Macroinvertebrate colonization of invasive *Fallopia* x bohemica leaf litter in a temperate stream

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ABSTRACT: We compared macroinvertebrate communities on leaf packs made of recently senesced leaves of native *Quercus* and *Acer*, and invasive *Fallopia* x bohemica. Leaf packs were left in Cascadilla Creek, a third-order temperate stream in central New York, U.S.A., for 7, 14, 28, or 56 days. After we removed them from the stream, we examined the leaf packs for biomass loss and invertebrate richness and abundance. While we expected to see a significant difference between leaf types, which would indicate a cascade effect of invasive vegetation on higher trophic levels, little variation was actually seen. The results of this study suggest that localized effects of *F.* x bohemica on invertebrate communities in streams are quite small if the invasive component represents only a small percentage of the total biomass of the system. Leaf breakdown rates also did not differ significantly between the invasive and either of the two native leaf types. We observed larger numbers of predators on leaves of *F.* x bohemica than on either of the native leaf types, which may impact leaf breakdown and consumer activity over a longer study period, but what we have seen so far is still inconclusive. Further study will have to better simulate true invasion conditions where native vegetation is not available to invertebrate communities, and incorporate a full season of leaf breakdown.

INTRODUCTION

Macroinvertebrates

Aquatic macroinvertebrates in temperate streams play a key role in the ecosystem by serving as the primary mechanism for transferring food and nutrients to higher trophic levels, both within the stream and in the nearby terrestrial environment (Stehr 1987). Leaves that wash into these streams from trees on adjacent banks in autumn provide most of the organic and inorganic inputs that fuel their food chains throughout the year (Webster et al. 1995). Aggregations of leaves on stream beds serve as both a food source and a substrate for colonies of invertebrates, which feed on the leaves themselves as well as smaller invertebrates, particulate organic matter, or other browse that gets trapped in the stream channel (Malmqvist and Sjöström 1984). These leaf packs are discrete habitat units that favor specialized invertebrate communities, and so are often used as the subjects of stream ecosystem studies (*e.g.* Malmqvist 1993).

Freshwater insects are traditionally segregated according to the morphology of their mouthparts because this significantly affects their feeding behavior, and thus their role in the community. There are four basic groups, called functional feeding groups: shredders, collector-gatherers, grazers, and predators. Shredders feed directly on the leaves that wash into the stream channel, helping to bring those nutrients into the system. Shredders play an important role in processing leaves in streams, converting coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM), which can be utilized by other invertebrates (*e.g.* Oberndorfer et al. 1984, Cummins 1989, Wallace et al. 1995). Collector-gatherers, either filter-feeding or deposit-feeding, and grazers feed on the FPOM and associated microflora. Predators feed on smaller invertebrates in the leaf pack colonies, serving as an important control on the other groups (Cummins 1973).

Many studies focus on the shredder group, because leaf breakdown in the stream is directly associated with the activity of their populations, which share an evolutionary relationship with the plant communities growing in their adjacent upstream surroundings. The point at which approximately 50% of the annual leaf input has been processed should correspond with maximum shredder biomass, and also tends to correspond with maximum invertebrate biomass in general. For slow-processing leaves this is around 600 cumulative degree-days; for fast-processing leaves 300 degree-days (Cummins 1973).

The functional feeding group framework is a convenient generalization of complex stream communities, however it does not pay much attention to the trophic roles of individual species (Mihuc 1997). Feeding roles of some invertebrates also vary seasonally, making categorization all the more difficult (Haapala et al. 2001). Species within a given functional feeding group are not necessarily redundant either. A study by Jonsson and Malmqvist (2000) found leaf breakdown decreased by half when they were colonized by only one species of shredder, as opposed to three. Although few similar studies have been published, it seems likely that intra-feeding group competition would encourage adaptive niche specialization and discourage redundancy (Jonsson and Malmqvist 2003).

Traditionally, the process of leaf breakdown within a stream is thought to occur in three separate and successive stages: leaching, microbial conditioning, and invertebrate consumption. This is being challenged by some scientists in favor of a more interactive model where the three stages may occur simultaneously. In the current model, bacterial and fungal communities in the leaf packs are the first to begin breaking down the leaves, conditioning them to the point where shredder colonization could begin. However, the alternate idea focuses less on microbes as enablers for invertebrates, and more on the two competing for the same resources (Gessner et al. 1999).

High breakdown rates observed in arctic and subalpine streams challenges the central role of temperature in breakdown rates, suggesting that other variables (nutrients, pH, stream biota, etc.) may be more interrelated than previously thought. Haapala et al. (2001) found that in lower latitudes microbes contribute more to breakdown, whereas in higher latitudes, invertebrates contribute more, suggesting that latitudinal gradients may make little difference over all (see also Irons et al. 1994).

The role of invasive plants

Exotic plants species which exclude native species and dominate the landscape are known as invasives. They generally follow a classic logistic growth pattern with their introduction followed by a lag period of variable length, and then exponential growth which continues until the carrying capacity of the invaded system has been reached (Baker et al. 1986). “Corridors of invasion” such as roads, waterways, and railroads are important pathways for the spread of invasive species, due to frequent disturbance and turbulence from passing vehicles, which is ideal for disseminating propagules (Harrison et al. 2002, Gelbard and Belnap 2003, Barney 2006). However, relatively few exotic species will actually become invasives, because of the large numbers of species that are introduced, and the disproportional impact they can have, the ecological and economic harm they cause throughout the world is large. The “Tens Rule” of invasive success, first proposed by Williamson and Fitter (1996), states that only one in ten introduced species will escape from cultivation, and from that pool one in ten will survive to self-sustaining populations to become naturalized in their new habitat. From those naturalized species one in ten will become invasive.

An exception to the Tens Rule is that species that are intentionally introduced, such as *Fallopia* x bohemica (a hybrid of *Fallopia japonica*, Japanese Knotweed), have a much better chance of success than those which accidentally get transported from one place to another, having been selected specifically for characteristics that will make them hardy and adaptable (Harrington et al. 2003). Intentionally introduced species are also often introduced in multiple locations over vast geographic areas, giving them a further advantage (Baker et al. 1986).

