many studies in the S&H2018 survey were categorised as ‘no effect’ of consumers on prey. In this case, manipulative generation of high and low consumer pressure and stress at one site are likely to span a small fraction of the full range of stress. In contrast, the pink shading in c and d spans a much higher fraction of the full spatial range of stress and selecting two or more sites (arrows) in this range allows a more rigorous test of ESMs.

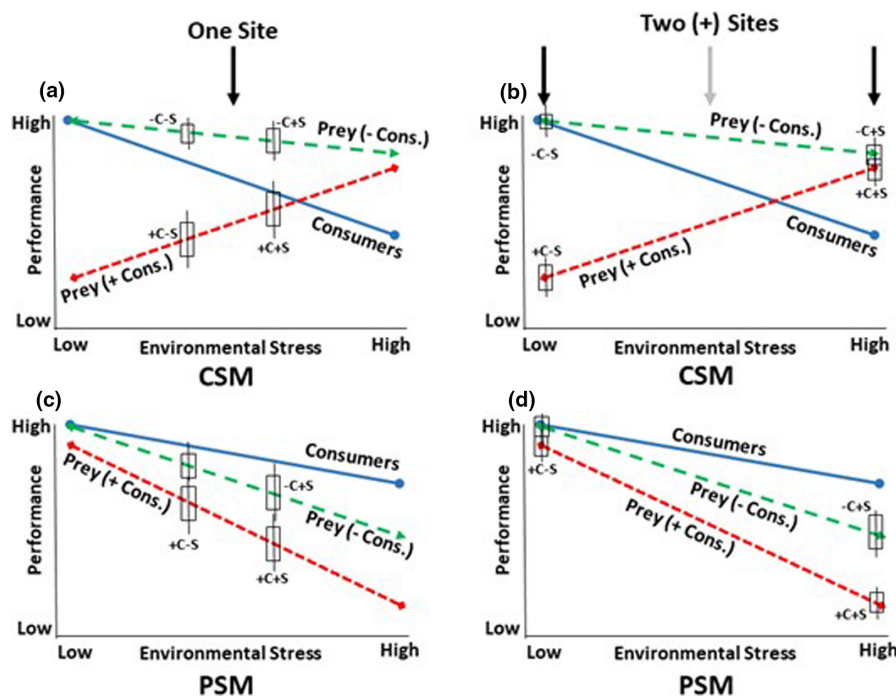


FIGURE 6 Consumer Stress Models (CSM, a and b) and Prey Stress Models (PSM, c and d) with contrasting designs and suggested results (box and whisker plots) used to test each. Note that the lines between (a) and (c) are identical to those between b and d, respectively, and are meant to represent reality, with boxplots representing different levels of stress achievable with one vs. two or more sites. The diagram envisions how results might occur if a single site (denoted by the arrow in a and c) is used or two or more sites (denoted by arrows in b and d) are used, with treatments of all combinations of high and low consumer pressure (+ or - C) and stress (+ or - S). The grey arrow suggests a potential intermediate site in b and d and implies that multiple sites could be incorporated into a more rigorous test.

be severely reduced by consumers with low environmental stress and minimally reduced at high environmental stress while direct environmental stress effects vary more gradually. With two sites representing more divergent environmental stress levels (Figure 6b), stress effects should be more readily detected. The difficulty of detecting consumer and environmental stress effects with single site studies is likely even greater for PSMs (Figure 6c), where among-replicate variability may make detection of either consumer or environmental stress effects difficult. Again, testing consumer and environmental stress effects at more extreme levels of both as in Figure 6d seems more likely to detect effects.

These problems point out difficulties in using literature surveys to test ESMs based on studies that mostly were not so designed. ESMs are complex, and besides the need for different levels of environmental stress and consumer pressure, tests need information on propagule input (recruitment, colonisation and immigration) and direct environmental stress effects on communities, not just individual species. A protocol for testing ESMs was laid out in the Discussion of Menge and Sutherland (1987) and of testing CSMs and PSMs specifically was discussed in Menge and Olson (1990). As noted here, few studies explicitly designed to test these ESMs have been published. I suggest that as global environments become ever more stressful, researchers should consider conducting appropriately designed studies to test effects in as many ecosystems as possible, and soon. For instance, evidence from insect assemblages indicates that the sensitivity of functional groups increases with increasing trophic status, with potentially destabilising results (Voigt et al., 2003). Model results echo these possibilities, suggesting the potential generality of such an effect (Vasseur & McCann, 2005).

