The Effects of the Hemlock Woolly Adelgid on Riparian Habitat and Macroinvertebrate Diversity in Connecticut Streams

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Abstract:

The hemlock woolly adelgid (Adelges tsugae) is an exotic scale insect that threatens eastern hemlock (Tsuga canadensis) populations throughout Northeastern US forests. Because hemlock forests cover over 800,000 ha of New England, and because the eastern hemlock is considered to be foundation in many essential ecosystem processes, the decline of this species has widespread ecological and economic implications. This study examines the aquatic macroinvertebrate communities associated with this species across a gradient of hemlock woolly adelgid induced mortality. Macroinvertebrates were sampled from 13 first and second order streams draining hemlock forests throughout Connecticut. Species composition, total abundance, species richness, functional richness, functional diversity, and functional evenness were compared between sites along a hemlock woolly adelgid impact gradient. 2-Dimensional ordination indicated that the hemlock woolly adelgid's impact has influenced macroinvertebrate species composition. In addition, disturbed sites, those that had the highest levels of hemlock decline, had the greatest levels of total species abundances, species diversity, functional diversity, and functional evenness. Predators, filter/collectors and shredders were inversely correlated to hemlock health while scrapers and gather/collectors showed no relationship to the level of adelgid impact. Impacted sites also had higher sapling densities and understory light levels, and lower stream pH. At least in the short-term, certain ecosystem functions, like the transport of energy throughout higher trophic levels, will likely be enhanced in severally impacted sites.

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Introduction:

Invasive plants, pests and pathogens are altering ecosystems on a global scale (Vitousek et al., 1996). Within the last century several well known invasive species have led to dramatic changes in the composition and structure of Eastern US forests. For example, the gypsy moth (*Lymantria dispar*), chestnut blight (*Cryphonectria parasitica*), and dutch elm disease (*Ophiostoma ulmi*) are all invasive species that have altered forest structure and function in the Eastern US by reducing populations of once dominant tree species to near functional extinction (Liebhold et al., 1995). Currently, the hemlock woolly adelgid (*Adelges tsugae*; hereafter HWA), an invasive scale insect from Japan, has reduced eastern hemlock populations significantly (Orwig et al., 2002) and threatens many of the ecosystem processes associated with this foundation species (Ellison et al., 2005). Hemlocks have a primary role in regulating both terrestrial and aquatic ecosystem processes, providing habitat structure, soil stabilization, soil moisture retention, soil chemistry modification, stream temperature moderation, runoff filtration, and hydrological regulation (Ellison et al., 2005). The loss of this species has altered nitrogen cycling (Jenkins et al., 1999), litter chemistry (Cobb et al., 2006), soil water chemistry (Yorks et al., 2003), ecosystem nutrient fluxes (Stadler et al., 2006), and forest vegetative communities (Orwig and Foster, 1998; Orwig et al., 2002; Small et al., 2005) and has many still anticipated effects upon eastern forest ecosystems.

Biology of the eastern hemlock

The eastern hemlock is a long-lived, shade tolerant conifer that extends its northern most range from Lake Superior westward into Nova Scotia, and along the

Appalachian Mountains southward into Georgia and Alabama (Rogers, 1978). Within this range hemlocks are found in a variety of habitat types, from subxeric to mesic sites, and from exposed slopes to enclosed ravines (Kessell, 1979). Due to their shade tolerance and shallow rooting system hemlocks have colonized sites that are inaccessible or impractical for logging, thus allowing mature, monospecific stands of hemlocks to developed throughout the Northeast (Whitney, 1990). As a result, many key ecosystem functions are regulated by this widespread climax species (Ellison et al., 2005).

Hemlocks cast a deep shade and respire at lower rates during peak temperatures than hardwood species (Catovsky et al., 2002). Therefore, the soils under hemlock cover are kept moist and cool and streams draining hemlock forests have more stable seasonal base flows and reduced diurnal temperature fluctuations (Ellison et al., 2005). In addition, hemlocks have a slowly decomposing leaf litter, low N turnover rates and thus produce nutrient poor soils (Jenkins et al., 1999). These physiological properties, along with the unique physical structure of hemlock trees, enable these forests to support specific salamander (Brooks, 2001), avian (Ross et al., 2004; Tingley et al., 2002), fish (Ross et al., 2003) and macroinvertebrate (Snyder et al., 2002) communities. Consequently, the widespread loss of the eastern hemlock could have profound effects upon associated terrestrial and aquatic ecosystems linked with hemlock forests. In addition, the eastern hemlock represents over 6.5 million m^3 of growing timber stock of in Connecticut and 85 million m^3 of growing timber stock in New England; the potential economic losses that might result due to the increased mortality of this species are therefore significant (Orwig and Foster, 1998).

Expansion of HWA

HWA first entered the eastern seaboard into Virginia in the 1950's (McClure, 1989). The HWA was first recognized within Connecticut forests in 1985, and by 1988 widespread hemlock mortality had been recorded in many forests throughout southern Connecticut (McClure, 1989). The HWA feeds on ray parenchyma cells in the young growth of hemlock stems, eventually defoliating and killing the infested tree (McClure, 1991). The HWA only completes part of its polymorphic lifecycle in the Northeast because of the absence of suitable spruce (*Picea*) trees, which are required to host its mobile, sexually reproductive, sexuparae generation (McClure and Cheah, 1999). Regardless, these insects are rapidly reproducing asexually without spruce hosts and have been dispersing readily through a number of biotic, abiotic, and anthropogenic vectors including wind, birds, and human traffic (McClure, 1990). Although the HWA is innocuous in its native range within Japan, a lack of natural predators and absence of host resistance has allowed the proliferation of this species in North America (McClure, 1989). Cold temperatures have limited the northward expansion of the HWA. However, experimental studies have shown that this insect is sufficiently cold hardy to tolerate the minimum winter temperatures of areas beyond its current range (Parker et al., 1998; Skinner et al., 2003). Scientists estimate that this species has increased its range at 30km/year, and is expected to continue this expansion northward (Skinner et al., 2003). Consequently, the eastern hemlock is threatened through much of its range by the HWA (Figure 1).

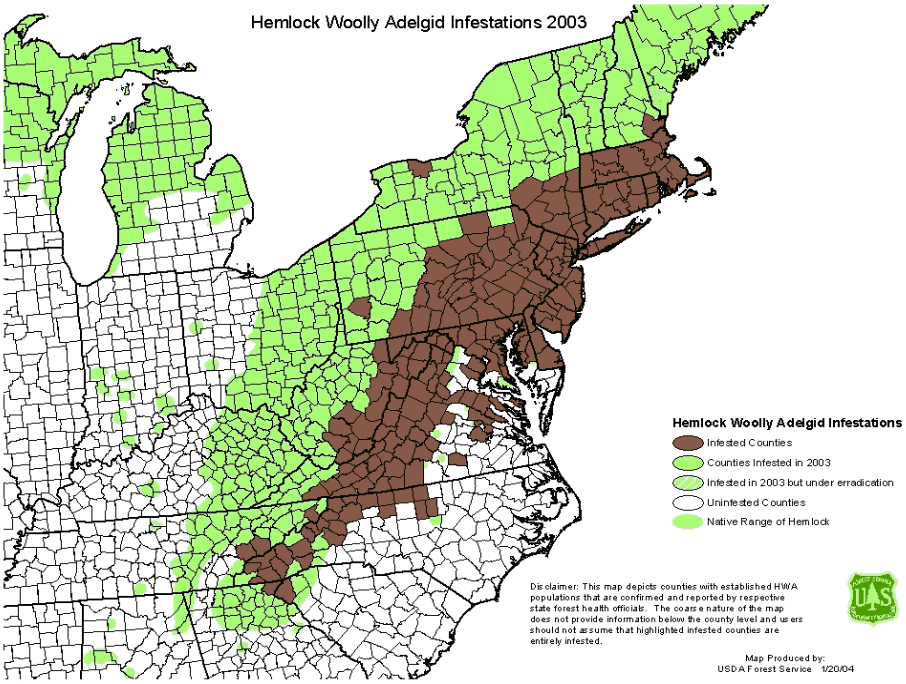

Figure 1. The range of eastern hemlock (*Tsuga canadensis*), shown in light gray, and the HWA (*Adelgid tsugae*), shown in dark gray

Consequences of hemlock decline

Historic declines of hemlock have been recorded in pollen records of the mid-Holocene (~5400 years BP) (Fuller, 1998). However, the full range of ecological impacts resulting from the loss of this dominant species remains unknown. The decline of hemlock in eastern forests, both presently (Eschtruth et al., 2006; Orwig and Foster, 1998; Orwig et al., 2002; Small et al., 2005; Stadler et al., 2005) and historically (Fuller, 1998), has led to an increase in the abundance of birch (*Betula*) species. In addition, following the loss of hemlock in eastern forests, researchers have found higher levels of N turnover, nitrification, and nitrate leaching (Jenkins et al. 1999), elevated concentrations of NO_3, Ca, K, and Mg cations (Yorks et al., 2003), higher dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and K fluxes (Stadler et al., 2006), and reduced organic soil moisture content (Cobb et al., 2006) in infested stands. In addition, hemlock decline influences the composition of avian (Ross et al., 2004; Tingley et al., 2002), salamander (Brooks, 2001) fish (Ross et al., 2003) and macroinvertebrate (Snyder et al., 2002) communities.

