The effects of disturbance on trophic levels, food webs, and species diversity

I am particularly interested in how minimizing impacts to trophic levels can preserve functioning in ecosystems and how this translates to benefits for mankind. I selected papers that would encapsulate the gamut of relationships between disturbance and trophic levels along with how this impacts humans. Rather than an intensive review of any one facet of this expansive subject, I decided to broadly explore a few topics that I found most interesting or pertinent to trophic level preservation. I included a paper about the restoration of trophic levels via apex predator reintroduction to illustrate the ability of degraded community structures to return to their prior states.

To begin, it is important to state my definition of “disturbance” for this review. I determined disturbance to be any event that affected the normal processes of a stable community. These events could have stemmed from natural causes such as fire, from anthropogenic causes such as predator removal, from invasions of exotic species, or from the removal of native species. According to Wootton (1998), disturbance can be a landscape-altering phenomenon and can have consequences that disrupt ecological processes and services.

The most popular ecological theory in disturbance is the intermediate disturbance hypotheses (IDH) which states that intermediate levels of disturbance allow for maximum biodiversity by ensuring that highly adaptable species do not have full access to all of the resources potentially available to them because their populations are kept in check via disturbance. At the low end of the disturbance spectrum, species can out-compete others and take over. At the high end of the spectrum, species cannot maintain adequate population sizes and therefore suffer extirpation. Apparently, immigration can alter the outcomes of intermediate disturbance by ensuring that new organisms quickly replace individuals that were lost to disturbance, thereby filling any niche opening that the disturbance had created.

Wootton (1998) proposes two potential outcomes to species affected by disturbance. It is hypothesized that disturbance may not play out according to the IDH theory, and that instead disturbance might affect organisms proportionate to their population size, thus creating biodiversity without creating limiting factors to competition. Another scenario that could develop is that disturbance would limit one population that would then recover and have an abundant resource available to it, which would limit competition. Certain levels of disturbance may lead to the affected population being more vulnerable to extirpation due to normal pressures such as predation. Disturbance can also increase competition on other levels in the food web by limiting a food source thus forcing predators to concentrate too heavily on another food resource. As a result of mortality or limiting population growth, disturbance can release a population from normal predation pressure, allowing the affected population to recover once predators themselves have been limited. The originally affected population may then out-compete other species. After performing various modeling on disturbance in different environmental scenarios, Wootton (1998) found that intermediate levels of disturbance seemed to maximize coexistence at lower levels in the food chain and did not benefit populations that exist in the higher trophic levels. Wooton also showed that disturbance reduces coexistence in open populations because the influx of immigration offsets the losses from disturbance.

After learning about the impacts of disturbance on populations, I wanted to uncover some information about food web complexity in ecosystems. Jenkins et al. (1992) hypothesize that the length of food chains may be dictated by the amount of available energy in the system, and that systems that contain
abundant energy tend to have more complex food chains. In turn they found that longer food chains are more susceptible to effects from disturbance. When disturbance occurs in an energy-rich system that has formed highly complex food chains, it is more likely to collapse the trophic structure than in simpler systems. This is a very important fact when considering where anthropogenic disturbances should occur.

Habitat fragmentation and loss

To talk more specifically about disturbance I will focus on habitat fragmentation. Dobson et al. (2006) found that disturbance in the form of habitat loss or degradation can lead to a loss of ecosystem services. The authors conclude that different ecosystem services will respond differently to habitat loss and that species at higher trophic levels are lost more rapidly in this situation. The paper determined that as disturbance leads to more habitat loss and degradation, species, along with their accompanying ecosystem services, will disappear from the food chain from highest to lowest ranks. It was very interesting to see that the services that will be lost change depending on the ecosystem in question. This means that the same species can provide different vital roles in different ecosystems. This illustrates a great benefit of trophic level preservation: If local extinctions occur and a very important ecosystem service is lost as a result, then immigration from a nearby intact system may be able to offset local losses.

In terms of maintaining the composition of species diversity in habitats that are being altered, Starzomski and Srivastava (2007) found that corridors enable resiliency in patches that have been subjected to disturbance. In contrast, patches that contained no connections to other nearby patches suffered local extinctions and had poor resiliency. Other contributing factors to poor resiliency and recolonization after habitat loss and disturbance can be explained by other variables that prohibited species from emigration and immigration such as edge effects of fragmentation. The authors determined that increasing habitat loss coupled with disturbance will cumulate in species extinctions at least at local scales if connectivity is not provided between habitat patches. Once trophic structures are altered in a fragmented area, they will have a better ability to return to normal states if connectivity is accounted for.

