

IN FOCUS

Stress as a modifier of biodiversity effects on ecosystem processes?



A limnephilid caddisfly larvae (*Anomalocosmoecus* sp.) removed from its case and an amphipod (*Hyalella* sp.) from Andean streams. Leaf litter of five different qualities was offered to these two detritivores in an experiment to test whether the stress-gradient hypothesis from plant ecology might apply to stream invertebrate communities. Photo and copyright: Patricio Andino.

Fugère, V., Andino, P., Espinosa, R., Anthelme, F., Jacobsen, D. & Dangles, O. (2012) Testing the stress-gradient hypothesis with aquatic detritivorous invertebrates: insights for biodiversity ecosystem functioning research. *Journal of Animal Ecology*, **81**, 1259–1267.

Does stress, defined as a reduction in growth by external constraints, modify biodiversity effects on ecosystem functioning? That is, are diversity effects stronger under stressful, as opposed to favourable conditions? The study by Fugère *et al.* (2012) in this issue borrows the stress-gradient hypothesis from plant ecology to explore this issue in an aquatic detritus-detritivore system. Although they find weak support for their hypothesis, the study opens the door for future experimental and theoretical investigations into the role of stress in modifying the relationship between the diversity of animal communities and ecosystem processes.

Humans are profoundly affecting global biodiversity, which potentially has consequences for biogeochemical processes and the benefits afforded to humans by ecosystems (Naeem, Duffy & Zavaleta 2012). Concern regarding these consequences has spurred intense research over the past two decades to assess the impact of changing biodiversity on the rates at which resources are captured and processed by biological communities (Cardinale *et al.* 2012). Much of this research has focused on plant communities, where long-term studies (Reich *et al.* 2012) and meta-analyses (Hooper *et al.* 2012) consistently show that increasing species richness enhances plant productivity. The prevalence of similar effects on plant litter decomposition is, however, less clear (Gessner *et al.* 2010; Hooper *et al.* 2012). This suggests that environmental context plays an important role in determining the influence of biodiversity loss on decomposition (e.g. McKie *et al.* 2009; Gessner *et al.* 2010; Kominoski *et al.* 2010).

In this issue, Fugère *et al.* (2012) take a step towards understanding context dependency of biodiversity effects by examining how a resource-quality gradient modifies the influence of consumer diversity on leaf litter decomposition. The starting point of the study is the stress-gradient hypothesis of plant ecology (Grime 1979; Maestre *et al.* 2009; Malkinson & Tielbörger 2010), which was proposed based on observations that in stressful environments, plant performance improves in the presence of neighbouring plants (e.g. Callaway *et al.* 2002). The stress-gradient hypothesis suggests that competitive interactions structure plant communities in favourable conditions, but that facilitative interactions are instrumental in stressful environments where they enhance the realized niche of species that could barely persist in such conditions otherwise (Maestre *et al.* 2009; Malkinson & Tielbörger 2010). Facilitation, in turn, allows for complementarity effects of co-occurring species on ecosystem process rates. This is the rationale based on which Fugère *et al.* (2012) propose that stress imposed on animal communities also might enhance effects of biodiversity on ecosystem processes.

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To fully understand this rationale, it is necessary to define stress – a concept adopted from physiology but now widely used in ecology as well. In plant ecology, stress has been distinctly defined as the reduction in growth or biomass production caused by an external constraint (Grime 1977). It is this definition that allows Fugère *et al.* (2012) to interpret a gradient in food quality as a stress gradient, reasoning that consumers cannot realize maximum growth on a low-quality diet. One might argue that using the stress-gradient hypothesis as a framework for examining a detritus-detritivore system is a stretch, because food is (almost) always beneficial rather than stressful to consumers, even if its quality is low. However, if Grime's (1977) definition of stress for plants is literally transferred to consumers (i.e. stress curbs growth), then the logic by Fugère *et al.* (2012) holds.