Many details about the short- and long-term effects of this displacement of native vegetation, however, are not known. Habitat heterogeneity in general promotes species richness, while disturbance, such as an invasion, promotes the dominance of a tolerant species (Cardinale et al. 2000). Beyond the general concept that lowered species richness has negative effects on ecosystem functioning, there is little specific information about the consequences of biodiversity loss with respect to individual systems and organisms (Loreau et al. 2001).

Japanese Knotweed has followed the traditional invasion pattern with a relatively short lag time (50 years) between introduction and rapid spread, and is now known as an aggressive invader throughout Europe and North America. Some studies have begun to suggest direct effects of Knotweed invasions on higher trophic levels because of the disappearance of native vegetation (Maerz et al. 2005).

The objectives of this study were to examine the interactions between Knotweed leaves as allochthonous organic material in streams (originating outside of the system and washing in from the bank) and their primary consumers: aquatic macroinvertebrate communities. I expected to see a large difference in the invertebrate communities that colonized Knotweed leaves as compared to two types of native leaves, *Acer* (Maple) and *Quercus* (Oak). Such a difference would support the hypothesis that the effects of an invasion create a cascade effect of changes throughout the system.

METHODS AND MATERIALS

Site description

I conducted my experiment in Cascadilla Creek, a non-invaded, third-order stream in the Cascadilla Creek drainage basin (Dahl and Peckarsky 2002) in Ithaca, N.Y., USA, in the Cayuga Lake watershed. The rocky streambed displays a natural complexity composed primarily of gravel and cobble, and the forested bank is buffered by native vegetation on either side of the channel.

Experimental organism

Japanese Knotweed (*Fallopia* x bohemica) is a classic invader, completely taking over habitat from native vegetation by aggressive growth (Baker 1986). It is an ideal early successional species in its native habitat (Chiba and Hirose 1993), where it can grow on slopes up to 40 degrees and up to 3800m above sea level (Beerling et al. 1994). It optimizes its photosynthetic potential by self-regulating its growth within clusters of shoots so that their relative heights allow for maximized leaf surface area exposed to sunlight (Suzuki 1994). As a result, shoots grow quickly and block practically all sunlight from reaching competing sprouts allow Knotweed to spread to the exclusion of other vegetation in areas in which it invades (Seiger 1997, Shaw and Seiger 2002, Maerz et al. 2005). Reproducing both sexually and asexually, it can utilize a wide variety of habitats, growing in a wide range of soils between pH of 3.7 and 8.5, with varying nutrient levels (Seiger 1997). Knotweed is now found throughout Europe and North America between 43 and 63˚ N in latitude (Beerling et al. 1994).

Maerz et al. (2005) found no native vegetation beyond ten meters into a Knotweed stand, even when native cover and richness were high in adjacent sites outside of the invasion front. This absolute invasion is also troublesome because Knotweed shoots die back in the winter, often leaving soils exposed and susceptible to erosion since no other vegetation is present to hold onto topsoils (Seiger 1997, Shaw and Seiger 2002).

Leaf collection and set up

We used leaves from Red Oak *(Quercus rubra)*, Sugar Maple *(Acer saccharum)*, and Japanese Knotweed in leaf packs to simulate naturally occurring leaf accumulation (*e.g*. Merrit et al. 1979). We collected the leaves in the fall of 2004 just after senescence and dried in open paper bags. We collected Oak and Maple leaves from trees on the bank of the study site, and the Knotweed from a stand near Cascadilla Creek, about a mile from the study site. We weighed dried leaves out into 3g packs, sewed them into plastic mesh bags, and tagged them with a unique identification number. We tied the bags to metal stakes hammered into the stream bed along a 70 meter transect. They were removed at intervals of 7, 14, 28, and 56 days between 24 October, 2004, and 22 December, 2004, coincident with natural leaf input. We removed 7 samples of each leaf type on each collection day. We collected water temperature data in the stream daily at 11am throughout the 56-day period. Seven samples of each leaf type were kept as processing controls: they were wet in the stream, pressed against a rock, and immediately removed. They were weighed and used as initial biomass for each leaf type to calculate percent mass lost over the course of the study.

Once we removed the leaf packs from the stream, we placed them in large ziplock bags and immediately brought them inside the lab to be rinsed and preserved. We rinsed the leaves, mesh bags, and ziplock bags into a basin, and preserved the rinsed material in 70% ethanol. Each sample was stained with Rose Bengal before being analyzed so that invertebrates could be more easily distinguished from small pieces of leaves and other debris in the samples. We then dried the leaves in an oven and weighed them.

Leaf pack sample processing

We rinsed the contents of each leaf pack again through a 500mm mesh sieve and examined them individually under a compound microscope. Invertebrates were separated out into morphospecies of the lowest taxonomic group possible and counted. We organized the samples by their unique identification number, so that we were not biased by the leaf type used and collection day during sample processing. We compared total numbers of each invertebrate morphospecies found based on leaf type used in the original leaf pack, and number of days spent in the stream.

The starting biomass for each leaf type was defined as the average of the oven-dried biomass of the Day 1 control leaf packs. We determined average percent remaining biomass for each leaf type on each collecting day using the difference between the starting biomass and the biomass of leaf packs collected on each subsequent collecting day. Breakdown rates for the three leaf types were said to be significantly different if they were not within two standard deviations of the mean from each other.

