

FORUM

Why should we constrain stress and limitation? Why conceptual terms deserve broad definitions

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Abstract

In his recent essay, Ch. Körner (2003) suggested that we need to clarify and narrow the meaning of limitation and stress. Current definitions and usage of these terms are not in any great need of revision. Limiting the use of 'stress' to only extreme situations is inappropriate because sometimes stress is indeed weak. What is needed is to use the terms within a comparative framework, a framework based on comparisons along gradients and among taxa. Recent studies on the factors controlling diversity have used such a comparative framework, and have increased our understanding of the relative roles of various types of stress. Redefining and narrowing general terms that relate to common processes would limit our ability to make comparisons and generalizations, and this should be avoided.

Keywords: Biomass; Comparative framework; Ecological understanding; Epistemology; Gradient; Production.

"Grasp the subject, the words will follow" – Cato the elder

"Broadly speaking, the short words are the best, and the old words best of all" – Winston Churchill

"All definitions are human devices, not parts of nature independent of human activity" – Allen & Hoekstra (1992)

In his recent essay, Ch. Körner (2003) attempted to clarify the meaning of limitation and stress. While clarification is an important and laudable goal, I found his essay to be neither clarifying nor particularly enlightening. It is with some hesitation that I state this, given our dire need to be clear and precise when dealing with the inherently slippery subject of ecological concepts and our continued need for open-minded dialogue. I certainly agree with Körner's point that we often use terms like limitation and stress with reckless sloppiness, but I do not agree with his remedy.

I have several goals in writing this essay. First, I aim to dispel the notion that there is any great need to revise,

and indeed narrow the usage of stress and limitation. I wish to succinctly explore the conceptual issues at stake when we go down the path of increasingly narrow definitions of terms that have enjoyed a certain generality. Third, I want to avoid *ad hominem* attacks, and while I will address some of his points, I also want to honor the courage and honesty of his goal of pushing our science forward by questioning dogma.

A central issue in Körner's essay is the definition of stress. I find Grime's (1979, 2001) definition entirely satisfactory. It is simple and universal. Stress is something that reduces the rate of biomass production. Therefore, both resource limitation and non-optimal conditions are forms of stress. Körner stated that deviations from optimality are the norm – and therefore we should expect nearly all individuals of all species to be under some kind of stress at nearly all times. Körner then stated that if this is the case, which of course is absolutely reasonable, then the notion of stress is useless because of its ubiquity. He then suggested that we should limit our use of the term stress to situations where stress is severe.

While I concur that deviations from optimum conditions are indeed the norm, to me this simply means that some amount is stress common. Stress exists along a continuum. Minor stress is probably unimportant to species distributions and to their relative abundances, as most species are adapted to survive and reproduce over some range of resource levels and conditions. I concur with Körner that stress is really most important when it is extreme enough to limit species presence in a community, or when it causes reversals in rank abundance. But of course that does not mean stress does not exist when it is small, so we cannot restrict the use of stress to extreme situations. This is like saying art is not art unless it is good art.

I would like to suggest that we translate Körner's point into questions that put stress and limitation into a comparative context. Under what circumstances does

nutrient stress limit, for example the distribution of *Lupinus perennis* or species richness or the presence of legumes? I think translating Körner's criticism into questions about the importance of stress and limitation might provide a better avenue toward progress than simply revising terminology. This is because the importance of stress and limitation lie in their comparative context, in terms of variation along stress gradients, and in terms of the biota in question.

Körner suggests that understanding limitation and adaptations to stress often involve the misconception that stress and limitation are negative, when this is not necessarily true, because if the stress were removed, the species in question might be replaced by competitively superior species. In other words, stress-adapted species are dependent on stress for their existence. I agree that this is a subtlety lost on some, but it is not a cause for narrowing our definitions of stress and limitation. I suggest that the solution to this misconception lies in our need to pay more attention to niche concepts and the role of interactions. There are certainly many clear cases where the limits of species distributions are caused by limitation of the fundamental niche; e.g. Ezcurra et al. (1991) showed that *Larrea* species have contrasting leaf orientations and morphologies that are adaptations to specific habitats, and consider other examples in Wisheu (1998), and there are also cases where the limitation is brought about by interactions – limitation of the realized niche (e.g. reduction of realized niche via competitive exclusion by a superior species, e.g. competitive displacement of one *Typha* species to greater water depths by another (Grace & Wetzel 1981), increased growth by understory species in treefall gaps (Denslow et al. 1990).