In the reported experiment with detritivorous stream invertebrates, Fugère *et al.* (2012) offered one of five species of leaf litter reflecting a resource-quality gradient to a limnephilid caddisfly (*Anomalocosmoecus* sp.), an amphipod (*Hyalella* sp.), or both invertebrates together. Subsequently, they assessed litter decomposition rate by determining leaf consumption normalized for body-mass specific metabolic activity, using an index named Leaf Processing Efficiency (LPE) (McKie *et al.* 2008, 2009). Limnephilid caddisflies are capable of cutting through tough leaf tissue, whereas the amphipod is supposed to feed mainly on the margins of leaf pieces. Fugère *et al.* (2012) reason that these differences in feeding patterns would increase the overall consumption of leaf litter, when both species feed on the same leaves simultaneously. However, the magnitude of this diversity effect would depend upon resource quality. Both species would easily consume high-quality litter, but on recalcitrant litter, the total length of leaf margins could possibly limit *Hyalella* feeding. Therefore, shredding activity of *Anomalocosmoecus* might be necessary to permit *Hyalella* feeding on low-quality litter. As a consequence, competitive interactions were presumed to be most important on a high-quality diet that was easily degraded by microbes, and facilitative interactions would enhance resource consumption on the low-quality litter.

In partial support of the stress-gradient hypothesis, Fugère *et al.* (2012) find that caddisfly–amphipod interactions shift from competitive to neutral with increasing stress levels defined along their resource-quality gradient. However, no support was found by Fugère *et al.* (2012) for the main feature of the stress-gradient hypothesis: that facilitation is important in high stress environments. A small literature survey conducted in parallel to the experimental study also provides mixed outcomes.

Are these results surprising? At least four non-mutually exclusive reasons indicate the answer is no. First, it is not clear whether shredding of leaves by limnephilid *Anomalocosmoecus* indeed facilitated food acquisition by *Hyalella*, although *Hyalella*'s mouthparts most likely make the species a less effective shredder of tough litter. Second, the

argument made by Fugère *et al.* (2012) deviates substantially from situations considered in plant ecology. It is conceivable, for example, that the degree of competition, rather than facilitation, increases with decreasing food quality (defined here as stress), because patches of palatable and nutritious food, especially patches colonized by fungi (Suberkropp 1992; Chung & Suberkropp 2009), are scarcer on recalcitrant litter. Third, tests of the stress-gradient hypothesis have produced mixed results even in plant ecology (Malkinson & Tielbörger 2010), suggesting that the postulated mechanisms are not universal. Fourth, the hypothesized interactions between the two species were limited to competition and facilitation. However, cannibalism and intraguild predation, which do not occur in plant communities, are common interactions among some detritivorous caddisflies (Klemmer *et al.* 2012) and amphipods (MacNeil & Dick 2012). Therefore, because death (predation) arguably has stronger consequences than hunger (competition), and mobile animals can more easily escape unfavourable environmental conditions than plants, species neighbouring effects that alleviate stress might not be as important for animals as for plants. Overall, this suggests that outcomes depend not only on specific context and associated mechanisms but also on how biodiversity effects at different trophic levels (e.g. consumers vs producers) are assessed.

The idea that stress may notably change the way in which species interact to affect ecosystem processes has been variously assessed in experiments focusing on plants. For example, Mulder, Uliassi & Doak (2001) found that diverse moss communities performed better than species-poor moss communities when exposed to a moderate experimental drought, and that this effect was mainly due to enhanced performance of those species that were most affected by drought when grown in isolation. Similarly, Steudel *et al.* (2012) considered the strength of diversity effects on algal biomass production along an experimental temperature and salinity gradient and observed that the relative biodiversity effects increased at elevated temperatures and salinities, although the absolute diversity effect did not. These results suggest that to some extent high plant species richness can act as an insurance policy against stress, although other patterns have also been observed – including a negative diversity effect on plant productivity in infertile soil despite a positive effect in fertile conditions (Fridley 2002). Fugère *et al.* (2012) are among the first to apply these concepts to animal communities.

Based on the data collected by Fugère *et al.* (2012) and some others, it would arguably be premature to conclude that stress plays either a minor or an important role in determining outcomes of biodiversity change on ecosystem processes. Given the multitude of possible interactions, especially when food-web and microbial interactions are added to the basic template of plant–plant interactions, it is likely that a complex interplay between species interactions, stress and resource availability

changes the relative importance of each factor across environmental gradients (Ellison 1987; Callaway 1997). The type of stress, the way it is assessed, and variation in responses to a particular stress type and level across species are likely to complicate patterns further. As a result, the overall net effect of species interactions on ecosystem processes may be negative, neutral or positive, and different outcomes may be expected for different processes in a given system.

