

FORUM

The value of stress and limitation in an imperfect world: A reply to Körner

Lortie, Christopher J.^{1*}; Brooker, Rob W.²; Kikvidze, Zaal³ & Callaway, Ragan M.⁴

¹NRES, University of Nevada Reno, Mail Stop 370, Reno NV 89557, USA;

²robb@ceh.ac.uk; ³zaal@science.s.chiba-u.ac.jp; ⁴callaway@selway.umt.edu;

*Corresponding author; Fax +17757844789; www.onepoint.ca; E-mail chris@onepoint.ca;

Abstract

A recent perspective paper offered by Körner essentially argued that 'limitation' and 'stress' are functionally useless terms for ecology except perhaps within limited contexts such as plant physiology or agriculture. We strongly disagree, and to this end argue that, although stress is not as precise as other concepts in ecology and is probably more difficult to apply to communities than to individuals, if ecologists want to communicate in a meaningful and interesting way about the distribution and abundance of species, we have to use multi-purpose terminology that allows us to scale from reductionistic, strictly quantifiable levels of analysis to more general conceptual levels. Here, we revisit the main arguments presented against these concepts and use three lines of counter-argument to support our conclusion that limitation and stress are necessary concepts for organizing and integrating general ecological inquiry. We discuss (1) the role of interactions between individuals in changing the limitation experienced by a species, (2) the importance of delineating whether stress is being applied to individuals or to the community, and (3) the evolutionary argument that fitness is never perfect since even adapted species are likely limited to some degree by the environment.

Keywords: Alpine vegetation; Community; Fitness; Gradient; Optimality; Physiology.

Preamble

Plant ecology has become a discipline that incorporates multiple scales and levels of organization simultaneously from individuals to populations to communities to ecosystems. This multiplicity is essential; however, it can sometimes also lead to multiple definitions and interpretations of a single term. In a recent perspective paper (derived in part from a previous book chapter), Körner argued that 'limitation' and 'stress' are vague terms that are often applied inappropriately to different phenomena (Körner 1998, 2003). We agree that these

terms refer to very broad concepts. We also believe that it is worthwhile to periodically revisit such common concepts and terms in the literature to clarify meaning. However, in this particular instance, not only do we feel that the perspective offered by Körner confuses the concepts more than clarifies, but we disagree with the conclusions reached because they do not correspond with fundamental ecological evidence.

Körner's perspective paper evaluated the utility of limitation and stress in a binary fashion, 'always or never', and our understanding of the main thrust of his argument is that these concepts are mostly useless for ecology, i.e. 'never', primarily because "neither high mountains nor deserts are stressful for those naturally living there, contrary to common belief (for instance Callaway 2002)" (Körner 2003). However, Körner does admit that limitation might be useful for physiology or agriculture. His case depends upon the assumption that plants living naturally do not experience limitation or stress because they have adapted to the place where they live. Körner accepts that it is possible for plants to be limited or stressed, but only when manipulated in some way that is outside of their natural, evolved historical experience – such as when ecologists experiment with them. Furthermore, Körner states that limitation loses its meaning for plants growing in assemblages because species are driven by their own habitat preferences independently of interactions. We disagree with these arguments. First, there is abundant empirical evidence that interactions between species can influence distribution, both positively or negatively, by modifying the abiotic limitations that an individual experiences. Second, there is no logical reason to believe that groups of species may be any more or less limited or stressed than the individuals that make up the groups, and it is essential to differentiate between the two levels. And third, the belief that plants have optimized their fitness to the

place they naturally occur implies that selection has been perfect and is no longer important for species growing there. We expand on these themes below, and explore how the stress concept can be conservatively applied to ecological systems.

The role of interactions

Körner defines limitation as “sub-maximal rates of processes, or yields of biomass, or certain biomass compounds.” This definition is straightforward and clear but then he rejects the possibility that limitation occurs for plants growing in their ‘natural’ habitats, i.e. along environmental gradients or in multi-species assemblages. Patterns forming the very foundation of ecology are at odds with this conclusion. Most organisms tend to be distributed in roughly bell-shaped curves along gradients of environmental variability. The shape of these curves suggests that species can exist in places where conditions are less than optimal for that species – e.g. at the ends of the curves. However, can interactions between species influence these distributions? In one of the first manipulative experiments to test the relative importance of interactions between species in determining distribution, Connell (1961) tested the importance of tolerance to physical factors, competition for space, and predation. He found that, at least in a marine intertidal system, the lower limit was mainly determined by competition while the upper limit was set by tolerance to extreme abiotic factors (Connell 1961). In a related recent experimental test of the general importance of plant-plant interactions along elevation gradients in the alpine, Callaway et al. (2002) removed neighbouring plants for 115 different target species in 11 different alpine environments worldwide. Similarly, they found that competition was common at the lower limits of the alpine meadow gradients while at the upper limits, i.e. higher elevations, facilitation or positive interactions were more frequent (Callaway et al. 2002). It thus seems reasonable to suggest that limitations can function throughout the distribution of a species and furthermore that the presence of interacting species can subsequently modify the relative importance of limitations at different points along a gradient.