Terrestrial – Aquatic Interactions

Because the eastern hemlock is a dominant riparian tree species in many eastern forests, its decline can be expected to affect both terrestrial and aquatic systems. The terrestrial environment provides the most significant energy influx into headwater stream ecosystems (Fisher and Likens, 1973). Further, important linkages exist via terrestrial inputs into aquatic systems and also through aquatic inputs into terrestrial systems (Jackson and Fisher, 1986). Changes in forest canopy structure have been shown to alter aquatic food webs and limit terrestrial and aquatic ecosystem interactions (England and Rosemond, 2004). Therefore, HWA induced hemlock mortality and decline can be expected to affect stream ecosystem structure and function.

Hemlock and hardwood forests support different macroinvertebrate communities (Snyder et al., 2002). Environmental variability, including changes in riparian vegetation across large spatial gradients, strongly influences the diversity and evenness of macroinvertebrate functional groups (Heino, 2005). In particular, functional diversity and evenness decrease with increasing canopy cover, and functional richness and evenness increase with decreasing pH. Long-term studies involving the manipulation of the rate and volume of leaf and woody debris inputs have demonstrated that macroinvertebrate communities are highly dependent upon and correlate strongly to these types of terrestrial inputs (Wallace et al., 1999). Specifically, litter exclusion limits macroinvertebrate shredder, gather, and predator functional group abundances. Macroinvertebrate shredder community structure also varies significantly between forests in differing stages of succession because these forests vary in their pools and fluxes of debris (Stout et al., 1993). Specifically, shredder abundances increase in disturbed sites due to enhanced levels of fast decomposing leaf litter from early succesional hardwood species. In addition, caddisfly abundances vary significantly depending on forest type (conifer or hardwood), and are likely influenced by detritus inputs (Molles, 1982). It then follows that macroinvertebrate assemblages can be expected to vary significantly along a gradient of hemlock decline, due largely to changes in the rate, volume, and type of debris inputs associated with hemlock mortality (Orwig and Foster, 1998).

The composition of riparian vegetation also controls the amount of light reaching streams (Davies-Colley and Quinn, 1998). The amount of solar radiation received in the stream channel controls stream temperature and rates of autochthonous, in-stream production. Scraping and grazing macroinvertebrates that feed upon photosynthesizing organisms, green algae and macrophytes, would be expected to increase in response to higher rates of autochthonous production. These increases in grazer populations could then be expected to support higher levels of predators, as grazers form a significant part of most predator diets (Wallace et al., 1999). Further, water temperature affects the amount of dissolved oxygen in headwater streams and therefore has indirect effects on macroinvertebrates respiration rates, and ultimately, distribution. In addition, as water temperature influences feeding activity of predatory fish on macroinvertebrates, changes in temperature regime can alter predation rates and consequently macroinvertebrate abundance (Kishi et al., 2005).

In summary, the direct linkages between stream systems and the surrounding terrestrial ecosystem exist through the following: the input of leaf and (coarse woody debris; hereafter CWD) for macroinvertebrate consumption, habitat formation through CWD input, and shading and light regimes as determined by riparian vegetation type. Indirect influences from the terrestrial system extend into: top down fish predation, which controls macroinvertebrate populations and therefore litter processing, to bottom up trophic interactions, as macroinvertebrate populations provide an important food source for fish. The loss of a dominant riparian species, like the eastern hemlock, has potential implications for macroinvertebrate assemblages and other ecosystem process that are regulated by these organisms.

Although macroinvertebrate communities have been compared between hemlock and hardwood forests (Snyder et al., 2002), no studies have documented changes in these aquatic assemblages over a gradient of hemlock decline. Comparisons between hardwood and hemlock sites alone have certain limitations. To begin, sites that support mature hemlock stands over hardwood stands may have distinct soils, exposure, slope, aspect, precipitation regimes and land-use histories that strongly influenced which tree species colonized and now dominate these forests. Thus, differences between hemlock and hardwood sites, from the micro-site to the landscape level, may confound the influences of the riparian canopy composition on macroinvertebrate communities.

This study seeks to document shifts in habitat structure, environmental conditions and macroinvertebrate assemblages over a gradient of HWA induced hemlock mortality.

Specifically, I will determine how species diversity and functional diversity change along this gradient. In addition, I wish to identify which macroinvertebrate feeding groups are most associated with hemlock streams, and which will change most dramatically in response to hemlock decline. This data will help address the underlining question of how ecosystem function might change in response to hemlock decline and mortality.

Methods:

Macroinvertebrates were collected from a total of 13 first and second order hemlock streams located throughout Connecticut (Figure. 2). Sites were located through the help of a scientist at the Connecticut Agriculture Experiment Station (Cheah, pers. comm.) and extensive field surveying. The most impacted regions of the state occur around the Connecticut River Valley and the least impacted in the northwest corner (Table 1). These were the areas where field surveying was most concentrated.

Macroinvertebrates were systematically sampled at 10 equally spaced sampling locations over a 100-meter transect established within each stream. At each of these sampling sites 20-second kicks were performed with a standard D-frame kick net with 250-micron mesh to sample a total area of .09 m^2. The samples for each stream were then be pooled and preserved in 91% isopropyl alcohol. All macroinvertebrates within this pooled sample were later identified to the family level. This taxonomic level corresponds to that outlined in the rapid bioassessment protocol set by the Department of Environmental Protection (EPA, 2006) and allows for sufficient resolution to determine functional feeding groups and pollution tolerance values for each taxon.

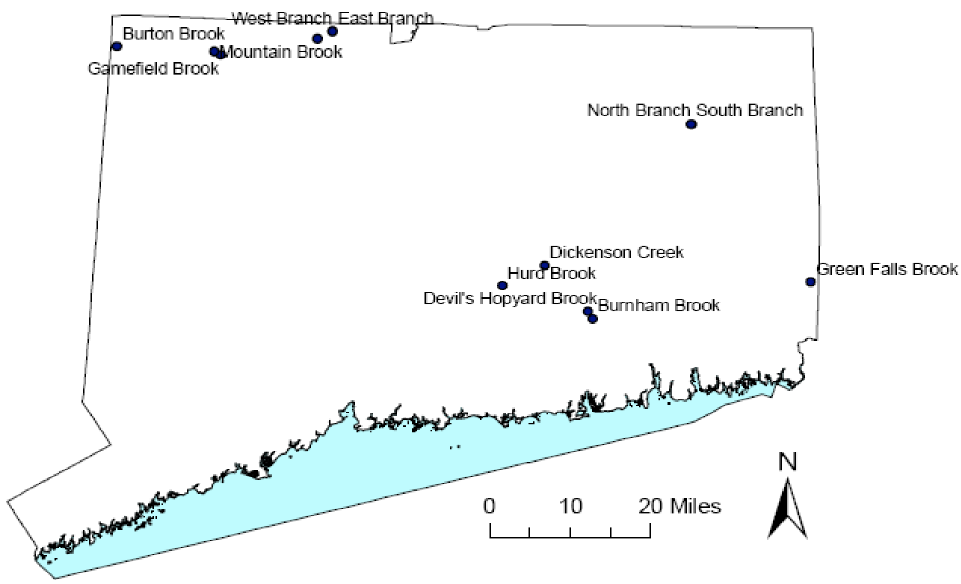

Figure 2. Map of Connecticut displaying 13 research sites located throughout the state

Table 1. A summary of the level of HWA impact and geographic location of 13 sites

Site	Site #	Level of Impact	Relative Health Value	County	N Coordinate	W Coordinate
Burton	1	low	78.2	Litchfield	41 59.348	73 28.531
Mountain	2	low	73.9	Litchfield	41 58.842	73 14.487
Gamefield	3	low	71.1	Litchfield	41 58.433	73 13.518
Old Forge	4	medium	67.2	Litchfield	42 00.406	72 59.572
North Branch	5	medium	64.7	Tolland	41 50.277	72 05.544
South Branch	6	medium	60.7	Tolland	41 50.268	72 05.562
West Branch	7	medium	59.2	Hartland	42 01.237	72 57.348
East Branch	8	medium	52.2	Hartland	42 01.237	72 57.348
Green Falls	9	medium	50.4	New London	41 31.703	71 48.600
Hopyard	10	high	48.5	Middlesex	41 28.478	72 20.587
Dickenson	11	high	45.7	Middlesex	41 33.798	72 26.765
Burnham	12	high	4.9	Middlesex	41 27.558	72 19.943
Hurd	13	high	0.9	Middlesex	41 31.470	72 32.910

At each stream, species and diameter at breast height (DBH) was recorded for all trees above 10 cm within a 5 meter riparian zone from the stream edge paralleling the 100 meter sampling reach. Each hemlock tree was given a foliar transparency value from 0-100 (0=full crown, 100=dead tree) to assess the health and vigor of the hemlock population and the level of HWA impact. Total basal area, percent hemlock, percent hardwood, percent standing dead tress (SNAGS) and relative health were then calculated for each sampling site. Relative health was calculated for each site by subtracting from 100 the sum of the product of each tree's foliar transparency value and the importance value (the percentage of the total basal area of each hemlock tree of each site):

Relative Health = 100 - (-$\sum$ of $I_i\ FT_i$ for each ith tree)

I_i = importance value of each tree (% of total hemlock basal area, including hemlock snags)

FT = foliar transparency value

This value was used to assess the overall hemlock health of each forest, which is assumed to be a proxy for the impact of HWA at each site. To make the scale of impact more intuitive, the relative health value was the inverse of the foliar transparency value: the most impacted forests had the highest transparency values and the lowest relative health values. Sites were placed into three categories, low, medium, and high HWA impact, based on their hemlock health values (low = 70 - 100, medium = 50 - 70, high < 50).