Another area of research concerning habitat fragmentation effects on trophic structure is centered on identifying whether certain species possess identifiable traits that leave them predisposed to elimination from the trophic regime. For example, specialists may suffer from habitat fragmentation if their prey base suffers population declines, while generalists may benefit by obtaining new resources (i.e., foraging areas). Cagnolo et al. (2009) found that fragmentation caused specialists to experience a decrease in abundance while generalists fared well by having new foraging opportunities in the form of open niches and new habitat patches. It was also found that all three trophic levels tested suffered an almost even decline in species richness after habitat fragmentation.

Invasive species effects on trophic levels

With many species exchanging environments in today’s world, I felt that investigating the effects of invasions on trophic levels was pertinent. France and Duffy (2006) found that communities which contain high species richness are less prone to invasions of exotic species because it is likely that every niche is occupied and all available resources are being used by established species. This provides further evidence that maintaining trophic structure provides additional ecosystem services by preventing the establishment of non-native species.

Carvalheiro et al. (2010) examined the impacts of invasion of a non-native shrub, *Gaultheria shallon* (native to North America) on parasitoid-herbivorous insect-plant food webs in heathlands, an
endangered British habitat. The authors established plots in heathlands containing the invasive G. shallon to measure plant diversity and collect insects. Nearly all insects were collected from native plants. Species richness of plants and herbivores was not significantly affected by G. shallon invasion, however species abundance of specialist herbivores was negatively impacted by invasion. In contrast, species abundance of generalist herbivores was found to have increased, despite the fact that these species were not feeding on the invasive plant. Abundance of generalist parasitoids was not significantly affected by invasion, while abundance of specialist parasitoids experienced a strong negative effect. These results demonstrate that the impacts of G. shallon invasion were propagated up through the food web, as species in higher trophic levels (parasitoids) experienced a greater effect due to the invasion than the herbivores, which themselves experienced a greater effect than native plants.

**Fire effects on trophic structure**

I include a short review of the results of fire disturbance on food webs and trophic structure. Prescribed fires are a common habitat management technique in the southeastern United States, and are used in part to preserve the endangered sandplain grassland ecosystem found in that region. Knight and Holt (2005) hypothesized that areas disturbed by fire will have greater numbers of herbivorous insects along the edges of the area rather than the interior. Non-mobile insects (i.e. flightless grasshoppers) located within burned areas are killed during fires, leading to heterogeneity in herbivory in the landscape. The authors examined three sites in Florida that were treated with a prescribed burn. In the burned areas, understory plants began to regrow 2-3 weeks following the burn. The authors sampled each of the three sites for insect diversity and abundance and insect herbivory along three transects: the unburned edge, the burned edge, and the burner interior. Two to three months post-fire, insect abundance was higher in the burned and unburned edge than the burned interior, however 5-6 months post fire, abundance along the unburned edge had decreased, abundance in the burned interior had increased, and abundance along the burned edge had remained constant. Post-fire herbivory may have life-long effects on plant fitness and population dynamics, since fire causes temporary reductions in populations of herbivorous insects during a critical period in plant growth. Plants may grow faster after a burn due to decreased competition and increased nutrient availability. These populations take longer to recolonize areas in the interior of a burned area than along the edge. Plants growing in the interior experience a longer reprieve from herbivory than plants along the edge, therefore, the size and shape of the burn is very important in determining how it will affect population dynamics.

After reading about these small-scale but very detailed experiments concerning trophic levels, I was interested in research occurring at larger scales where I feel that broader impacts are occurring. In terms of large-scale effects of trophic decline on terrestrial species, I thought it would be useful to include papers that cover recent carnivore and ungulate population declines. I begin this portion of the review with a paper by Laliberte and Ripple (2004) which focuses on range declines of carnivores and ungulates. After reading the previous papers in this review and taking into account what I have learned concerning cascading effects of species removal in trophic structure, it seems only logical to wonder what current ecosystem functioning is like with the absence of these two fundamental species. Some great points highlighted in this paper included the general concern that the extirpation of carnivores from formerly inhabited regions is having negative effects on trophic cascades as evidenced by the population boom of mesopredators and over-browsing by herbivore populations. Of 43 species ranges that were examined,
18 had suffered range contractions that were greater than 20% and the remaining 25 had lost less than 20% of their range. It was very interesting to learn that some species such as Dall sheep (*Ovis dalli*) lost 50% of their range, yet the habitat within their former range has remained similar to when they occupied the area. This is promising news for potential reintroductions. Unfortunately this was not the case for other species such as grizzly bear (*Ursus arctos horribilis*) and gray wolf (*Canis lupus*), whose vast historic ranges have undergone significant changes following the removal of these species. The maps of species range contractions in this paper really helped me see what areas are probably not playing with a full trophic deck.