Körner argues that limitation loses its meaning if one is dealing with a natural community, such as tundra, which is dependent on stress for its continued existence. However, experimental warming increased production in tundra vegetation, but it did not increase competition intensity (Hobbie et al. 1999). Therefore, alleviating some of the temperature stress simply increased production, but it did not result in a collapse of the community. We could certainly expect that with enough warming, tundra vegetation would be replaced, as Körner suggested. Alleviating the stress of nutrient limitation in tundra caused it to be replaced by competitively superior vegetation (Shaver et al. 2001), as would the stress-tolerant grasses and sedges of sandy oak barrens, if fertilized and watered. So we need to recognize that while stress-tolerators are often dependent on stress to keep competitively superior species out (as Körner also noted), the very same stress tolerators will usually respond positively to the reduction of said stress. For example, shade tolerant tropical shrubs grow faster when light limitation is reduced (Denslow et al. 1990). Stress

still reduces biomass production in these situations.

It has been suggested that Körner was trying to reduce the negative connotation of stress because stress is actually good for the “biodiversity-oriented dimensions” at the community level. There is ample evidence that when the size of the sampling unit is large (i.e. at large grain sizes), species richness tends to increase with production, that is, biodiversity is highest at low stress (e.g. Currie & Paquin 1987; Hawkins et al. 2003). At smaller grain sizes where one is dealing with the number of coexisting species, species richness is often maximal at intermediate amounts of production and stress, but this is by no means a universal pattern (e.g. Mittlebach et al. 2001). There is also ample evidence that removing the stress of low nutrient availability usually brings about a reduction in diversity (e.g. Shaver et al. 2001). Recent multivariate studies have explicitly addressed the relative roles of soil stress, shade stress, and disturbance on species richness (e.g. Grace & Pugsek 1997; Weiher 2003), with the aim of comparing the relative contributions of multiple aspects of stress. It is this kind of comparative framework that leads to greater understanding.

Perhaps Körner is right in suggesting limitation and stress are muddled concepts in need of revision. Perhaps a large number of practicing ecologists simply do not get the subtle nuances associated with their use. And perhaps even more ecologists have trouble adequately qualifying their use because of a lack of understanding that the importance of these factors is dependent on context and point of view. Even if these things were true, which I doubt, the solution is not to narrowly redefine limitation and stress, but to enlighten our colleagues about the differences between them and to focus our attention on comparisons.

I was interested in writing this essay in order to address the question of what motivates scientists to have a burning desire to revise and narrow terminology. My interest comes from my own brush with narrow versus broad definitions when dealing with the idea of assembly rules. My work on assembly rules (e.g. Weiher & Keddy 1999) has taken a broad view, that assembly rules are about the general constraints that limit community composition – whatever the mechanism. The view was not entirely radical, as others (e.g. Belyea & Lancaster 1999) have taken a similar view. Some ecologists however, took issue with this, and felt that assembly rules were really about patterns caused by competition, or at least interactions, which was what Diamond (1975) had in mind when he first used the term (although Diamond has since agreed that the idea was more general than competition, pers. comm.). My point is that some ecologists seem to be uncomfortable with the idea

that some terms or concepts can have a general and perhaps fuzzy meaning.

Now I do not begin to profess as to why this is the case, but I do think it is something that is worth bringing up. It is worth bringing up because we spend time, energy, and journal space debating things that seem to me are more about feelings and personal preferences than substance. I myself have been frustrated with the various definitions of niche, and have only recently learned to accept that niche may have multiple acceptable definitions. In retrospect, my own issue with niche definitions was mainly emotional. I felt one definition was clearly superior, so we should banish the others, and it bothered me that others were so confused.

I do not accept the notion that the clear thinkers among us are necessarily the ones pushing for terminology reform. Many of the ecologists I most admire seem quite at ease with general definitions which include a little complexity and wobble in their usage. It seems to me that general concepts like stress and limitation ought to apply to a wide range of situations.

Wittgenstein stated that the meaning of a word comes from its use in language; what we do with the word, not from some internal idea or feeling (Wittgenstein 1963). We need general conceptual terms like stress and limitation to apply over a wide range of situations because this is how we make generalizations and make comparisons among different habitats. If we restrict our conceptual terms to specific cases, we diminish our ability to make progress.

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