Air temperature, the time since the last precipitation event, pH, water temperature, and turbidity were recorded at each site. Canopy density was measured using a spherical densiometer every 10 meters along the transect in the middle of the stream channel.

Channel width and the amount of downed woody debris were recorded for every 10-meter segment of the 100 meter transect.

Functional groups were assigned to each of the 16 macroinvertebrate families that were present based on the functional feeding groups proposed by the EPA's Rapid Bioassessment Protocol (EPA, 2006). Species richness, functional richness, species evenness, functional evenness, species diversity and functional diversity were calculated for each stream. Species and functional diversity were calculated using the Shannon-Wiener diversity index:

$H' = -\sum P_i \log P_i$

P_i = represents the proportion of the total number of species or functional groups present in the ith species or functional group)

Species and Functional evenness, or equitability, was also calculated for each stream using the Shannon-Wiener equitability index:

$EH = H' / \log S$

H' = Shannon-Wiener diversity value

S = total number of species or functional groups in each stream community

Results:

The 13 sites selected were distributed along a gradient ranging from highly impacted (hemlock health value = .9) to unimpacted (hemlock health value = 78.2) (Figure 3). Non-metric multidimensional scaling of all 13 sites with a 2-demensional ordination of species composition produced a stress value of .015 (Figure 10). Using only 12 sites (excluding the least similar, site 13, Hurd) 2-dimensional ordination produced a stress value of 5.128 (Figure 11). Macroinvertebrate species abundance was inversely correlated to hemlock health (r^2 = .746, p-value = < 0.001) (Figure 4). In addition, species evenness and functional evenness were inversely correlated to hemlock health (r^2 = .363, p-value = .0295 and r^2 = .569, p-value = .00289 respectively) – as hemlock health increased species and functional evenness decreased moderately (Figure 5). Both species and functional richness showed little or no relationship with hemlock health (r^2 = .0783, p-value = .354 and r^2 = .0422, p-value = .501 respectively). Functional diversity was inversely correlated to hemlock health at the .05 significance level (r^2 = .342, p-value = .0358), whereas species diversity was inversely correlated to hemlock health at the .10 significance level (r^2 = .271, p-value = .0684) (Figure 6).

Predators were the most abundant functional group across all research sites, followed by filters/collectors, shredders, gather/collectors, and scrapers. Predators were the most common functional group in three of the four sites with a hemlock health value equal to or below 50. In the four sites with the highest hemlock health value predators were the most common functional group in one site, whereas shredders were the most common in two sites, and filter/collectors in the last site. Predators and filters/collectors showed a strong positive correlation with poor hemlock health (r^2 = .658, p-value = <0.001 and r^2 = .597, p-value = .00196 respectively) (Figures 7 and 8). Shredders showed a weaker inverse relationship with hemlock health at the .10 significance level (r^2 = .300, p-value = .0526) (Figure 9). Scrapers showed no correlation with hemlock health (r^2 = .0185, p-value = .658), and gather/collectors showed no correlation to hemlock health (r^2 = .00345, p-value = .849).

PH across the 13 sites showed a positive correlation to hemlock health (r^2 = .409, p-value = .0184) (Figure 12) (for a summary of environmental data see Table 2). In addition, both functional diversity and functional evenness showed moderate correlations to pH at the .05 and the .10 significance levels respectively (r^2 = .3801, p-value = .0248, and r^2 = .2956, p-value = .0548) (Figures 13 and 14). The amount of CWD found in the stream did not show any correlation with hemlock health (r^2 = .0818, p-value = .343). The percentage of standing dead trees (SNAGS) did correlate positively at the .10 significance level with the amount of CWD measured in each stream (r^2 = .2294, p-value = .0977). Densiometer readings were positively correlated to hemlock health and percent live hemlock of the total measured basal area (r^2= .469, p-value = .00974 and r^2 = .378, p-value = .0254 respectively) (Figure. 15). Hemlock health was inversely correlated to the abundance of saplings and the density of saplings increased in sites with more hemlock mortality (r^2 = .555, p-value = .00346) (Figure 16).

Table 2. A summary of forest composition and some environmental data collected at each site

Site	Total BA	% Hemlock	% Hardwood	% Hemlock SNAGS	# Sapling	Channel Width	Densiometer	Total CWD	Ph
Burton	30744.48	75.56	24.44	7.86	4	1.94	94.9	3	8.97
Mountain	32154.57	64.23	35.77	0.00	17	3.47	95.6	11	9.2
Gamefield	22776.96	72.18	27.82	0.00	5	2.63	96.9	7	8.4
Old Forge	20528.83	50.89	49.11	0.00	13	1.97	92.2	18	8.43
North Branch	35465.99	64.06	35.94	5.75	4	5.75	95.1	23	8.76
South Branch	52442.71	65.67	34.33	1.24	1	7.11	95.5	29	8.71
West Branch	33664.57	43.13	56.87	2.07	6	2.96	94.9	12	8.73
East Branch	23163.25	66.45	33.55	2.89	6	3.28	96	0	8.5
Green Falls	24206.66	73.59	26.41	4.02	4	3.63	92.2	21	9.08
Hopyard	30348.85	76.47	23.53	3.55	4	3.62	94.8	4	8.55
Dickenson	25452.36	66.22	33.78	2.27	5	5.75	93.2	3	8.28
Burnham	9122.32	13.45	86.55	117.50	26	4.25	86.1	6	8.09
Hurd	10120.93	1.65	98.35	212.14	33	1.85	93.1	38	8.3

Discussion:

Relative health values provided an accurate measure of hemlock health and an adequate measure of HWA impact. Based on relative health scores, the least impacted sites clustered in the extreme northwest of the state, whereas the most impacted clustered around the Connecticut River Valley where the most HWA have been documented (Cheah, pers. comm.). Although other factors, such as the elongate hemlock scale, might also be causing some hemlock decline (McClure, 1980), it is likely that the HWA is the main cause of widespread hemlock mortality (Orwig et al., 2002).

The most impacted site, Hurd (site number 13), had a hemlock health value of .09 and was the most dissimilar site in terms of species composition, separating from all other sites in 2-demensional ordination space (Figure 10). This site had one family, the *Ptilodactylidae*, or riffle beetle, in much greater abundances than any other site. Deforestation has been shown to increase the productivity of this family in freshwater streams (Bojsen and Jacobsen, 2003) and members of this family have been shown to commonly feed on detritus (Funk and Fenstermacher, 2002). Therefore, the high levels of CWD found in Hurd (Table 2) may explain, in part, the abundance of members of the *Ptilodactylidae*.

Once Hurd was excluded from non-metric multidimensional scaling analysis, the second most impacted site, Burnham (site number 12), with a hemlock health value of 4.9, separated farthest from all other sites in 2-dimensional ordination space (Figure 11). Sites 10 and 11 clustered closest to Burnham, and were also highly impacted; both sites also have hemlock health values below 50 (Table 2). The four least impacted sites, sites 1-4, with high hemlock health values (> 65), clustered on the opposite end of the 2-

dimension ordination space. Overall, based on species composition, sites that are on opposite ends of the hemlock health spectrum separate in 2-dimensional ordination space in a fairly clear patter: sites that are impacted cluster on the extreme right, while unimpacted sites cluster to the extreme left of the 2-dimensional ordination space. These results indicate that hemlock health has a strong influence on macroinvertebrate species composition.

My results differ from those of Snyder et al. (2002), who found that macroinvertebrate species and functional diversity was higher in hemlock streams than in hardwood streams. Their findings more accurately test the long-term changes in macroinvertebrate community structure that might occur as hardwood species colonize disturbed hemlock forests. Sites that once supported hemlock forests, and those that have a mature mixed hardwood forest, likely have distinct biotic and abiotic conditions that controlled which tree species colonized these sites. These conditions might influence macroinvertebrate community structure and diversity, ultimately limiting relevant comparisons between the study by Snyder et al. (2002), which compared hemlock and hardwood forests, and this study across a hemlock health gradient.

This study documents changing stream habitat and macroinvertebrate communities that result from the loss of the eastern hemlock within the last twenty years. Enhanced macroinvertebrate diversity might be supported by increased rates of CWD and litter inputs, more canopy gaps and allochthonous production, and lower stream pH. Because my sites have experienced a disturbance, that of riparian canopy mortality, stream macroinvertebrate diversity might be enhanced initially (Connell, 1978) but decline to the original level once a hardwood riparian canopy develops, as is predicted (Eschtruth et al., 2006; Orwig and Foster, 1998; Orwig et al., 2002; Small et al., 2005; Stadler et al., 2005). Therefore, this increase in diversity might by a short-term phenomenon.