One important point to consider is that stress related to resource quality as examined by Fugère *et al.* (2012), or resource abundance (e.g. Fridley 2002), could have different effects compared with abiotic (e.g. salinity fluctuations or low temperature) or biotic (e.g. disease vectors or predator presence) stressors that limit the conversion of available resources to biomass. Therefore, further examining the significance of stressors in diverse settings, including the effects of multiple stressors acting in concert, holds much potential to provide insights into the mechanisms behind biodiversity effects, and lack thereof, on plant production, litter decomposition and other ecosystem processes. Such mechanistic understanding would not only constitute a major scientific advance but also be sorely needed in view of the profound environmental changes that occur increasingly over large spatial scales (Cardinale *et al.* 2012; Naeem, Duffy & Zavaleta 2012).

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References

- Callaway, R.M. (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*, **112**, 143–149.
- 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., Kikodze, D. & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Anne, L., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.
- Chung, N. & Suberkropp, K. (2009) Contribution of fungal biomass to the growth of the shredder, *Pycnopsyche gentilis* (Trichoptera: Limnephilidae). *Freshwater Biology*, **54**, 2212–2229.
- Ellison, A.M. (1987) Effects of competition, disturbance, and herbivory on *Salicornia europaea*. *Ecology*, **68**, 576–586.
- Fridley, J.D. (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia*, **132**, 271–277.
- Fugère, V., Andino, P., Espinosa, R., Anthelme, F., Jacobsen, D. & Dangles, O. (2012) Testing the stress-gradient hypothesis with aquatic detritivorous invertebrates: insights for biodiversity ecosystem functioning research. *Journal of Animal Ecology*, **81**, 1259–1267.
- Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. & Hättenschwiler, S. (2010) Diversity meets decomposition. *Trends in Ecology and Evolution*, **25**, 372–380.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Process*. John Wiley, Chichester.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. & O'Connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105–108.
- Klemmer, A.J., Wissinger, S.A., Greig, H.S. & Ostrofsky, M.L. (2012) Nonlinear effects of consumer density on multiple ecosystem processes. *Journal of Animal Ecology*, **81**, 770–780.
- Kominoski, J.S., Hoellein, T.J., Leroy, C.J., Pringle, C.M. & Swan, C.M. (2010) Beyond species richness: expanding biodiversity–ecosystem functioning theory in detritus-based streams. *River Research & Applications*, **26**, 67–75.
- MacNeil, C. & Dick, J.T.A. (2012) Intraguild predation may reinforce a species–environment gradient. *Acta Oecologica*, **41**, 90–94.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.
- Malkinson, D. & Tielbörger, K. (2010) What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos*, **119**, 1546–1552.
- McKie, B.G., Woodward, G., Hladysz, S., Nistorescu, M., Preda, E., Popescu, C., Giller, P.S. & Malmqvist, B. (2008) Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivore richness, evenness and density. *Journal of Animal Ecology*, **77**, 495–504.
- McKie, B., Schindler, M., Gessner, M.O. & Malmqvist, B. (2009) Placing ecosystem functioning in context: effects of biodiversity change and two abiotic perturbations in a stream field experiment. *Oecologia*, **160**, 757–770.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001) Physical stress and diversity–productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Science of the USA*, **98**, 6704–6708.
- Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science*, **336**, 1401–1406.
- Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F. B. & Eisenhauer, N. (2012) Impacts of biodiversity loss escalate through time as redundancy fades. *Science*, **336**, 589–592.
- Studel, B., Hector, A., Friedl, T., Löffke, C., Lorenz, M., Wesche, M. & Kessler, M. (2012) Biodiversity effects on ecosystem functioning change along environmental stress gradients. *Ecology Letters*, Doi: 10.1111/j.1461-0248.2012.01863.x.
- Suberkropp, K. (1992) Interactions with invertebrates. *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher), pp. 118–134. Ecological Studies, Vol. 94. Springer-Verlag, Berlin.

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