RESULTS

Site and Abiotic Factors

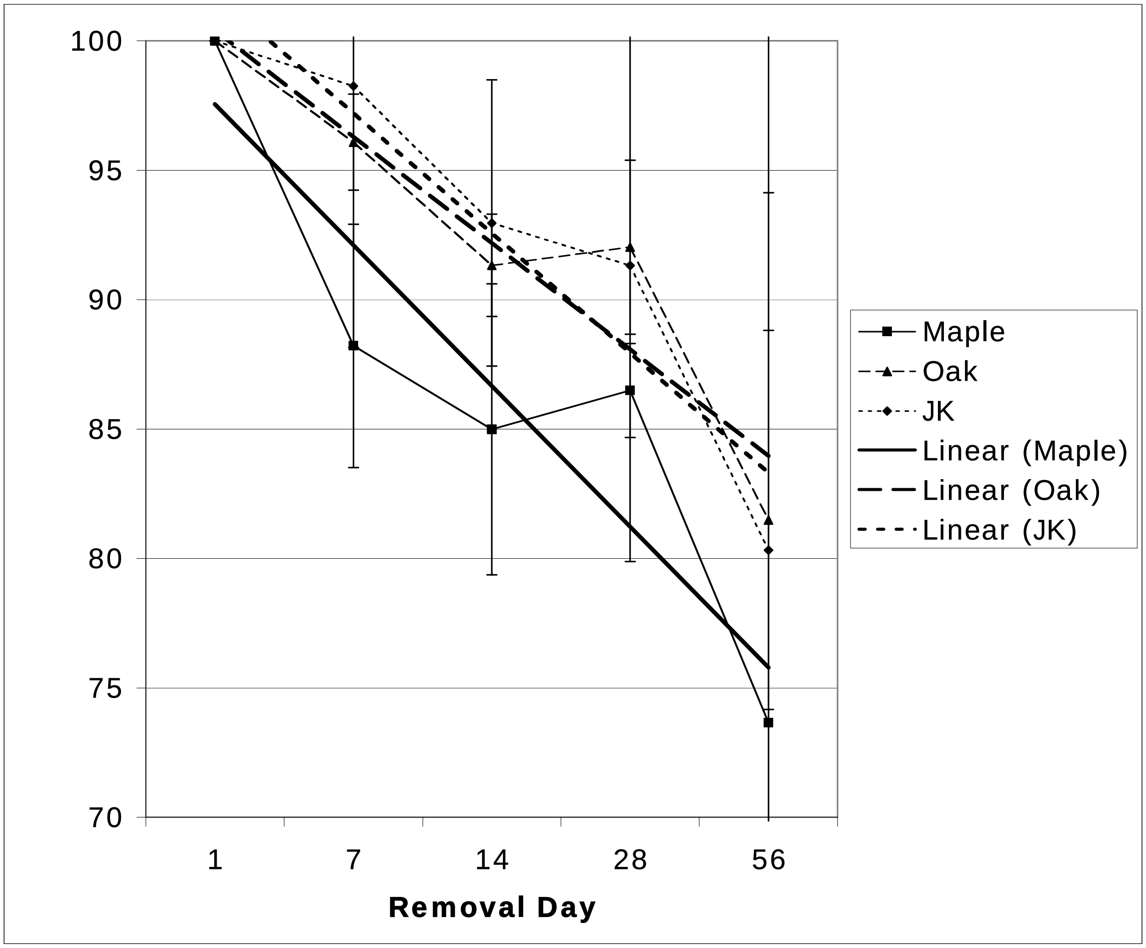
The water temperature in the stream reached a high of 12˚C on 1 November, Day 9 of the study. After dropping to 0˚C on 16 and 17 November (Days 24 and 25, respectively), it rose again sharply to hover between 4 and 8˚C for the rest of November. In early December, around Day 40, temperatures in the stream dropped again, reaching 0˚C on 16 December, Day 54, where they stayed for the rest of the study period. The stream did not freeze over, although there was occasional icing in places.

Leaf biomass

Leaf packs of all three leaf types lost mass steadily throughout the study period (Figure 1). We compared the biomass remaining in each leaf pack on each collection day to the initial biomass for the leaf species and averaged them, showing two standard deviations from the mean. Decomposition in the stream for all leaf species most closely followed a linear model; r^2 values for Maple, Oak, and Japanese Knotweed were 0.88, 0.84, and 0.90, respectively. Oak and Maple were significantly different on two out of the four removal days (not including the Day 1 processing controls). Knotweed was not significantly different from either of the other leaf types on any of the removal days. Maple and Oak leaves showed a slight increase in average percent biomass retained between days 14 and 28, but between all other collection days for all leaf types the leaf packs lost mass.

The Maple leaf packs processed the most quickly, retaining less biomass on each collection day than those of either Oak or Japanese Knotweed, and ending on Day 56 with an average of 73.7% of the starting biomass. Knotweed leaf packs retained the most biomass on Days 7 and 14, but nearly matched the percent biomass remaining in the Oak leaf packs on Days 28 and 56, ending just below Oak at 80.3% of their starting biomass. On Day 56, Oak leaves still retained 81.5% of their starting biomass. Maple and Oak were within two standard deviations of each other on Days 14 and 56, and significantly different on Days 7 and 28. Standard deviations for the Knotweed biomass were quite large and always within two standard deviations of the other two leaf types.

Figure 1. Average biomass remaining in the leaf packs of each leaf type on each collection day, expressed as a percentage of the average biomass of the Day 1 processing controls.



Faunal communities

We found one salamander (*Eurecea bislineata*) in one of the Japanese Knotweed leaf packs removed from the stream on Day 14, but all other fauna in the leaf packs were invertebrates. Overall, 58 different morphospecies of macroinvertebrates were identified in the leaf packs, from 11 different orders (Table 1). In total, 13500 individuals were found. The four most abundant morphospecies found were Tricoptera in the superfamily Hydropsychoidea and the family Hydropsychidae, Diptera in the family Chironomidae, Ephemeroptera in the family Baetidae, and Plecoptera in the family Perlodidae. These four dominated the total invertebrate communities by far in all three leaf types, as the only morphospecies that regularly made up at least 10% of the community on their own, and over 90% of the community when combined together. Other morphospecies found on average at least once per leaf pack were Arachnids, Diptera in the families Tipulidae, Empididae, and Anthericidae, Ephemeroptera in the family Ephemeridae, Tricoptera in other families, Copopods, and Nemotodes. These morphospecies, combined with others found only sporadically, never exceeded 10% of the invertebrate community make-up for any given leaf pack.

Table 1: Total macroinvertebrate abundance by leaf type for the ten most abundant morphospecies observed.