Type of litter inputs

Conifer needle litter has been shown to not be the preferred food source for many macroinvertebrate feeding groups. Maloney and Lamberti (1995) tested macroinvertebrate preference to different litter input types and found that hemlock needles supported the fewest macroinvertebrates and decomposed at a slower rate than hardwood litter. Therefore, the shift from a hemlock to a hardwood canopy, and from hemlock to hardwood litter inputs in those streams with severe hemlock mortality, might help explain the increase in macroinvertebrate abundances and functional diversity. High levels of disturbance encourage hardwood litter production, which in turn supports increased shredder abundances (Stout et al., 1993). I found that the most impacted sites also had the highest abundances of saplings (Figure 16) and shredding macroinvertebrates (Figure 9). Thus, HWA disturbance encourages the growth of early successional hardwoods that in turn can support higher shredder abundances.

Rate and amount of coarse woody debris inputs

CWD have been shown to provide a significant refuge for macroinvertebrates. France (1997) found higher abundances of macroinvertebrates in streams with increased CWD inputs from clearcutting. However, clearcutting would lead to rapid CWD inputs, while HWA induced mortality creates prolonged input of CWD over a longer temporal scale. In addition, the most severe HWA impacted sites lost hemlock populations several years ago, and therefore my instantaneous CWD measurements might not accurately represent the debris loads these streams have experienced. However, it seems logical to infer that in both instances the increases in CWD offers increased food sources for certain macroinvertebrates, and increased refuge and habitat for certain macroinvertebrate groups. Thus, the differences in macroinvertebrate abundances across the hemlock health gradient tested in this study might in part be explained by increased CWD inputs.

Although I found no direct correlation between CWD measurements and macroinvertebrate diversity, at either the species or functional level, the percentage of standing dead tress (SNAGS) increased dramatically in impacted sites (Table 2) and the percentage of SNAGS correlated positively to CWD inputs. The increase of SNAGS in these sites likely contributed more CWD inputs, which in turn encouraged macroinvertebrate productivity and diversity.

Amount of light reaching stream

Gaps in hemlock canopy cover increased the amount of light reaching the stream (Figure 7). We can infer that photosynthesizing organisms, those that are able to colonize the rapid waters of headwater streams, would increase in abundance as a direct result. Boucherle et al. (1986) tested the effects of the historic widespread decline of hemlock on lake trophic structure and concluded that the distribution of cladocerans, diatoms, chrysophytes, and bacterial pigments all increased in response to hemlock decline. Although instream, allochthonous production accounts for a small portion of the total stream energy budget (Fisher and Likens, 1973), organisms that graze on plant life in streams would be expected to increase along with increasing photosynthetic activity in sites with poor hemlock health. Although the diversity and abundance of scraping organisms showed no significant correlation to hemlock health, other researchers have found that in general, macroinvertebrate functional diversity and functional evenness both increase with decreasing canopy cover (Heino, 2005). Therefore, increases in light levels may support more macroinvertebrate production in general, as my data indicate, and not exclusively scraping organisms.

Stream pH

Stream pH can be an important determinant of macroinvertebrate community structure (Eyre et al., 2005). I found that stream pH decreased in sites with poor hemlock health (Figure 12) and that sites with lower pH had higher levels of both functional diversity and evenness (Figure 13-14). Several possible mechanisms might be responsible for the lowering of pH in HWA impacted streams including: increased hemlock needle litter due to HWA induced defoliation (McClure, 1991); increased rates of respiration and decomposition as a result of higher macroinvertebrate productivity (Figure 4); and the increased leaching of cations (Yorks et al., 2003). While it is reasonable to assert that to a certain extent stream pH will enhance functional evenness and diversity, as others have documented (Heino, 2005), after a certain threshold, acidic water will limit diversity (Hall et al., 1980). However, as the lowest recorded stream pH in all 13 sites was 8.02 (Table 2), pH in these streams could likely be decreased by several degrees of magnitude before macroinvertebrate community structure and diversity are dramatically altered (Dangles and Guerold, 1999).

General Hypothesis of Species-Diversity

Along the hemlock health gradient studied, sites with the highest levels of disturbance had the highest levels of species and functional diversity and evenness. McCabe and Gotelli (2000) found that in controlled experimentation in a northern New England stream, disturbance limited species abundance. However, in rarefied samples species richness increased along an intensifying disturbance gradient. Their results fit the model proposed by Huston (1979) in which ecosystems out of equilibrium have decreased rates of competitive exclusion and hence allow for increased niche utilization and species diversity. If we consider disturbance as a factor causing ecosystems to be prevented from achieving an equilibrium state, then disturbance could be expressed as an inverse to an equilibrium state. With this assumption in mind, data from this study best fit the model proposed by Huston, in which disturbance prevents an equilibrium state, and thus encourages species diversity by allowing low rates of competitive exclusion. My analysis would suggest that in declining hemlock forests, as the impact of the HWA becomes more pronounced, macroinvertebrate diversity will increase (Figure 6). Thus, as disturbance events increase in intensity or frequency the ecosystem is brought further from equilibrium and species diversity is encouraged (see Figures 17-18 for visual representations of these relationships).

Stream ecosystem function

Biodiversity, in terms of species diversity, functional diversity and functional evenness, influences ecosystem properties (Hooper et al., 2005), may enhance ecosystem productivity (Spehn et al., 2005), and provides enhanced functional stability (McCann, 2000). To more precisely study ecosystem function there is also a clear need to identify those specific functional traits that affect specific ecosystem functions (Naeem and Wright, 2003). Therefore, to understand the role of macroinvertebrate diversity in stream ecosystem function it is important to identify specific functional traits and the ecosystem properties they drive. For example, shredding macroinvertebrates are responsible for controlling a number of stream ecosystem functions including but not limited to: leaf litter processing, converting course particulate organic matter (CPOM) to fine particulate organic matter (FPOM), encouraging the production of FPOM feeders, enabling the downstream transport of FPOM, increasing the organic content of stream sediments, and speeding the decomposition of CWD by exposing surface areas to bacterial colonization (Wallace and Webster, 1996). We could then postulate that some or all of these ecosystem functions will be enhanced, or in the least augmented, as a result of changes in shredding macroinvertebrate functional diversity across the hemlock health gradient tested.

Other ecosystem functions will likely change in response to shifts in functional feeding group composition across a HWA impact gradient. Specifically, the diversity of predators and filter/collectors increased along a declining hemlock health gradient. Therefore, ecosystem functions that are regulated by predators, prey growth and fecundity rates (Wallace and Webster, 1996), might occur at higher rates in sites with increased HWA impact. Lastly, ecosystem functions driven by filters, the removal of FPOM from suspension, and the delay of the movement of FPOM downstream (Wallace and Webster, 1996), might occur at increased rates in more disturbed sites.

Summary

Macroinvertebrate species composition differs between sites of varying levels of HWA impact and hemlock health. The increase in macroinvertebrate abundances, diversity, and evenness seen along the decreasing hemlock health gradient might be related to changes in the type of litter inputs, the amount and rate of coarse woody debris, the amount of light reaching the stream channel, and changes in stream pH. My results fit the model proposed by Huston, where species diversity increases in non-equilibrium states. This increase in functional diversity in sites with HWA disturbance will likely enhance certain ecosystem functions, like the generation of FPOM and the delay of FPOM transport. However, these changes in ecosystem function might be short-term phenomenon. It remains unclear whether the high levels of diversity in sites with high levels of HWA impact will be maintained as a new canopy develops. In fact, if HWA disturbance fits Huston's model, it is likely that diversity will decline if disturbance events become less intense or frequent as the forest canopy matures and stabilizes.

Conclusions:

Although it is clear that over the last century invasive species have dramatically altered forest ecosystem structure, little is known of the underlying mechanisms driving these alterations or how they directly affect forest ecosystem function. Studying how functional diversity changes as a result of species invasions is a key step in further understanding the ramifications of the loss of a foundation species, such as the eastern hemlock. Because the eastern hemlock might already be functionally extinct throughout much of its range, it is important to document changes in eastern forest structure and function as they are currently occurring.

This field study documented that macroinvertebrate communities have changed in response to hemlock decline. My data reveal that stream habitat changes in several significant ways in response to hemlock decline. Further, my analysis indicates that these ecosystem changes have yet to adversely affect macroinvertebrate communities. Specifically, species abundances, species and functional diversity, and species and functional evenness all increase along a gradient of HWA impact. However, this increased level of diversity is likely a short-term phenomenon and the result of rapid environmental changes that resulted from HWA disturbance

Once a mature forest develops within the riparian area, the high levels of diversity experienced in disturbed sites will likely decline to previous levels. Or perhaps, because hemlock forests have been shown to support higher levels of macroinvertebrate diversity than hardwood forests, diversity will be even lower if the eastern hemlock fails to recover. However, at least in the short-term, ecosystem functions such as leaf-litter processing and the movement of energy throughout trophic levels will likely be enhanced in streams experiencing high levels of HWA induced disturbance.

Changes in macroinvertebrate community structure, ecosystem function and stream habitat will also likely influence higher stream trophic levels. Macroinvertebrates form a significant portion of headwater food webs. Increased macroinvertebrate abundances will likely support increased stream fish productivity, at least of those fish, such as the brown trout (*Salmo trutta*), that can tolerate the higher stream temperatures that will likely accompany hemlock decline. Because stream temperature influences the feeding behavior, respiration and reproduction of freshwater fish species, hemlock associated species such as the brook trout (*Salvelinus fontinalis*), will not benefit from hemlock decline. Because CWD also form a significant habitat and refuge for upland and lowland fish, changes in these inputs along a HWA impact gradient might also support increased fish productivity. However, the destabilization of the forest hydrological regime that can result from deforestation could adversely affect fish communities. Overall, whole stream ecosystems and food webs will likely change due to shifts in stream habitat and macroinvertebrate community structure that result from HWA induced hemlock decline. However, without testing fish populations directly, it is hard to determine how shifts in lower trophic structures and environmental conditions will influence these communities.