A great deal of research has compared limitations of different species, i.e. their ability to tolerate lower resource levels and the consequences of this for competitive interactions (Tilman 1988) and more recently biodiversity (Tilman et al. 1997). Although adding a growth-limiting resource often changes the assemblage of species (Körner 2003) such that “watering the desert, fertilizing the tundra, – or removing shade – creates a completely new assemblage of species, with the former

‘limited’ ones being eliminated” this does not mean that plant species which live there are determined solely by limitation. A variety of processes determine what assemblage of species is found in a particular ‘limited’ environment including dispersal limitation, stochastic processes, disturbance, or possibly even interactions with other species from less ‘limited’ environments to name a few. Furthermore, there might be more than one different limiting resource, different limiting resources for different species, or the limiting resource is important only in the context of other species. Nonetheless, the consideration of differences in limitation for different species within a community, particularly in the context of interactions with other species, is certainly a crucial avenue of research as it is highly unlikely that all species within a community will respond in the same way to watering, warming, CO₂ deposition, or removal of shade – all of which humans are busy imposing at an alarming rate. Both direct and indirect interactions between species will also change depending on the new set of limitations generated by these global perturbations which will in turn influence the limitations themselves.

Limitation and stress at the community level

Körner argues that “a given assemblage of organisms is nature’s answer to a certain combination of growth limitations.” This statement is flawed because he fails to differentiate between processes occurring at the level of the individual and those at the community. Individuals have growth limitations, not communities. The process which leads to a new assemblage of species or the potential elimination of resource-limited individuals with change is not simply an increase in resources but an indirect consequence of this, i.e. competition from individuals with different limitations, which is likely a community-level process since populations of species commonly occur with other species. Körner seems unwilling to make this distinction throughout the paper. While subsequent statements like “alpine vegetation is not cold limited” (Körner 2003) are necessarily true by way of the definition for ‘alpine vegetation’, he is nonetheless mixing scales again and is referring to the community and not individuals within it. Individuals within ‘alpine vegetation’ can still be limited by the environment (and Körner realizes this but then argues at the community level). In fact in many environments, not just the more ‘extreme’ ones we have been discussing here, removal of a species from its natural environment and growth in more controlled favourable conditions can often increase the biomass of the individual plant. The famous study of Clausen et al. (1940) first demonstrated this limitation in the field for *Achillea lanulosa*,

ecotypes which demonstrated substantially different growth and morphological characteristics as abiotic parameters changed along a transect in California. For example, plant height decreased with increasing elevation suggesting that the plant was limited by the environment even in communities in which it naturally occurred (Clausen et al. 1940). Hence, biotic communities can be classified in many ways by the general habitats in which they occur including whether or not it is a stressful or extreme limiting environment. However, whether a particular species within that community or vegetation type is necessarily stressed or limited cannot be inferred from its community classification. This is why we do manipulative experiments. We try to determine which specific processes are important within and between each of these general classifications for habitats and communities, and in doing so gain a better understanding of individual species occurring within each.

Perhaps this is where some of the confusion arises. Different ecologists are simply referring to different levels of organizations. Körner quotes Callaway et al. (2002) as concluding that plants living in alpine environments are stressed. However, we demonstrated that for some species a change in position on an elevation gradient resulted in a shift from negative to positive interactions with neighbouring plants (Callaway et al. 2002). We do not conclude that alpine vegetation is stressed nor do we try to make inferences at this level at all. Our sample unit of interest was individual species (both experimentally and statistically) and by using a large number of species in many alpine environments we hoped to determine if plant-plant interactions change predictably with change in position within alpine meadow gradients. We did however use the term stress as surrogate for the complex and interrelated changes in abiotic parameters which undoubtedly changed as elevation increases. Nonetheless, our subject of interest was relative change in the interactions between *species*, and the short-hand use of the concept stress allowed us to generalize across many different sites and locations.

Fitness is never perfect

In sharp contrast to Körner (1998) who holds the view that “limitation exists only for the non-fit”, we do not consider limitation to be a clear-cut, black or white type process where either a plant is limited or not, nor do we consider fit plants to be existing without limits in a state of perfect local adaptation. Just as Körner proposes that ‘single individuals’ will almost always be functioning a long way from their ‘maximum’, we propose that individuals will almost always be limited *to some extent* by the environment. Körner proposes that “once the

ability to cope with environmental extremes has evolved, such extremes become elements of ‘normal’ life” (Körner 2003) and cites anecdotal evidence that most specialist species either die or are suppressed by natives when introduced to a new habitat. However, there are several evolutionary criticisms of this line of reasoning. Are species ever perfectly evolved to environmental extremes such that these extremes cease to have a negative effect upon the plant? No. Organisms must be analysed as integrated wholes not just collections of single traits and this means that non-optimality can also be rendered as a result of adaptation to certain specific conditions (Gould & Lewontin 1979). In other words, there are trade-offs between different sets of traits and often multiple selection processes exist with low temperatures, soil moisture, and nutrients sometimes co-occurring which reduce the likelihood of achieving local adaptation.