Invertebrate Morphotypes	*Quercus*	*Acer*	*Fallopia*	*All*
Hydropsychidae (Trichoptera)	599	958	537	2094
Chironomidae (Diptera)	1738	2220	1799	5757
Baetidae (Ephemeroptera)	987	1255	881	3123
Perlodidae (Plecoptera)	364	427	654	1445
Tipulidae (Diptera)	70	97	45	212
Ephemerellidae (Ephemeroptera)	21	38	32	91
Arachnida	30	22	36	88
Simuliidae (Diptera)	52	43	36	131
Copopoda	30	16	20	66
Nemotoda	14	7	18	39
Total	3905	5083	4058	13046

Nearly all of the most common mophospecies increased in abundance throughout the course of the study (Figure 2); most displayed a rapid increase in numbers on all leaf types. One notable exception was the Perlodidae, whose abundance peaked in the middle of the study (Day 14 for Japanese Knotweed; Day 28 for Maple and Oak) and had declined significantly by Day 56. The Perlodids were also more abundant in the

Knotweed leaf packs, while the relative abundances of other morphospecies were more consistent among different leaf types (Figure 2.4). Baetid abundance increased throughout the study on Maple and Oak leaf packs (although on Maple they experienced a significant dip on Day 28). However, on Knotweed they displayed a U-shaped abundance curve: declining between Days 7 and 28, and picking up again by Day 56 to just below Day 7 numbers. Some other morphospecies that were not as abundant overall (Arachnids, Copopods, and Nemotodes) displayed more variable and irregular abundance curves.

Figure 2.1 The relative average abundance, per leaf pack, of Hydropsychidae.

Figure 2.2. The relative average abundance, per leaf pack, of Chironomidae.

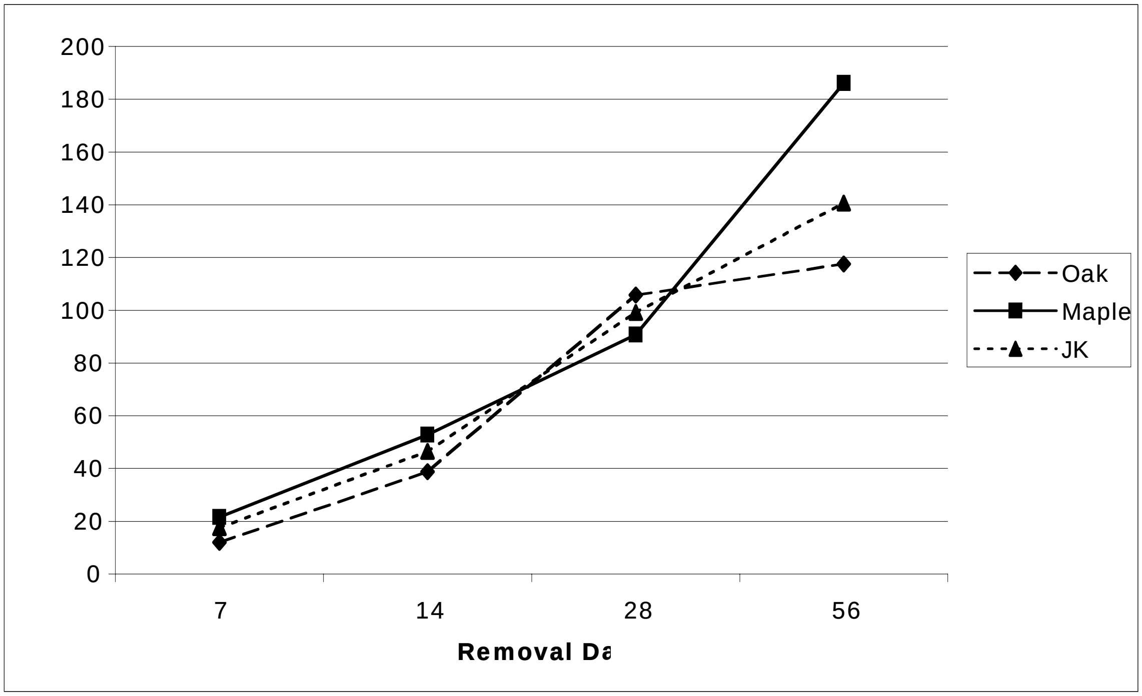


Figure 2.3. The relative average abundance, per leaf pack, of Baetidae.