While it is clearly important to try to preserve the unique habitat, ecosystem functions, and aesthetic mystique associated with hemlock forests, my findings might provide some balance to the predominate unconstructive view of ecological invasions. Namely, it seems clear that from the perspective of stream ecosystem function, the HWA has not been completely detrimental. Further, as invasives are commonly thought to decrease biodiversity, at least in the short-term, both macroinvertebrate functional and species diversity has been enhanced by the HWA in Connecticut streams. The diversity of the forest canopy might also increase in the wake of hemlock decline, as a variety of common temperate hardwoods, birch (*Betula*), oak (*Quercus*), and maple (*Acer*) species, regenerate in what were almost monospecific stands of hemlock forest. Thus, if we are to judge the effects of forest invasions from the perspective of biodiversity and ecosystem function, this study might offer a counter argument within the current debate.

Although others have documented the specific organisms associated with the eastern hemlock, it remains impossible to predict the new associations that will evolve in forests undergoing the dramatic changes brought by the HWA, and how these associations will influence ecosystem function and biodiversity. It seems sensible to assume that the new forest will be something entirely unique, in terms of structure, function and aesthetic appeal, much like the former one was.

Recommendations for Further Study:

Several steps could be taken to continue or add important components to this study. Stream temperature loggers would have enabled an accurate measure of the changing stream environment and provided a more detailed explanation of the changing stream habitat. In addition, as was originally intended, sampling for stream fish would also provide a more complete picture of how the HWA has altered the stream ecosystem. Lastly, more research sites, especially those in the hemlock health range of between 5 and 40 would provide a more accurate HWA impact gradient and more statistical power.

Acknowledgments:

I would like to thank Carole Cheah for helping me locate research sites and introducing me to her important work with the biological control of the hemlock woolly adelgid. Matt Palmer has also provided me with important support, helping me design this study, assisting me during the editing process, and contributing statistical tests for this paper. Lastly, I would like to thank Halima Duncan, for her help collecting data,

locating sites and revising this paper – I would not have been able to complete this project without her.

Figures:

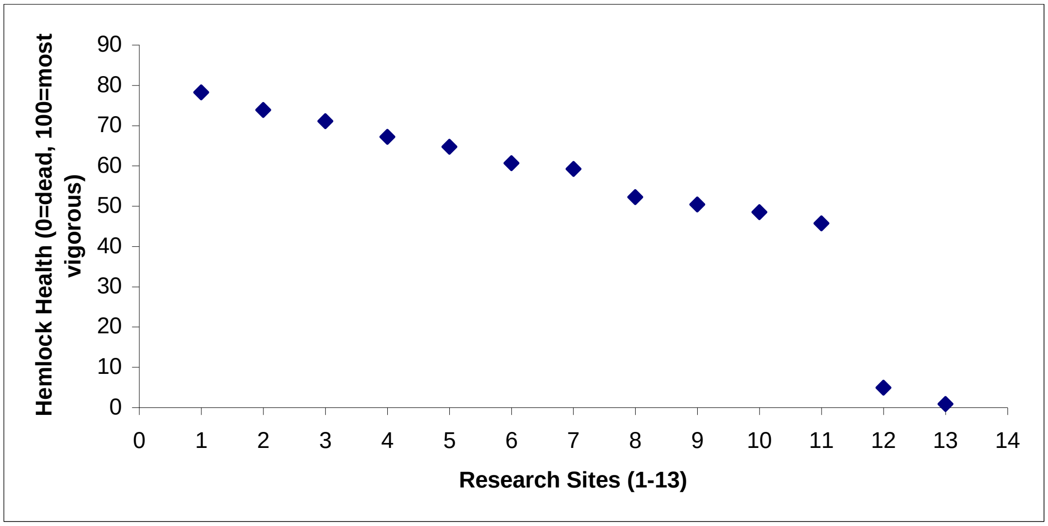

Figure 3. Research sites followed a strong gradient of hemlock health and HWA impact (site 13 is most impacted with a hemlock health value of .9 while site 1 is the least impacted with a health value of 78.2).

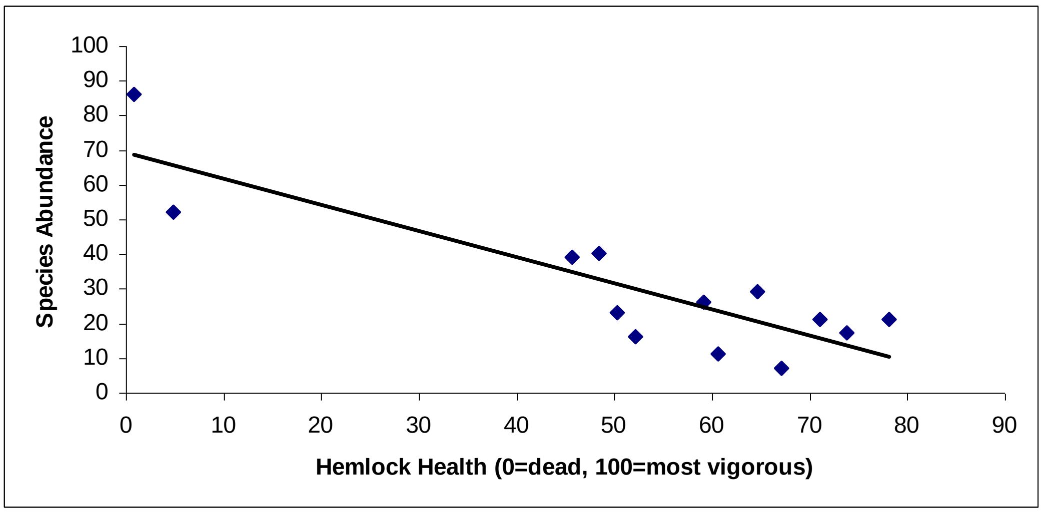

Figure 4. The inverse relationship between hemlock health (i.e level of HWA impact) and the abundance of macroinvertebrates, sites with the highest levels of hemlock mortality also have the greatest abundance of macroinvertebrates.

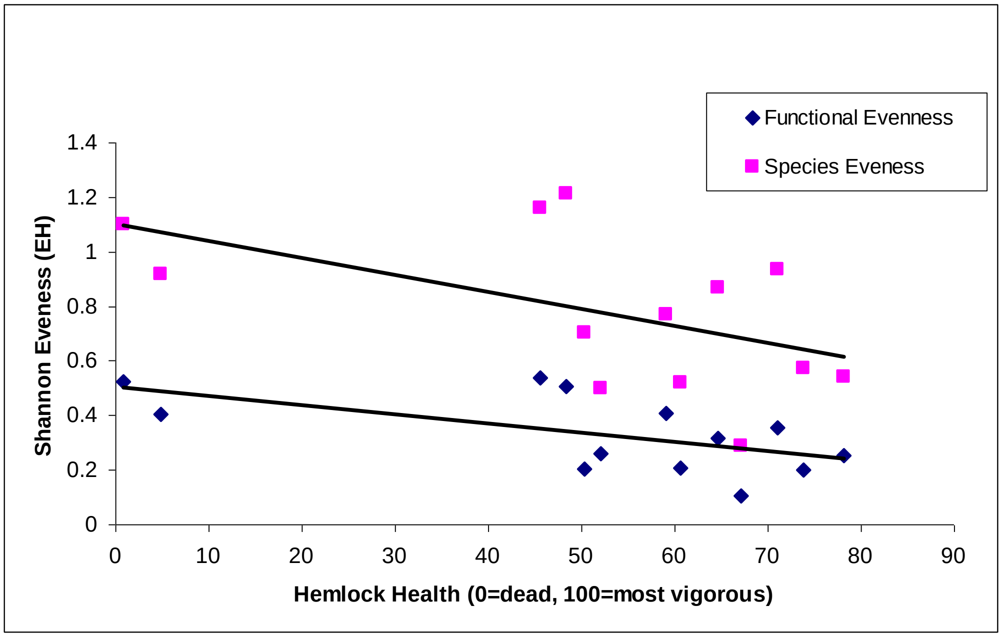

Figure 5. The inverse relationship between hemlock health and species and functional evenness, both species and functional evenness are highest in sites with poor hemlock health

