Tri-trophic Cascades and Indirect Interactions

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Bell, T., W.E. Neill and D. Schluter. (2003) The effect of temporal scale on the outcome of trophic cascade experiments. *Oecologia*. 134, 578-586.

Researchers in this study analyzed the results of 90 published trophic cascade experiments in order to test their hypothesis that the outcome of freshwater trophic cascade experiments is dependent upon the duration of the experiment. Specifically they looked at experiments where zooplanktivorous fish were either present or absent in the system, including a 4 year long study performed by the researchers themselves. The results of both the meta-analysis of the literature as well as the results of the 4 year experiment showed that the effects of aquatic trophic cascades do not diminish over time. Although the authors speculate that there may be a bias in the literature to only publish experiments which garner positive results they still conclude that generally speaking a short term experiment will adequately predict the long term pattern for trophic level biomass.

Brown, D.G., and A.E. Weiss (1995) Direct and indirect effects of prior grazing of goldenrod upon the performance of a leaf beetle. *Ecology,* 76(2), 426-436.

The authors look at how the grazing history of a plant can affect the nutritional quality of the leaves as well as the growth and fecundity of the herbivore which feeds on it. The authors fed leaves from un-grazed and grazed goldenrod to larvae and adults of *Trirhabda canadensis* (chrysomelid beetles) and measured the effects on consumption rates, biomass conversion, growth rates, as well as final mass. The results showed that previously grazed goldenrod had a direct negative effect on *T. canadensis* larvae growth however when *T. canadensis* adults fed on leaves which had been recently defoliated by larvae it had direct positive effects on growth and egg production. Ultimately a decrease in foliage consumption by the adults feeding on defoliated leaves negated the positive effect. The authors concluded that prior grazing history has complex effects on herbivores including altering food availability and quality.

Dalin, P. and C. Bjorkman. (2003) Adult beetle grazing induces willow trichome defence against subsequent larval feeding. *Oecologia*. 134, 112-118.

Previous literature has suggested that herbivore grazing on plants can increase trichome densities which may help to prevent future herbivory. To test this theory the authors looked at the effects of different defoliation treatments of the plant *Salix cinerea* on leaf beetle larvae. They measured larval growth and feeding habits. Larvae that fed on plants which had been previously grazed by adult beetles consumed less leaf area and showed greater dispersed feeding than those which fed on plants which had not been subject to previous herbivory. However, these results were only seen in whole plant treatments, larvae fed in petri dishes showed no significant differences between previously grazed plants versus ungrazed. The authors do not offer an explanation for why this is, but reiterate that experimental design can alter the conclusions in a study.

Dennis, P. et al. (1997) The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. *Journal of Applied Ecology*. 34, 433-443.

The authors looked at the effects different livestock grazing regimes have on the coleopteran fauna upland grasslands. The two livestock treatments considered were a sheep treatment and a sheep/cattle treatment. A previously lightly grazed plot was used as a control. Pitfall traps were used to sample beetle fauna. Results showed that the best grazing regimes to encourage beetle diversity were ones which incorporated varied rotation over time.

Dyer, L.A. and D.K. Letourneau. (1999) Trophic cascades in a complex terrestrial community. *PNAS*. 96, 5072-5076.

Researchers look at the effects of a top predator on three lower trophic levels in a tropical wet forest by periodically adding predatory clerid beetles to understory shrubs. They added the beetles to both naturally occurring shrubs and reproductive fragments. They found that the addition of a top predator resulted in a trophic cascade through three levels. There were fewer predators, greater herbivory, and smaller plants with less leaf area. These effects also cascaded to additional plants of the same species and so the authors suggest that additional plant species with the same herbivores may also be affected. This example of a four-level terrestrial trophic cascade is rare in the scientific literature.

Gomez, J.M., and A. Gonzalez-Megias. (2002) Asymmetrical interactions between ungulates and phytophagous insects: being different matters. *Ecology*. 83(1) 203-211.

In order to evaluate the effects of ungulates on phytophagous insects, researchers carried out a 3 year field experiment in which they manipulated the presence of domestic sheep, Spanish ibex and the chrysomelid beetle *Timarcha lugens*. They looked at muliple variables: beetle abundance, effects on the shrub *Hormathophylla spinosa*, reciprocal effects of the beetles on the ungulates and shrubs, the reproductive output of *H. spinosa*, and the abundance of an associated weevil species. As predicted, removal of the ungulates resulted in an increase in both the chrysomelid and weevil abundance, as well as an increase in *H. spinosa* reproductive output. Alternately, removal of *T. lugens* did not have an effect on the ungulates but had a delayed effect in the third year on weevil abundance. In conclusion the researchers point out that herbivores of highly dissimilar size can compete with one another for resources and thus removal of one may effect the other.

Halaj, J. and D.H. Wise. (2002) Impact of a detrital subsidy on tropic cascades in a terrestrial grazing food web. *Ecology*. 83(11), 3141-3151.