The gold standard for conducting literature surveys in contemporary ecology is to employ meta-analysis (Cadotte et al., 2012; Gurevitch et al., 2018). Why not use meta-analysis to evaluate ESMs more quantitatively? Briefly, most literature surveyed did not include information needed to apply this tool, again, because most papers were not aimed at testing ESMs. For example, categorising a site into where along environmental stress and recruitment gradients it might lie requires quantification of these gradients or at least a qualitative assessment of differences among sites and how they relate to extremes for that system. In many cases, the assembled studies provided data on stressor means and variation, sometimes in a time series, in the region under study, but rarely site-specifically. More detailed studies also offered quantification of the stressor by site, but rarely was this information placed within the wider context of the total environmental stress gradient. Recruitment information was even sparser. Twenty-nine studies across both Included and Excluded data sets either showed recruitment information, mentioned that it was high or low, or allowed inferences of its relative magnitude, but this information was infrequently related to the metrics in experimental treatments. An indirect way of inferring if recruitment was high or low

would be to determine if competition was strong or weak, as modelled in Menge and Sutherland (1987). With high recruitment, competition in the absence of consumers should be high, and vice versa. In the assembled datasets, however, competition was almost never tested (see Tyler, 1995 for an exception) although in some cases, other studies within the same system did test competition (e.g. Menge, 1976, 1995). Inverse relationships between species sharing space, light or some similarly depletable resource can suggest competition, but as is well-known, such correlations do not provide satisfactory evidence of the existence of competition (Barner et al., 2018; Connell, 1980, 1983; Freilich et al., 2018). I urge future researchers to test ESMs, that is, use multiple sites with contrasting and quantified environmental conditions and prey influx rates, and determine the relative importance of consumers, competition, and direct effects of environmental stress on basal species. Even better would be to conduct tests of the actual responses of key consumers and prey to different levels of environmental stress to have direct quantification of the performance of each component to variation in environmental stress. Still another advance would be to expand ESMs to include effects of productivity, and to conduct research allowing tests of the effects of facilitation in the context of ESMs (e.g. Bruno et al. 2003).

Caveats

The CSM-PSM scenario was envisioned for a consumer–sessile prey interaction, for example, predator–basal species or herbivore–resource, and based on the idea of differential mobility at each level driving the direction of the interaction (Menge & Olson, 1990). What if the interaction was predator–herbivore, that is, with two mobile trophic groups? In this case, both groups would be able to avoid stressful conditions and thus, this similarity could underlie the ‘No Effect’ examples. Both Included and Excluded datasets included these three general types of consumer–prey interaction: predator–herbivore (17 in Included and 12 in Excluded), herbivore–resource (73 in Included and 75 in Excluded) and predator–basal (25 in Included and 2 in Excluded). I examined the possibility of trophic bias in the No Effect examples in Included versus Excluded datasets by counting the number of predator–herbivore No Effect examples in both the Included and Excluded data sets and found that the proportion of predator–herbivore cases was almost identical in each set (3 of 23 = 13% in Included set; 8 of 64 = 12.5% in Excluded set). Though sample sizes are small, it appears that this potential bias did not explain the high number of No Effect results.

CONCLUSIONS

The differences between this and the earlier survey seem attributable to whether the datasets included single-site studies. I by no means intend to demean such research,

much of which is excellent but typically has different goals than testing ESMs. For the reasons discussed here, I argue that, unless single-site studies can be demonstrated to incorporate environmental stress extremes that reflect wider environmental stress gradients and that environmental stress affects both prey and consumer, such studies should not be used in tests of ESMs. My analysis suggests that to the extent that such surveys provide generality, CSMs appear to be the most frequent outcome of consumer-prey interactions across all ecosystems. PSMs seem far less frequent, and these results together suggest that prey generally are more resistant to stress than are their consumers. What remains unclear is whether particular categories of consumer and prey tend to sort more into one type of interaction than another, or if certain types of stress favour one class of models over the other. The implications of this analysis suggest that with intensifying climate change, consumer effects on prey should diminish, not increase.

AUTHOR CONTRIBUTION

BAM devised the study, did the surveys, analyzed the data, and wrote the manuscript.

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PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14240>.

DATA AVAILABILITY STATEMENT

No new data were used in this paper. Literature surveys are shown in [Tables S1](#) and [S2](#), and are also in the Figshare data repository at DOI: 10.6084/m9.figshare.22677610.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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