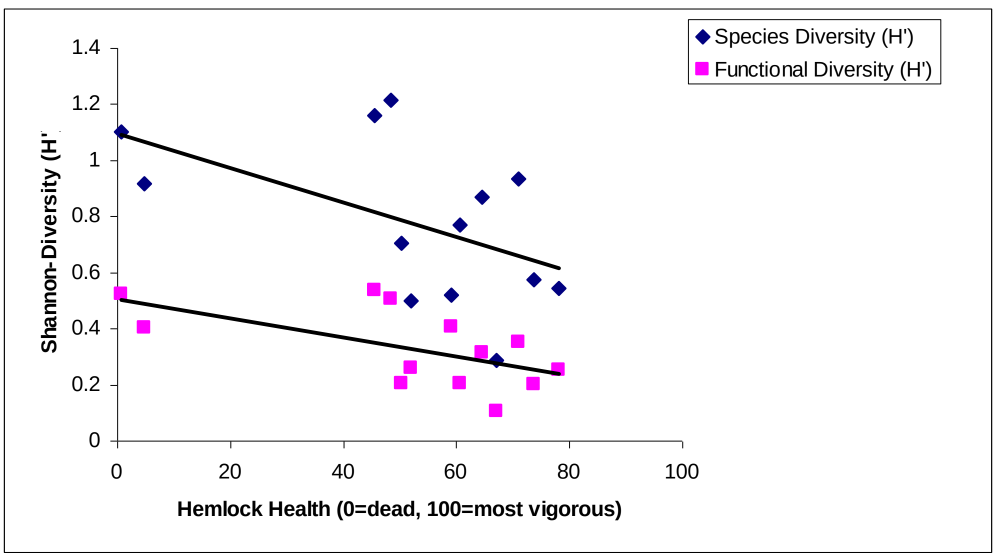

Figure 6. The inverse relationship between hemlock health and species and functional diversity, both species and functional diversity are highest in sites with poor hemlock health

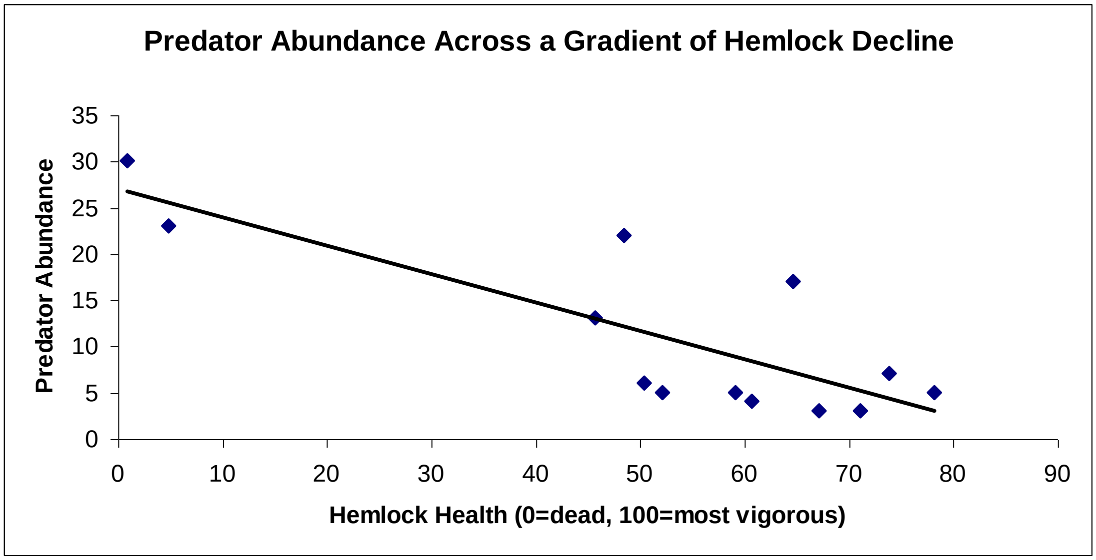

Figure 7. The abundance of predators showed an inverse relationship to hemlock health, those sites with the most hemlock mortality had the highest abundance of predators.

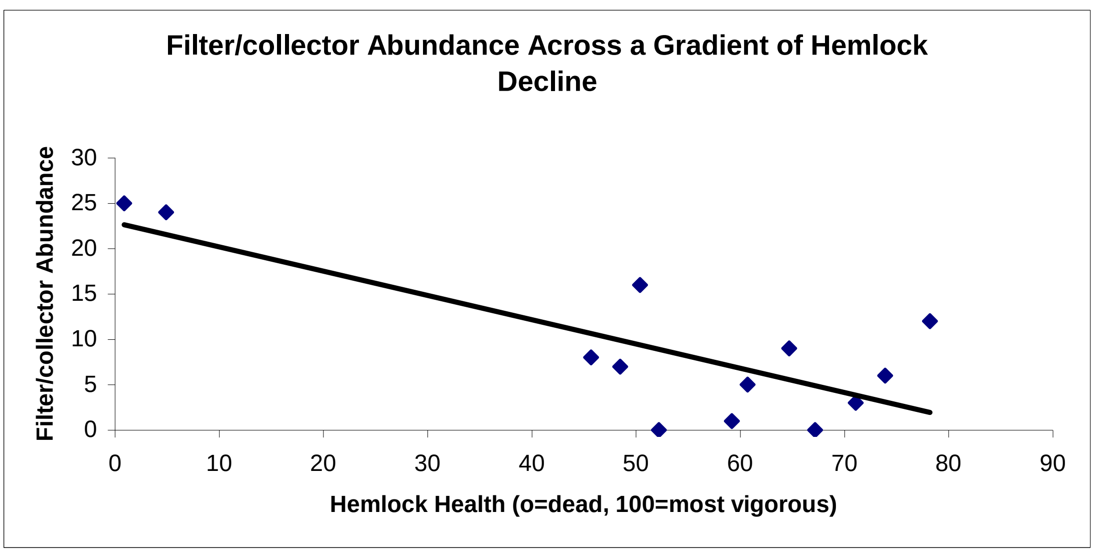

Figure 8. The abundance of filter/collectors showed an inverse relationship to hemlock health, those sites with the most hemlock mortality had the highest abundance of filter/collectors.

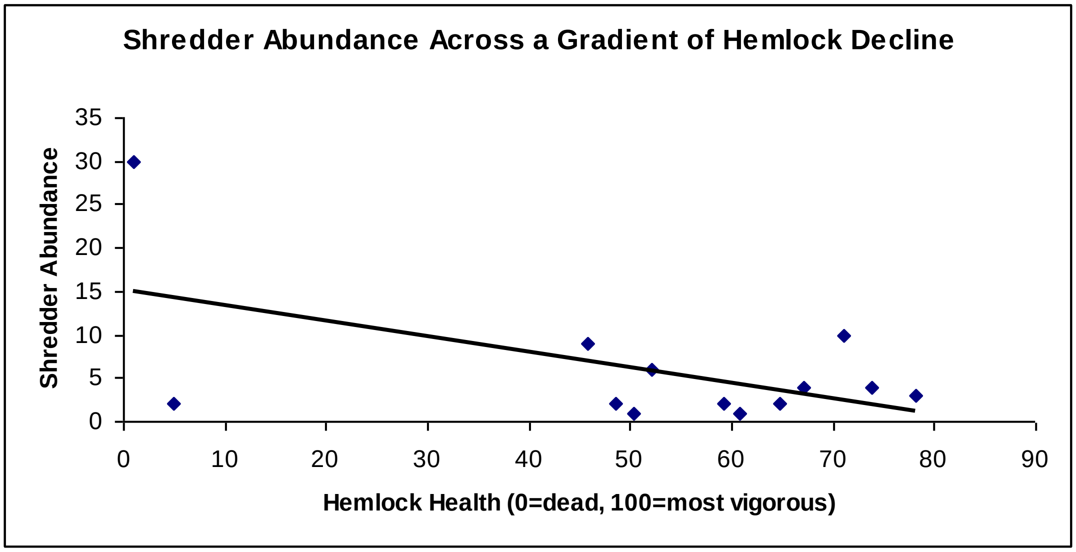

Figure 9. The abundance of shredders showed an inverse relationship to hemlock health, those sites with the most hemlock mortality had the highest abundance of shredders.

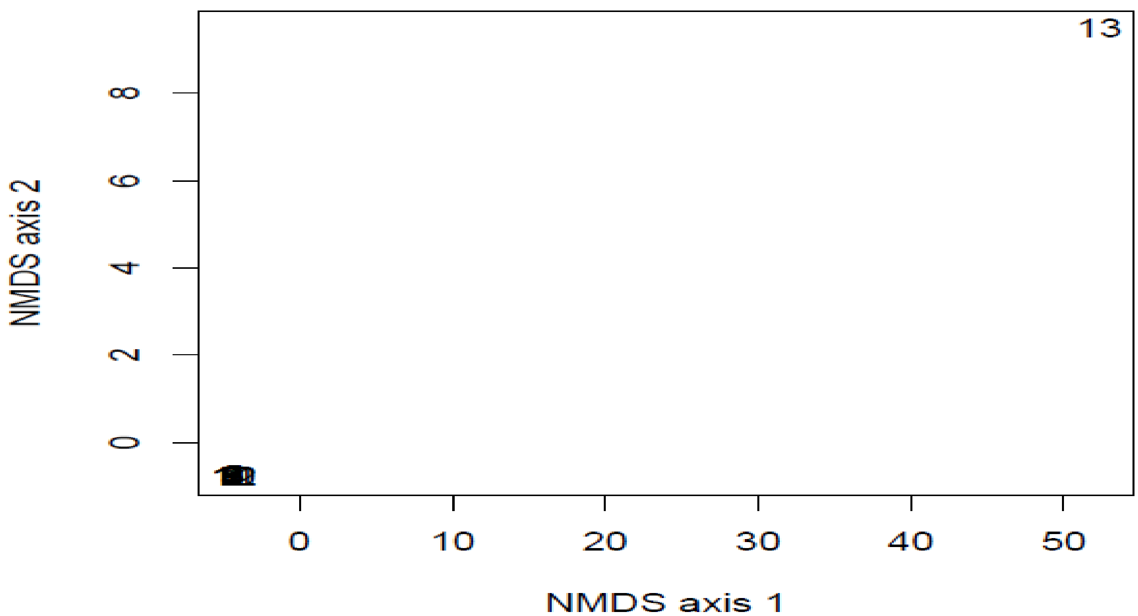

Figure 10. 2-Demensional ordination with all 13 sites using species composition, stress value = 0.015

