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1A

A trophic cascade is a response to a perturbation of a single species or gild that is felt throughout all trophic levels of the food web. Traditionally trophic cascades have been described as bottom-up or top-down, indicating whether the propegation of the pertubation is felt at the trophic levels above the perturbed species or below. For instance, depressing the sea-otter population increases the sea-urchin population, which subsequently consumes the kelp forest, is a classic example of top-down cascade. Polis studies on small islands provide a great example of a bottom-up cascade. Here, the populations of insects, spiders, lizards and plants subsist mainly on nutrients that wash on shore from the sea – primarily drift seaweed, and also bird guano. Convincing evidence for this dependence comes from the clear trend between abundance and island perimeter, rather than island area. A cascade is seen when the bottom of the chain is perturbed, this time when El Nino cycles bring rains, allowing an abundance of green plants to grow on the island (presumably from dormant seeds – a great example of Chesson's storage effect). This cascades up the trophic levels, increasing abundances of insects, spiders, and lizards, and even adding new top predators in the form of songbirds and parasitoid wasps.

Despite the Polis example, cascades tend to be predominately top down, which Don Strong explains as follows. Bottom-up systems have donor-control, meaning that changes in the upper trophic levels do not effect them, only changes in the donor (lower trophic level) populations matter. That's the definition of being bottom up, but its often overlooked – for instance Frank et al. 2007 describe any positive correlation between predator abundance and prey abundance as evidence for bottom up – but the perturbation

they are studying is the decrease of a top predator fish and the response on the herbivore fish populations. Bottom up systems ought to have no correlation, not a positive correlation, if the top predators are the ones perturbed. The reason donor control is so important is that perturbations typically affect the top of trophic levels, for a variety of reasons. Often we prefer to hunt/eat the top predator (salmon, lions, wolves). Top predators tend to have smaller population densities and longer generation times, so they easily suffer from increased mortality, even when it is due to some anthropogenic change that effects all trophic levels – the lower ones can respond and adjust faster with their larger numbers and faster growth rates.

Don Strong's other element in trophic cascades is the role of diversification. Diverse food webs are less likely to cascade because other species can pick up the slack. For instance, in the top-down kelp forests of Alaska, the otter is the chief urchin predator, and decreasing otter numbers have had a substantial cascade effect on the urchins and kelp forests. Meanwhile, the California kelp forests have abundant other urchin predators such as lobsters, which have damped the impact of the cascade when otter populations have declined.

Convincing examples of trophic cascades are rare. As Don Strong observes, cascades are mostly likely to be found in simple food chains under predominately top-down regulation. For these reasons, they are predominately thought to be marine, where food web can be relatively simple, since predation is far less specialized (basically following size hierarchy), while terrestrial systems are often more complex. Additionally, they are more likely when much of the biomass goes into production, as in the case with marine plankton, while comparatively little biomass goes into production in terrestrial forests.

Theoretical work also sheds light on the importance and magnitude of trophic cascades through more general work on food webs. For instance, Yodzis (1988) demonstrates that for many food webs, the effect of press-perturbation will be indeterminate on the other elements of the food web.

Climate change provides an interesting and potentially very dangerous threat of trophic cascades, where its effects might not be isolated to a single trophic level. For instance, higher temperatures may reduce cold, nutrient rich up-wellings that drive phytoplankton abundance, while top predators such as polar bears may also be removed from the system. Understanding these effects is particularly important in marine systems, which received amazingly little attention in the ecological climate change analysis in this

week's *Science.*

2B

A

Chesson divides all mechanisms for maintaining diversity (coexistence mechanisms) into equalizing or stabilizing mechanisms. The basis for each can be seen from the classic (de-dimensionalized to make Alan Hastings happy) Lotka-Volterra equations:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(1 - \alpha_{ii}N_i - \sum_{j \neq i} \alpha_{ij}N_j) \tag{1}$$