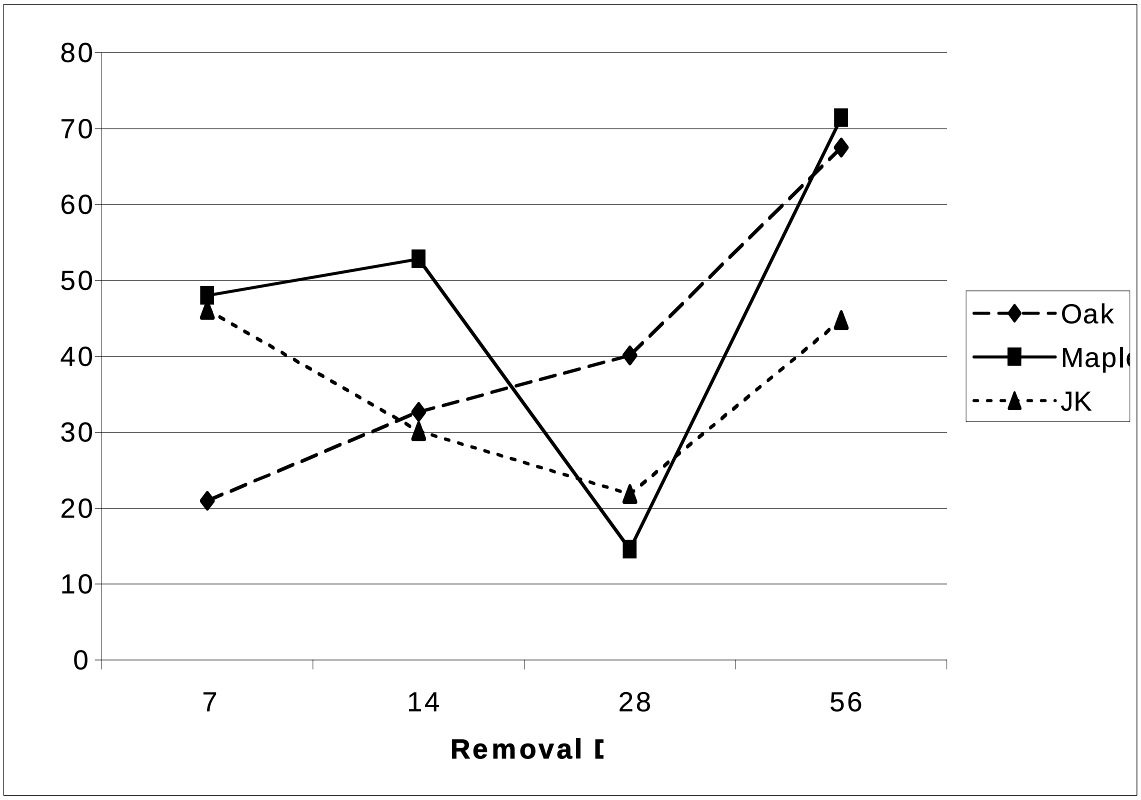
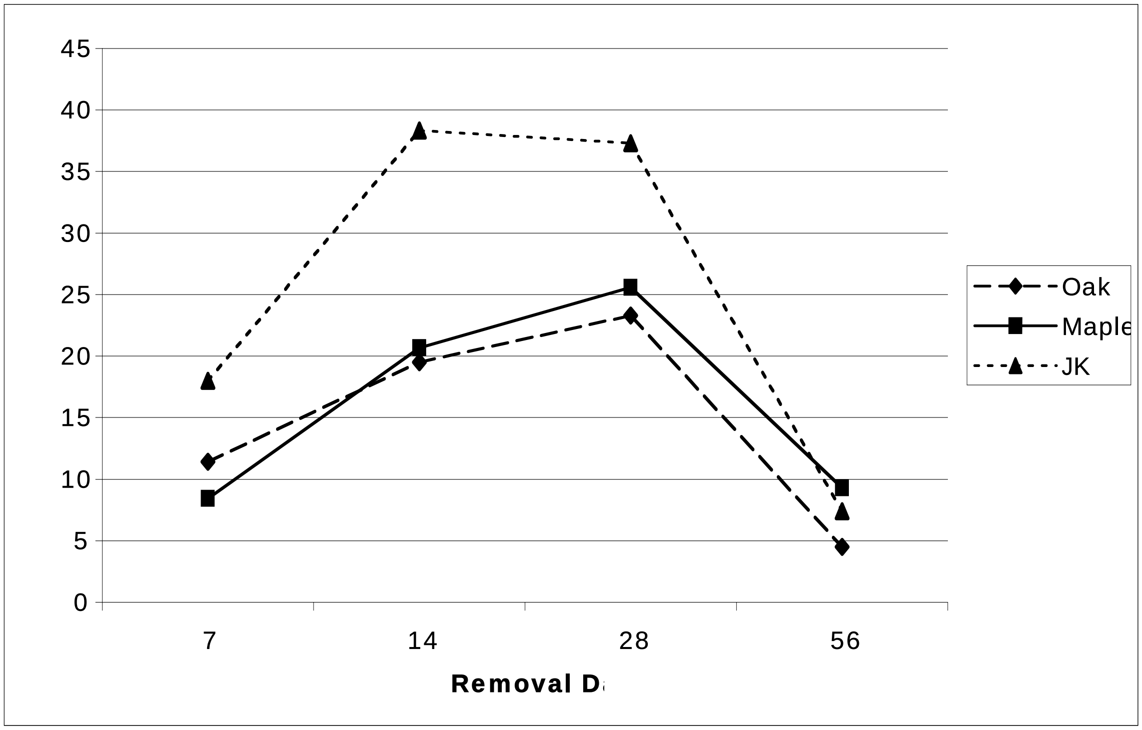


Figure 2.4 The relative average abundance, per leaf pack, of Perlodidae.



The invertebrate community compositions did not differ greatly between leaf types, but changed more dramatically between collection days (Figure 3). Among the four dominant morphospecies, Chironomids increased rapidly over the study as Baetids and Perlodids declined. On Day 7, the most abundant morphospecies was the Baetid, making up around 40% of the populations of each leaf type. Hydropsychids, Chironomids, and Perlodids each made up just under 20% of their respective populations. By Day 14, the Chironomid component had increased to just over 30% in all leaf types, while the Baetid component had decreased to 30% or less. By Day 28, the Chironomid component was over 50%, and the Baetids had shrunk to less than 20%. Hydropsychids and Perlodids held 10-20% of their populations, but on Day 56 the Perlodids had been reduced to less than 5%. Chironomids stayed around 50% and Hydropsychids and Baetids around 20% each.

Figure 3.1 Macroinvertebrate community composition by leaf species on Day 7.