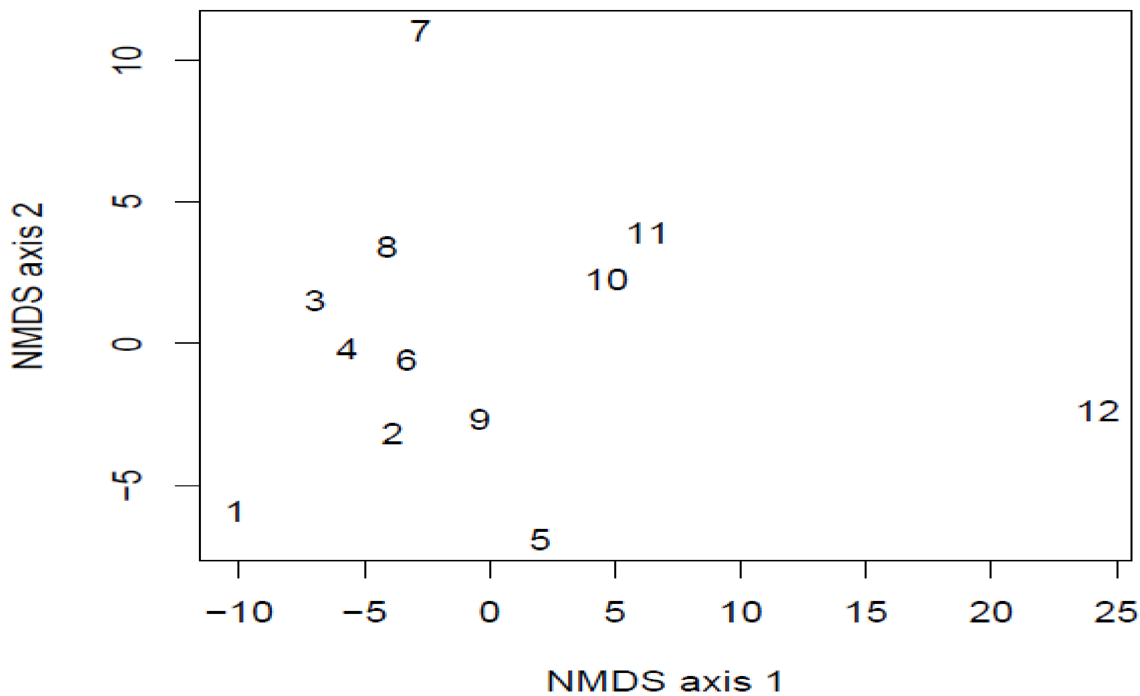

Figure 11. 2-Demensional-ordination with 12 sites (excluding site #13, Hurd) using species composition, stress value = .5.128

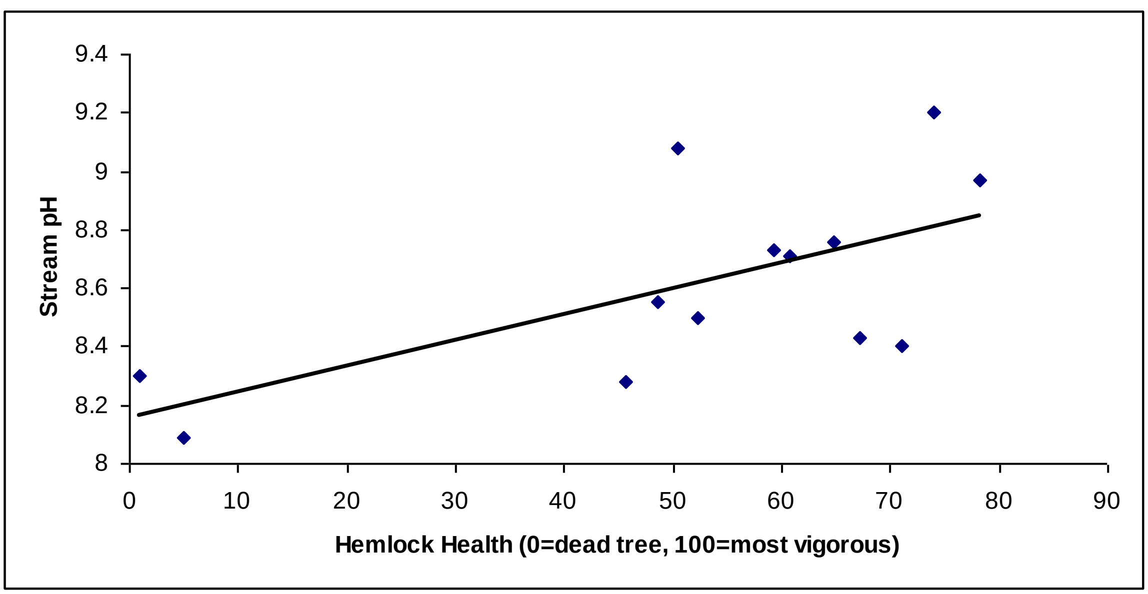

Figure 12. pH increased with hemlock health across 13 sites

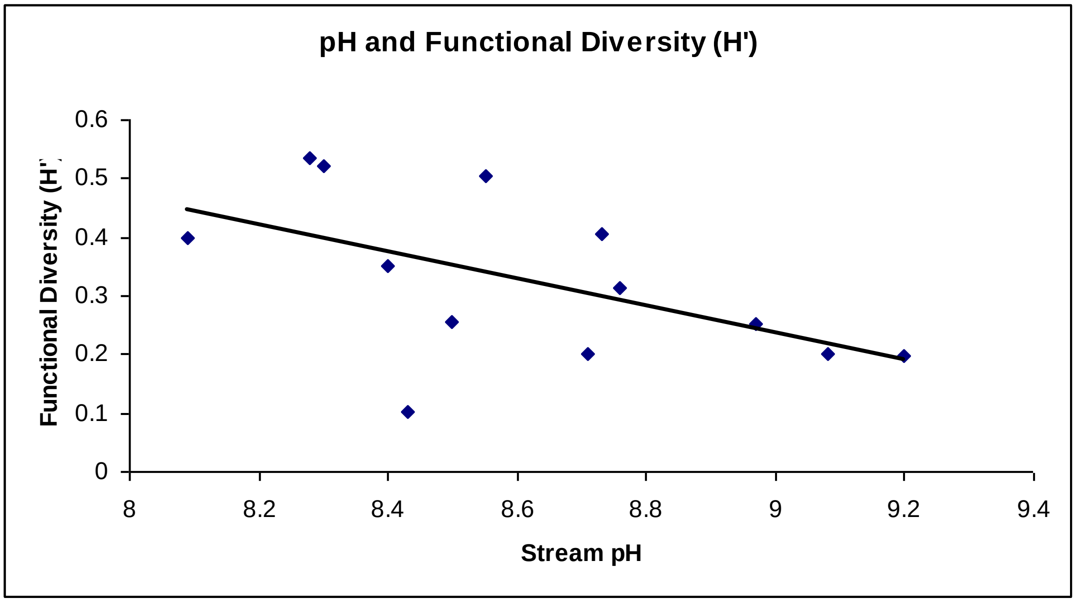

Figure 13. Functional diversity (E') showed a moderate inverse correlation to stream pH across the 13 sampling sites.

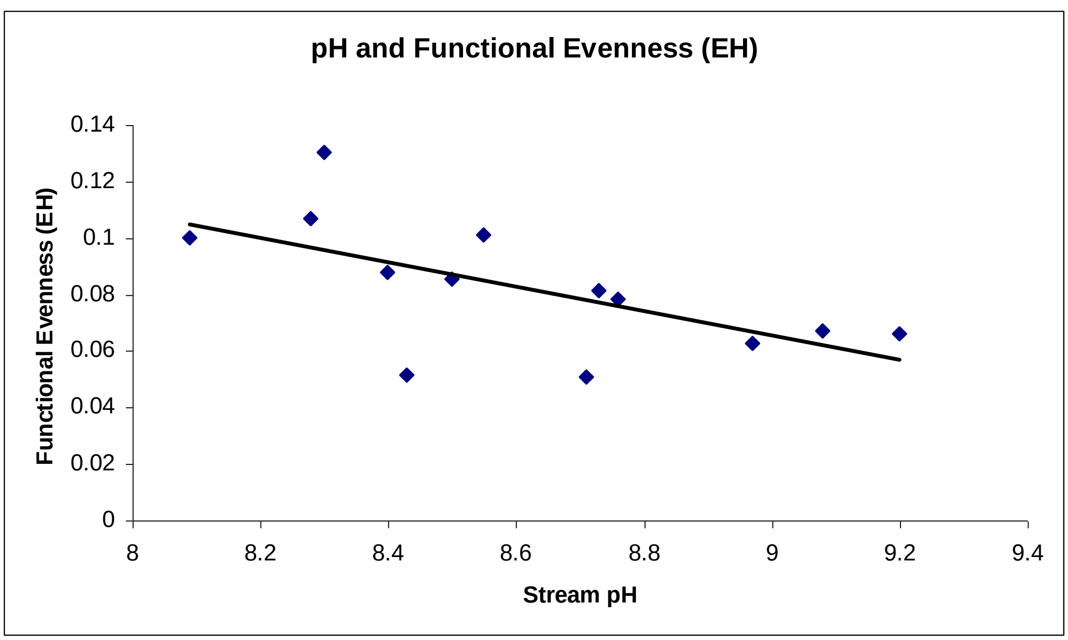

Figure 14. Functional evenness (EH) showed a moderate inverse correlation to stream pH across the 13 sampling sites.