Equalizing mechanisms make α_{ii} and α_{ij} more similar, which can be done by increasing niche overlap in the MacArthur Levins framework. Meanwhile stabilizing mechanisms make intraspecific competition α_{ii} greater than interspecific competition α_{ij}, which can be thought of in the MacArthur Levins framework as decreasing niche overlap. As we the stability analysis of the Lotka-Volterra equations show, only stabilizing mechanisms can guarantee equilibrium coexistence. Equalizing mechanisms simply slow the rate at which one species can drive another to extinction. In the limiting case, equalizing mechanisms leave the community totally neutral, and the only way diversity is lost is by drift. Anything that decreases fitness differences between organisms serves as an equalizing mechanism. Meanwhile, stabilizing mechanisms come in a variety of forms. Decreased niche overlap, as in the MacArthur Levins case of limiting similarity for coexistence, and also density dependent predation or prey switching, can operate independent of fluctuations. Fluctuation dependent mechanisms include nonlinear responses and the Storage effect. The storage effect can be thought of as spatial or temporal niche for an organism. As an example, perhaps two species of plants would compete for resources (i.e. nitrogen), but one is dormant in spring and the other is dormant in fall. While its competitor is dormant, the active species can store (hence the name) enough resources such that it can survive when both are growing in the summer, even if it is the weaker competitor. This temporal heterogeneity is also the answer to the paradox of the plankton, posed by EG Hutchinson in 1961 and answered by him six years later – changing the rules of the game so that each species has a time

when it does best allows for coexistence. The effect is not limited to temporal niches – Huffaker's experiment with mites on oranges provides an excellent example of spatial niches. The mites cannot coexist on the oranges, but the metapopulation persists because the prey can recolonize open patches faster than the predator, then become driven extinct when the predator reaches them, only to become an open patch again since the predator must leave (consistent with Hastings (1980) model).

B

I personally find the most convincing explanation of latitudinal gradients to come from Weins and Donoghue, which falls into the **Time** catagory of the Willig et al. review on latitudinal gradients. They make a phylogenetic tree of many taxa that include both tropical and temperate populations, and show that temperate clades are always included inside tropical clades. This suggests that the tropical clades are simply older than the temperate clades. Even if diversification has gone on at the same rate in temperate and tropical zones, because the process has been going on for much longer in the tropics, it has many more species. This is understandable if we imagine that early life developed in an environment similar to the tropics, while temperate zones are purged of their diversity by glaciation events, and have to be re-invaded each time by more tropical species. Meanwhile the equator represents a relatively unperturbed, old zone where diversification just keeps plodding away. The evidence in support of this includes both the phenomenal observation from the phylogenetic trees and our knowledge of past glaciation events.

I also find rather intriguing the **Rates** hypotheses discussed by Willig et al., The basic idea states that the rate of diversification (speciation - extinction rate) is higher at the equator than at the poles. This could be due to a higher speciation rate at the equator (more facilitation, or because of more radiation, more mutations, faster generation times, and hence faster evolution), or slower extinction rate at the poles (again, perhaps due to more facilitation, larger population abundances due to more energy/radiation/productivity, etc), or some combination of both. An article in the last issue of *Ecology Letters* compared the different combinations of these. Jim Brown's metabolic theory of Ecology predicts that all rates increase with temperature proportional to a Boltzmann factor, $e^{E/KT}$, and hence we should expect a higher rate of diversification in the tropics. However, Weir and Schluter, looking at the age of sister taxa of birds and mammals across different latitudes, argue

that in fact both extinction rate and speciation rate increase with *increasing* latitude. However, Weir and Schluter did find that the extinction rate was proportionally higher in the poles, hence overall the tropics should have a faster diversification rate.

Finally, I also enjoy the synthesis attempt of Willig et al., which shows how different hypotheses may inform different measures of diversity. While typically the original explanation and most hyoptheses focus on describing total species richness, Willig et al. observe that some, such as the "Greater land mass in the tropics" might be used to explain greater beta diversity, while "greater energy" and "greater productivity" in the tropics may have more to do with alpha diversity. This suggests an interesting way to partition the problem of latitudinal gradients.