On a positive note, a study by Ripple and Beschta (2004) in Yellowstone National Park showed that when apex predators are restored to their former ecosystems, they are able to reverse the negative effects on the habitat caused by their absence. Overbrowsing by elk (*Cervus canadensis*) in Yellowstone National Park has changed aspen (*Populus* sp.) stand location and abundance. This has had cascading effects that have affected variables such as river temperatures and beaver (*Castor canadensis*) abundance. In attempts to avoid predation from reintroduced wolves, elk have modified foraging habits which is allowing aspen to recolonize and resulting in benefits to beaver populations.

**Conclusion**

From the papers I chose, I can see there is a distinct difference between natural disturbance and disturbance via anthropogenic sources. Natural communities seem to have an inherent ability to recover in the aftermath of natural disturbance, while human disturbances are mostly associated with habitat loss and therefore recovery is not possible. In light of the number and significance of the ecosystem services that we rely on, preserving intact trophic structures will ensure we can continue to receive these benefits from natural systems. From what I have read, I can see that more research is needed to understand how disturbance affects multiple trophic levels. There is a gap in the empirical research for disturbance effects on the trophic levels of terrestrial communities. It seems that large scale experiments of this nature have previously been difficult to carry out due to numerous variables such as emigration and immigration. Fortunately, advances in stable isotope technology may open the door to examining food web links in vast systems. Almost every paper I read was in agreement that rare, specialist, and high trophic level species are most affected by disturbances. Since these species are so critical in shaping and maintaining healthy ecosystems, future research should focus on identifying the links between these species and their environments. I also feel that based on the results found by Jenkins et al. (1992), it would be best to determine the complexity of food webs in an area before undertaking any type of disruption.
Annotated Bibliography


The authors in this paper look to identify if there are particular traits that will leave species more vulnerable to extinction in the midst of habitat fragmentation. For example, previous research has shown that larger body size is correlated with larger space requirements and lower population densities. Species of this nature can be difficult to maintain in highly developed regions. They examined species-specific and food-web traits such as body size, natural abundance, trophic position, and specialization. They studied trophically-linked communities of plants, leaf-mining insects, and their parasitoids. Their results showed that large and small species were equally affected by habitat loss; species abundance was correlated to their response for habitat declines with rare species being affected in a greater proportion than more abundant species. Specialists suffered more than generalists and declines in richness occurred almost evenly at all three levels tested in the trophic structure. I thought this paper did a great job providing empirical results concerning effects of habitat declines on terrestrial species. Linking the species specific traits to vulnerability of declines with fragmentation made this paper fairly unique amongst the literature.


This study documented the response of native plants, herbivorous insects, and insect parasitoids to the invasion of a non-native shrub to the ecosystem. The authors found nearly no herbivory of the invasive shrub, and that species richness of native plants and herbivores was not affected by the invasion. Abundance of generalist herbivores and parasitoids either increased or was unaffected, while abundance of specialist herbivores and parasitoids decreased. The results demonstrate that the impacts of the invasion were propagated up through the food web, as species at higher trophic levels experienced great effects due to the invasion. The results of this study were quite interesting; however I felt that the authors placed too much emphasis on species richness rather than abundance or an index of the two. Colonization by non-native invasive species may not necessarily cause species extirpations, but may result in dramatic decreases in abundance that can ultimately lead to local extirpation.


This was a very interesting paper that linked ecosystem services to the loss of species and habitat. I really thought the connections made by the authors in this paper were fascinating. They were able to determine connections between the loss of a position on the trophic level and what ecosystem service would be lost as a result. To perform modeling, the authors assumed a loss in species diversity with increasing habitat loss. They classified services into a range that spanned from type A which provided the production of wood and fiber, erosion control, plant cover, carbon storage and storm protection to type E services which relied on rare species and therefore their losses would equate to a large loss of services. Species in the type E category mostly reside in the upper portion of the trophic level or are keystone species that reside in the lower levels. These species are mostly associated with
services such as controlling prey beneath them and recreation and tourism. Type C contained species that are associated with medicinal uses, and services such as pollination. I personally thought they could have used better examples between losing higher links in the trophic level and service declines. For example the connections between apex predator losses and subsequent habitat degradation from overbrowsing seems more viable than recreation to me. After quantifying what trophic levels fall into a particular “type” they construct a table which shows what services will be lost depending on the type of ecosystem. Through modeling they are able to show that with habitat loss and degradation species higher on the trophic level will be lost first along with the services provided by them and as the disturbance continues this will continue down the food chain. Although the author did not adequately speak to connections between apex predator conservation and healthy ecosystem functioning, an interesting connection was made between requiring large tracts of intact habitat to enable ecosystem services from the very important lower levels in the food chain such as decomposers. This in turn would lead to the preservation of habitats large enough for predators.