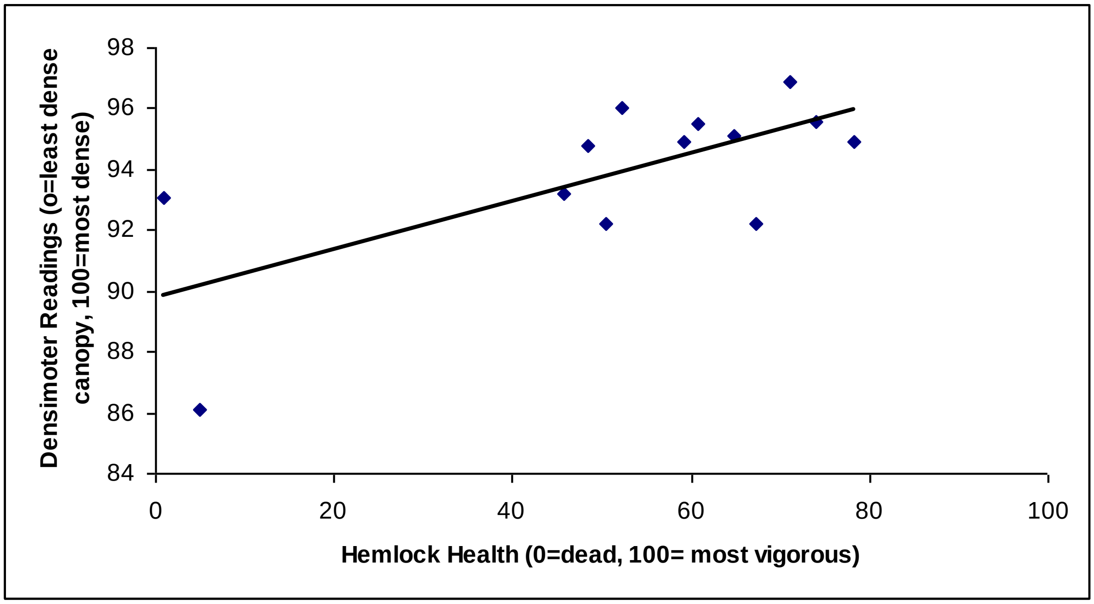

Figure 15. The relationship between the health of the hemlock canopy and the amount of light reaching the stream channel, here the healthier hemlock forests had higher shading levels as measured through densiometer readings.

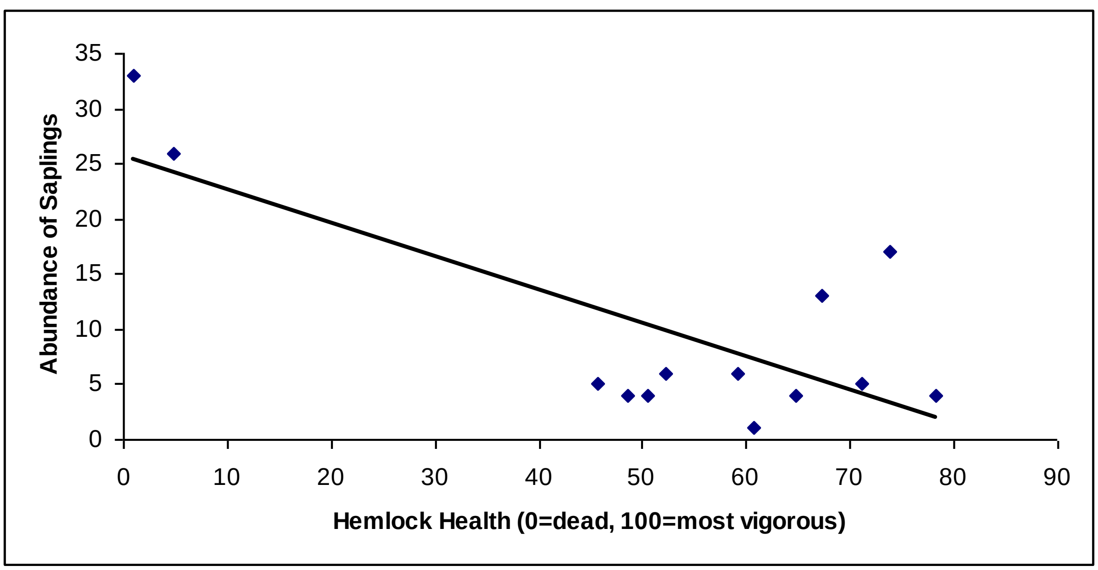

Figure 16. The abundance of saplings showed an inverse relationship with hemlock health, more saplings were present in sites with high levels of HWA impact

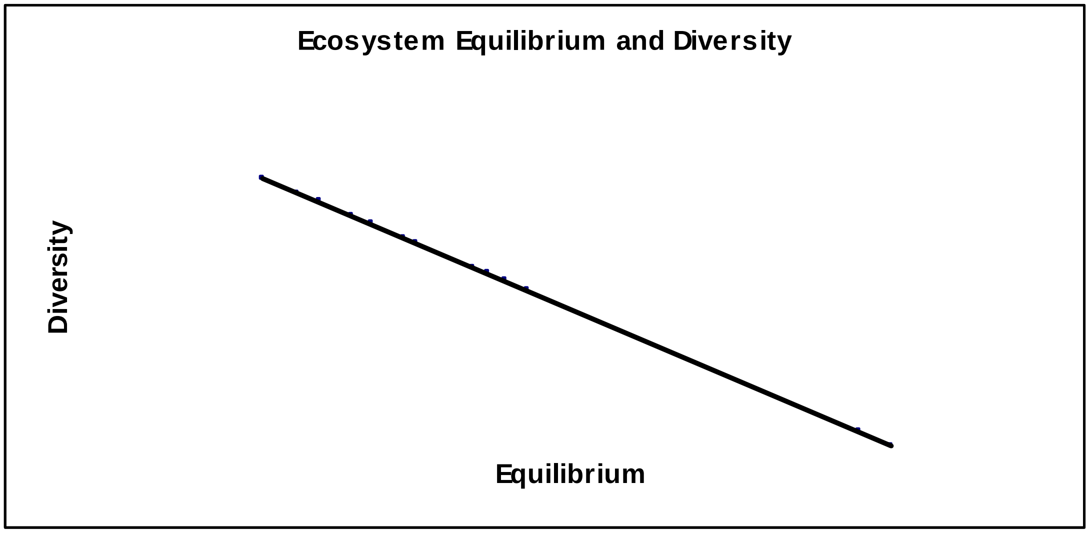

Figure 17. A simplified graph of Huston's General Hypothesis of Species Diversity in which low diversity occurs at high levels of equilibrium (although the relationship might not be exactly linier)

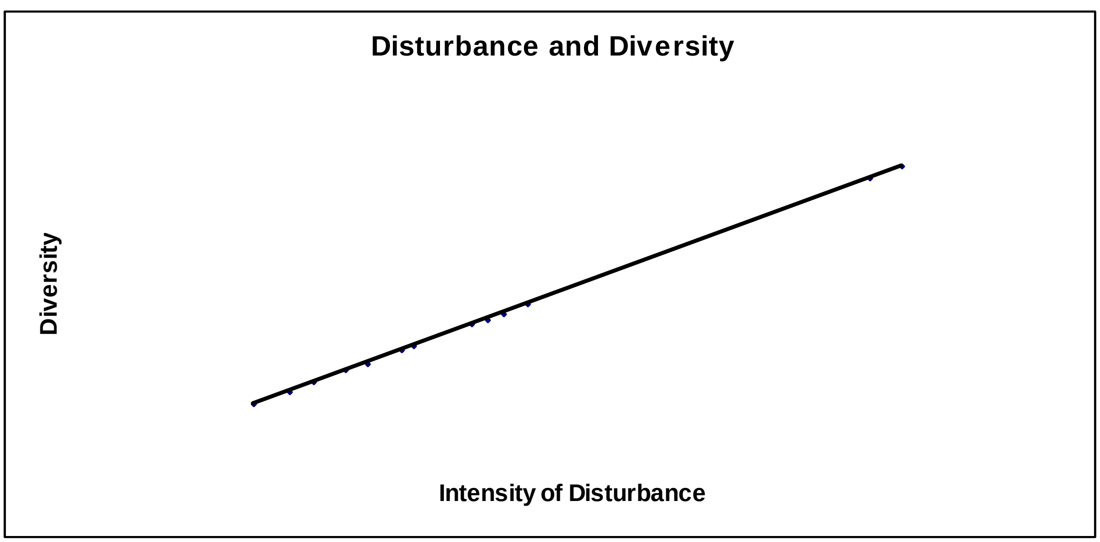

Figure 18. The relationship between the intensity of disturbance, which functions here as an inverse for an equilibrium state, and diversity, as the intensity of Disturbance increases so to does diversity (again, the relationship might not be exactly linier)

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