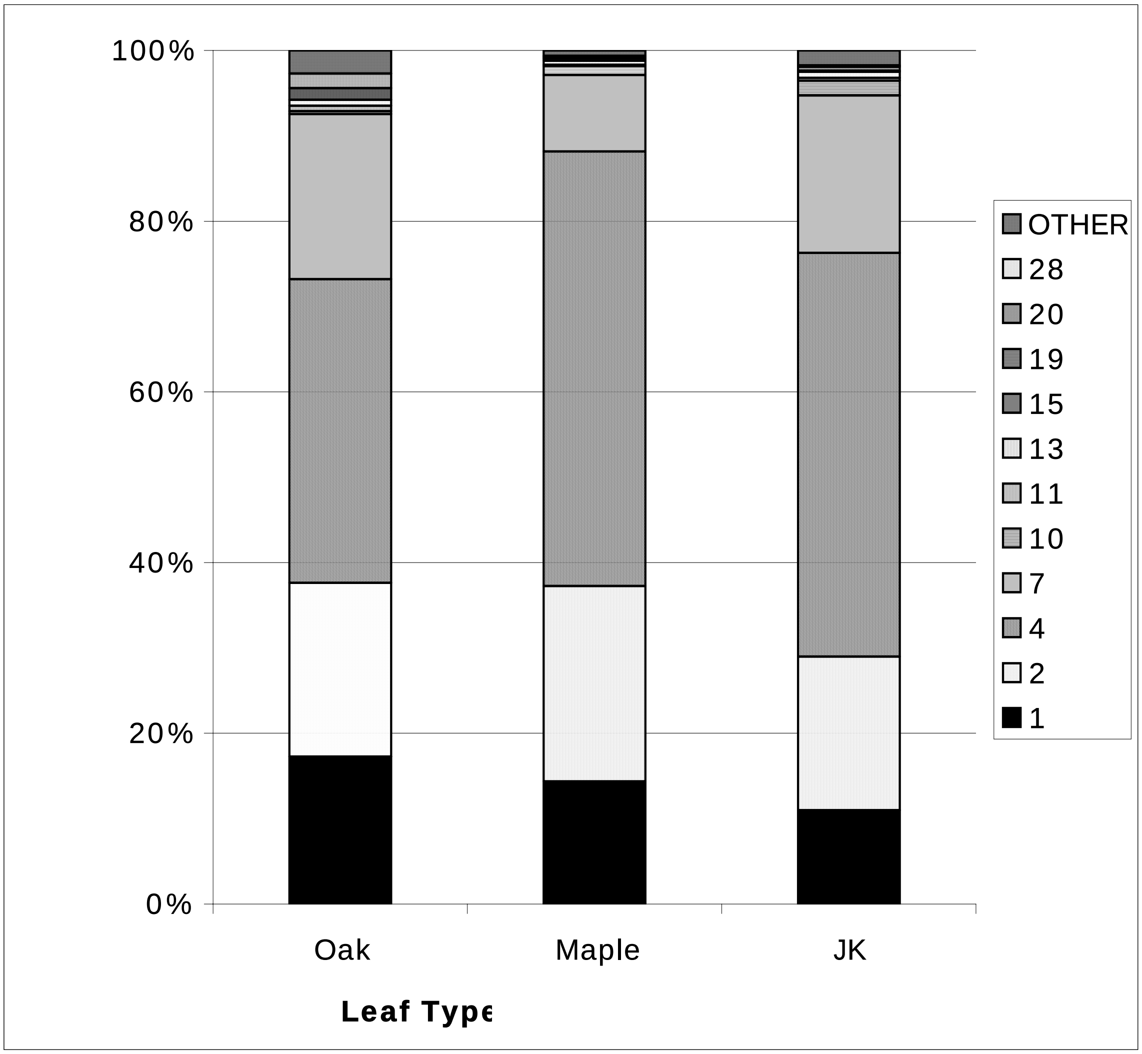


Figure 3.2 Macroinvertebrate community composition by leaf species on Day 14.

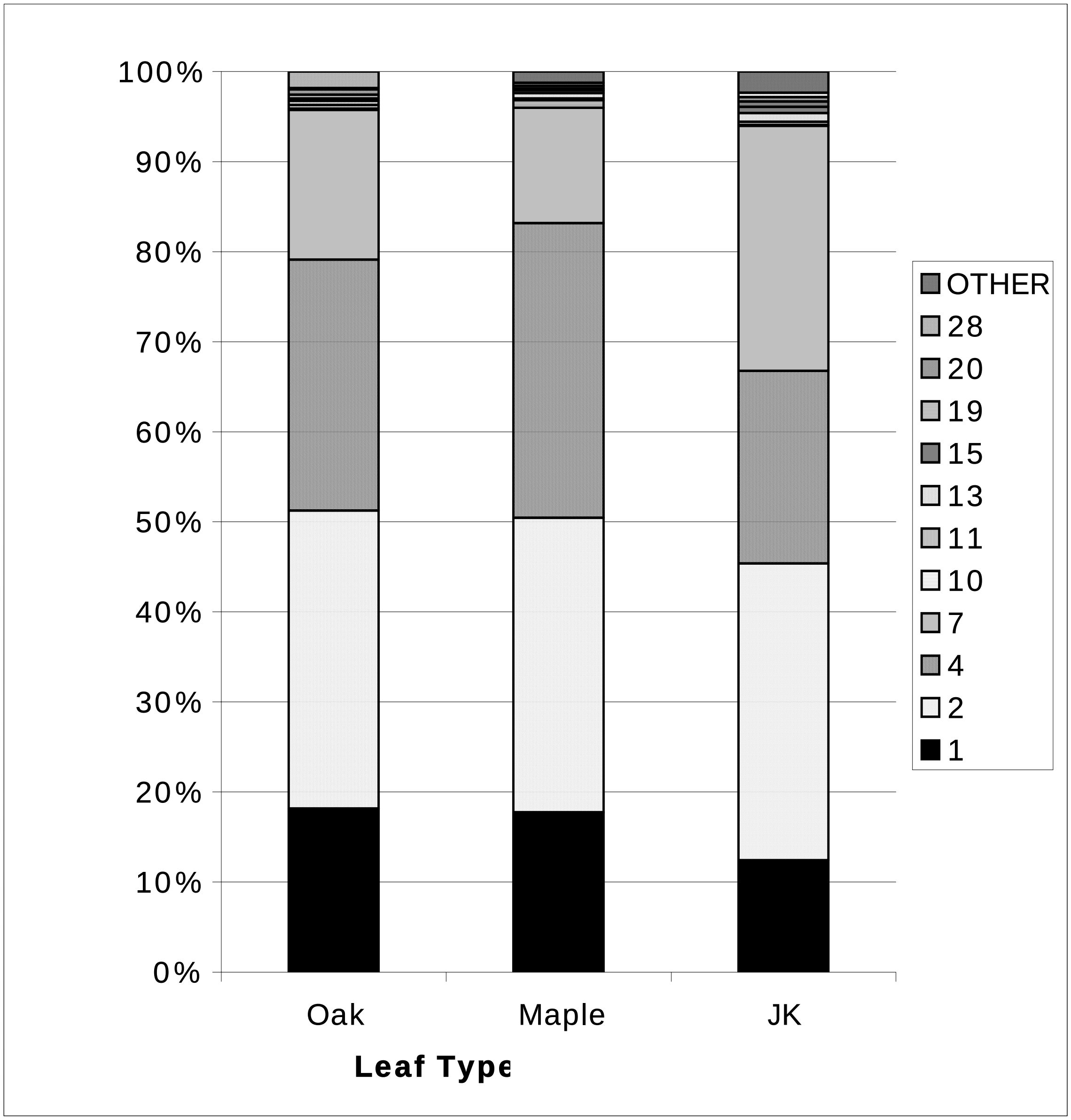


Figure 3.3 Macroinvertebrate community composition by leaf species on Day 28.