It is theorized that the addition of an energy subsidy, in this case a detrital one, can change the strength of a trophic cascade. In this study researchers hypothesize that a detrital subsidy within an agroecosystem will enhance the effects of the trophic cascade. To test this, the researchers combined predator removal treatments with detritus addition treatments within cucumber and squash plots. The addition of detritus increased numbers of Collembola, a common detritivore and also increased ground beetle and wolf spider densities however there was no strong evidence supporting a trophic cascade because no changes in fruit yield were seen in any of the experimental treatments. The authors offer a variety of reasons for why strong trophic cascades were not seen.

Halaj, J. and D.H. Wise. (2001) Terrestrial Cascades: How much do they trickle? *The American Naturalist*, 157(3), 262-263.

Researchers address the question of how frequently trophic cascades really occur in terrestrial systems. Using meta-anaylsis, field experiments on trophic cascades were analyzed to determine their over-all occurrence and strength. The authors report that they found extensive support for the existence of trophic cascades in arthropod dominated terrestrial communities. They found that predator removal typically resulted in an increase in insect herbivores which led to an increase in plant damage. However, that being said, there was rarely a decrease in overall plant bio-mass. So although it is now clear that the trophic cascades in terrestrial communities exist, the question remains…do they really have a significant impact?

Koppel, J.V., et al. (2005) The effects of spatial scale on trophic interactions. *Ecosystems*, 8, 801-807.

In order to better understand why food chain models fail to predict the dynamics typically seen in empirical trophic cascade studies the authors of this paper consider the effects of spatial configuration of consumers and their resources on trophic interactions. What follows is a theoretical discussion for how the scale of interactions between consumers and resources is an important consideration for how changed land uses may impact communities.

Letourneau, D.K., and L.A. Dyer. (1998) Density patterns of Piper Ant-plants and associated arthropods: Top-predator trophic cascades in a terrestrial system? *Biotropica*. 30(2), 162-169.

Researchers look at abundance patterns of top predators, ants, herbivores and plants in Costa-Rican wet forests in order to make inferences about four-trophic level cascades in terrestrial communities. They hypothesize that the forests which have the highest top predator densities will have the low ant densities, high herbivore densities, and low plant densities. Ultimately researchers found this to be true when the top predators were beetles however when spiders represented the top predators there was less of an effect, suggesting that less-effective top predators result in three level trophic cascades.

Letourneau, D.K., L.A. Dyer, and G. Vega C. (2004) Indirect effects of a top predator on a rain forest understory plant community. *Ecology*, 85(8), 2144-2152.

Authors in this study examined the effects of top predator additions to rain forest understory plants. Researchers compared vegetative cover, herbivore damage, plant longevity and plant species richness between patches with predator additions and patches without. Results showed that vegetative cover, longevity, and species richness were highest in control patches suggesting that understory communities may be vulnerable to disturbances which affect predator populations.

Marquis, R.J. and C. Whelan. (1996) Plant morphology and recruitment of the third trophic level: subtle and little-recognized defenses? *Oikos*. 75(2), 330-334.

The Authors in this paper suggest that plant morphology which allows for predators and parasitoids to more easily access the plant may be directed by the third trophic level. They theorize that because herbivore damage is reduced by predators and parasitoids there may be selection on plants for easier access. In this study they exclude ants and mites but look instead at predators such as birds, lizards, fish and beetles. Some of the traits they believe may be involved are pubescence, stem shape, perch shape, and leaf morphology. However, the subtlety of these changes in morphology makes this hypothesis a difficult one to prove empirically.

Martinsen, G.D., E.M. Driebe and T.G. Whitham. (1998) Indirect interactions mediated by changing plant chemistry: Beaver browsing benefits beetles. *Ecology*, 79(1), 192-200.

Researchers examine why chrysomelid leaf beetles are attracted to cottonwood resprout growth caused by beaver herbivory. They hypothesize that the resprout growth has higher levels of defensive chemicals which are sequestered and used by the beetles, and that they are also higher in nutritional value. Experiments in the lab showed that beetles which were fed the resprout growth were better defended against predators and also developed faster and weighed more as adults. The authors conclude that the indirect effects of beaver herbivory could have important consequences within a community.

Otto, S.B., et al. (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology*, 89(1), 134-144.

Researches look at how changes in predator diversity can alter how an ecosystem functions. To do this they set up a full factorial predator removal within a tri-trophic food web. When predator diversity decreased, herbivore biomass and survivorship increased, which led to an increase in the amount of plant biomass consumed. However researchers found the effects of additivity, compensation and interference also influenced the interactions between predators, herbivores and plants. They note that things such as predator identity and phenology also need to be considered in order to accurately predict how species loss may alter ecosystem function.

Polis, G.A., et al. (2000) When is a trophic cascade a trophic cascade? *Tree*. 15(11), 473-475.

This “Perspectives” article in the journal, Tree, discusses the prevalence of trophic cascades in science textbooks and science literature and addresses the need for better clarification of the terminology used so that the scientific community as a whole can agree on what really constitutes a trophic cascade.