While Körner (2003) does admit that “deviation from physiological optimality is normal life at most places on earth”, he fails to acknowledge that fitness is never perfect – even if a species is adapted to immediate local conditions such as cold temperatures. Hence, limitation can still exist for the fit. There are also many factors which can prevent a species from reaching local adaptation even though it is present in that habitat. Some species may be unable to evolve traits necessary to reduce the effects of a particular factor within a habitat either due to genetic constraints i.e. lack of appropriate genetic variability (including unfavourable linkages or pleiotropy) or due to trade-offs between defence, survival, or growth (Bradshaw & Hardwick 1989; Sibly & Calow 1989), or simply due to limitation in the environment to be able to do so (Bryant et al. 1983). Yet other species or even genotypes within a species may even respond facultatively through phenotypic plasticity (Calow 1989). Some species may also employ alternative strategies to deal with environmental extremes instead of tolerance such as dormancy, and furthermore, traits which have an immediate fitness value now in terms of coping may have been initially selected for other reasons (Gould & Vrba 1982). In short, limitation is still a valuable conceptual tool for understanding ‘normal’ life since most ‘normal’ life on Earth involves deviation from both physiological *and* adaptive optimality. Finally, with respect to the anecdotal evidence that Körner cites to support his position, that specialists die when moved or are suppressed by natives, unfortunately this is often not the case. Natives are frequently not very successful in suppressing introduced specialist species, i.e. *Centaurea* species, *Alliaria petiolata*, *Heracleum mantegazzianum*, *Mimosa pigra*, *Echium plantagineum* and probably hundreds of others – hence the growing public concern with the success of introduced/invasive species worldwide in virtually every ecosystem on Earth.

Conclusions: how to effectively apply stress

Körner argues that “if any deviation of life conditions is treated as stress, then we have just invented a new word for ‘life’ and the term ‘stress’ becomes useless” (Körner 2003). We disagree. Stress is merely an adjective that can be applied to the word ‘life’. What Körner is really arguing is that ‘life’ is always to some degree about severity of the environment. However, “a world of infinitely large populations is impossible because most environments can support only limited numbers” (White 2001) seems like a reasonable initial premise for life. It also seems reasonable to assume that different environments can support different numbers of individuals and that one way these differences might be manifested is through variation in the severity (i.e. stress) of particular environments in time or space. Furthermore, the erroneous restriction of stress (like limitation) to a simple, singular concept without applications at multiple levels and scales reduces its ability to explain or describe some of the most fascinating phenomena in ecology – including different physical environments. Admittedly, it is tempting to refer to stress very generally when describing an environment as stressful, but this does not reduce its explanatory power when the specific attributes under consideration are clearly identified. For instance, “position on a stress gradient” is short-hand for “at this point in space and time, this particular suite of abiotic parameters is constraining this species (e.g. changing the relative reduction in biomass) in the following way”. While the usage itself may sometimes be a simplification for convenience, including the attribute of stress to describe and compare relative changes in complex and often interrelated changes in abiotic parameters does not lead to the conclusion that stress is life, but rather that life is often stressful.

Acknowledgements. This opinion paper is a product of discussions among the Alpine Pals at NCEAS in Santa Barbara, California. Funding was also provided by National Geographic, The National Science Foundation, and the Andrew W. Mellon Foundation to RMC and an NSERC PDF to CJL.

References

- Bradshaw, A.D. & Hardwick, K. 1989. Evolution and stress – genotypic and phenotypic components. *Biol. J. Linn. Soc.* 37: 137-155.
- Bryant, J.P., Chapin, F.S. & Klein, D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357-368.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikvidze, D. & Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848.
- Calow, P. 1989. Proximate and ultimate responses to stress in biological systems. *Biol. J. Linn. Soc.* 37: 173-181.
- Clausen, J., Keck, D.D. & Hiesey, W.M. 1940. Experimental studies on the nature of species. I. The effect of varied environments on western North American plants. *Carnegie Inst. Washington Publ.* 520.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710-723.
- Gould, S.J. & Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* 205: 581-598.
- Gould, S.J. & Vrba, E.S. 1982. Exaptation – a missing term in the science of form. *Paleobiology* 8: 4-15.
- Körner, C. 1998. Alpine plants: stressed or adapted? In: Scholes, J.D. & Barker, M.G. (eds.) *Physiological plant ecology*, pp. 297-311. Blackwell Science, Oxford, UK.
- Körner, C. 2003. Limitation and stress – always or never? *J. Veg. Sci.* 14: 141-143.
- Sibly, R.M. & Calow, P. 1989. A life-cycle theory of responses to stress. *Biol. J. Linn. Soc.* 37: 101-116.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ, US.
- Tilman, D., Lehman, C.L. & Thomson, K.T. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci.* 94: 1857-1861.
- White, T.C.R. 2001. Opposing paradigms: regulation or limitation of populations? *Oikos* 93: 148-152.

Received 3 November 2003;
Accepted 24 February 2004.
Co-ordinating Editor: S. Díaz.