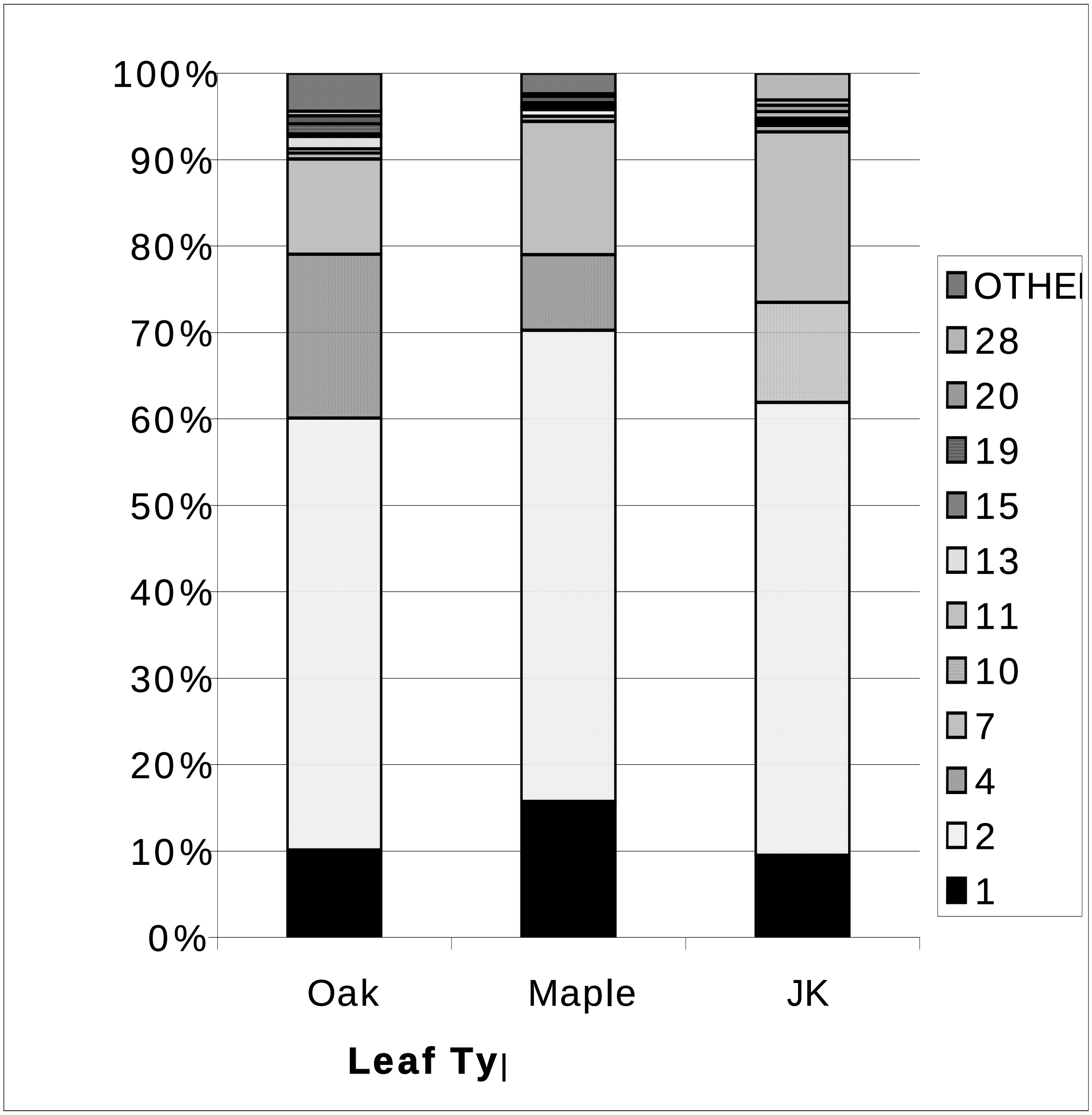
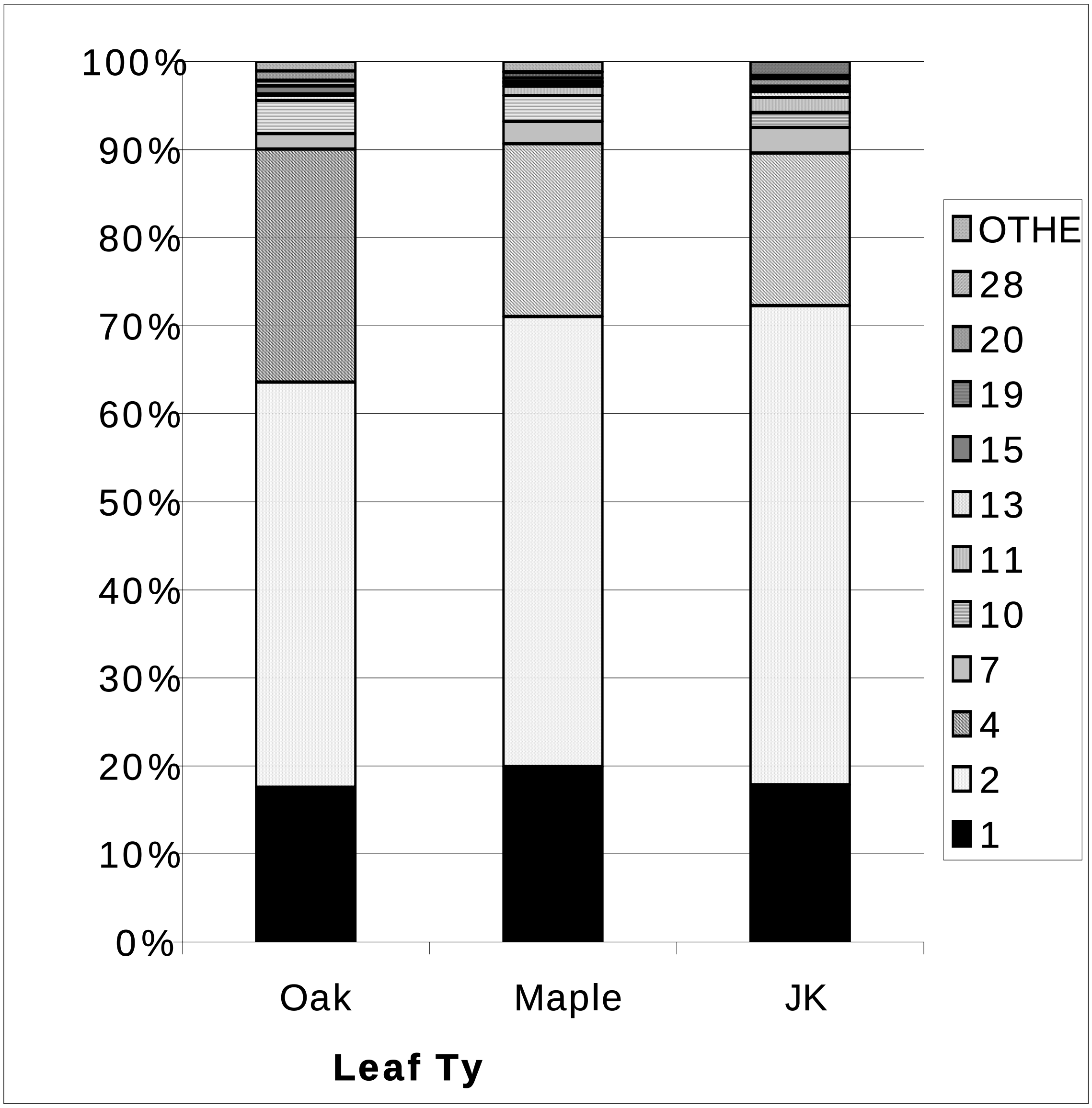