Most studies concerning the relationship between biodiversity and non-native invaders have been centered on sessile species, mainly plants. This study was interested in expanding this research into crustaceans to see how competition between established natives would affect a new colonizer and how these interactions might reverberate through trophic levels. They performed this by examining the colonization of eel grass beds. They found that areas with high biodiversity were less permeable to invasions than areas with lower diversity. I thought this paper tied in nicely with the papers that focus on habitat fragmentation and preserving community assemblages. It illustrates that another added benefit to keeping ecosystems intact is preventing invasions of new species.


The authors of this paper try to determine the influences that shape food webs and how disturbance can alter food webs on a local scale. They test two hypotheses. The first hypothesis states that food webs are structured based on the randomness of environments which will affect population densities. The second states that food chain lengths are determined by the available energy that is able to be transferred to the upper trophic levels. I feel that this hypothesis might be sound but it seems that available energy may be captured by species that can out-compete others and therefore lead to a shorter food chain. The authors also wanted to capture the effects of disturbance while estimating the accuracy of these two hypotheses. Water-filled containers were set up that had differing amounts of leaf litter added to them for productivity. These containers were made to represent water filled cavities in trees found in rain forests. The found that the more energy put into the system was linked to larger and more complex food webs. They also found that disturbances such as drought and low temperatures shortened food webs. Food chains that were longer and more complex were reduced in the face of disturbance and shorter chains suffered no declines.

Three recently burned sites in Florida were examined for insect abundance and plant herbivory. Two to three months post-fire, insect abundance was higher along the edge of the burned area (including unburned and burned plots) than the interior of the burned area, however 5-6 months post fire, abundance along the unburned edge decreased, abundance in the interior had increased, and abundance along the burned edge had remained constant. These results have important implications for plant and associated insect populations in areas managed using prescribed burns. This paper detailed an elegant experiment with clear and interesting results.


This paper focuses on overlaying current ranges of 43 North American carnivores and ungulates with the human footprint map. Of 43 species ranges that were examined, 18 had suffered range contractions that were greater than 20% and the remaining 25 had lost less than 20% of their range. I was surprised that these numbers were so low. I had thought current landuse changes would have resulted in much more drastic range declines. Using Ilevs electivity index to compare the proportion of area used by the species to the proportion of area available they were able to assign values for species preferences and avoidance of areas. Negative values were associated with avoidance, 0 for neutral and positive values for preference. They found that species were most likely to persist in areas with low human density and most species showed negative values near higher human densities. I think this paper provides a good layout of areas that may be lacking important links in trophic structure due to the absence of these species or it may also provide a good reference for areas where trophic links have now been replaces with other species.


The authors linked fear of predation with the maintenance of biodiversity in Yellowstone National Park. This review did a fantastic job of linking the changes in elk foraging behavior to benefits to beaver and riparian zones in Yellowstone National Park. With wolves returned to the landscape, elk cannot forage near streams which are their preferred habitat. This is allowing the re-growth of riparian species which is benefitting beavers. I really like this review but I wonder if there is a more solid way to identify these connections.


Determining the effect of connectivity and patch reductions on communities was the goal of this study. The authors gradually reduced patch size and corridors to examine the rates at which species would start to decline from positions in the trophic level. They also created disturbance in the patches to examine the coupled effects of disturbance and habitat loss. Habitat loss alone did not affect richness but when coupled with disturbance it became clear that patches that maintained corridors to nearby patches were more resilient than patches with no connections to intact habitats. Patches that had no corridors suffered local extinctions and were much less resilient after the pressure of habitat loss was alleviated. I thought this paper took into account two very important variables that are happening on
the landscape scale. Given current landuse patterns the authors feel that this experiment is representative of actual pressures on the landscape and they advise maintaining corridors at the very least for the preservation of biodiversity.


The main focus of this study was to determine if the intermediate disturbance hypotheses could be accurately applied to multi-trophic levels. The intermediate disturbance hypothesis has mainly been applied single trophic levels and therefore may not serve as a good tool in determining the effects of disturbance in real multi-trophic systems. After performing modeling to account for different community structures, Wootton found that intermediate disturbance hypothesis best suits single trophic systems and is not an appropriate fit for multi-trophic systems. It was found that species diversity is enhanced at lower trophic levels that experience intermediate disturbance but populations on higher levels in the food chain do not benefit from this disturbance level and therefore do not have higher diversity as a result. I really enjoyed this paper because it gave a thorough background on disturbance and trophic levels, referenced previous studies, and tested many conditions that occur in different systems. It serves as a fantastic baseline in terms of determining trophic structure in various environments.