Figure 3.4 Macroinvertebrate community composition by leaf species on Day 56.



Macroinvertebrate species richness also did not differ much between leaf types. On Day 7 Oak, Maple, and Knotweed leaves hosted, on average, 8.2, 7.4, and 8.6 morphospecies, respectively, per leaf pack. The numbers increased slightly to 8.7, 9.7, and 11.2 on Day 14, and 13.4, 11.4, and 12.4 on Day 28. On Day 56 Oak richness dropped back to 10.4 species per leaf pack, on average, while Maple and Knotweed continued to rise to 11.7 and 13, respectively.

DISCUSSION

Macroinvertebrates

Macroinvertebrate abundance increased regularly throughout the study on all taxonomic levels, regardless of leaf type. Between leaf types little difference was seen in the invertebrate community composition. My hypothesis that we would find great differences in richness and abundance of invertebrates, suggesting a cascade of changes throughout the higher trophic levels of the system proved incorrect. However, some changes to the experiment could reveal much more information in further studies.

As the study incorporated only the beginning of the season, following the first 56 days after leaf litter input to the stream, the macroinvertebrate populations did not have a chance to maximize the full potential of the leaves. By the end of the study, the leaf packs retained 73.7% or more of their initial biomass, and were still losing biomass steadily. Native floral and faunal communities in forested temperate streams have adjusted their life history patterns over time so that maximum annual invertebrate biomass coincides with the point at which decomposing leaf litter provides optimum food and habitat supply in the stream (Cummins et al. 1989). Generally, this corresponds with 50% processing, the point at which half of the initial leaf biomass remains. Up until this point, macroinvertebrates are increasing in both abundance and biomass per individual; after this point abundance begins to decline as individuals compete for resources, but individual biomass remains relatively high (Cummins et al. 1989, Haapala 2001).

While biomass of individual invertebrates was not measured in the current study, my data on abundance are consistent with this theory. As the leaves in the leaf packs continued to decompose, more potential food and habitat were made available to macroinvertebrates, which continued to colonize and increase in numbers over the duration of the study. If the study had continued to include an entire season, it is likely that we would have seen invertebrate abundance peak when 50% of the leaf litter had been processed, and begin to decline shortly thereafter.

The notable exception to this general trend of increasing abundance was seen in the Perlodid stoneflies, which peaked in the middle of the study and then declined by the end. It is unclear why this happened, although it was consistent throughout all three leaf types. The Perlodids were also the exception to the equivalent abundance of morphospecies among different leaf types. For the most part, the other morphospecies occurred in comparable numbers regardless of leaf type. However, Perlodidae was more abundant in the Japanese Knotweed samples than in those of either Maple or Oak. As the dominant predator found in the invertebrate communities, the Perlodids played an important role in the system with respect to the activity of the herbivores and leaf breakdown. Predators have been found to slow leaf breakdown rates significantly by decreasing herbivore and detritivore populations (Oberndorfer et al. 1984). While increased predator abundance did not coincide with decreased herbivore abundance (such as the other three dominant morphospecies: Hydropsychids, Chironomids, and Baetids, all collectors) in this study, in the long term there may be more of an effect as herbivore populations continue to grow.

Declines seen in other, less abundant morphospecies are more likely to be attributable to collection errors or small sample sizes than any larger phenomenon. Morphospecies which occurred less than once per leaf pack on average were not included in the calculations, as their presence was likely due to incident drift. Their numbers were not large enough to say anything conclusive about their populations.

Species richness also increased throughout the study, although only slightly and not showing notable differences between leaf species either. As the leaves broke down in the stream, it is likely that they attracted an increasingly greater variety of macroinvertebrate fauna that colonized the leaf packs.

Leaf biomass

The decomposition rates here were linear. However, some similar studies have reported exponential rates (Haapala 2001). A longer study may have seen rates slow and approach a more exponential shape as the leaves continued to break down.

Air-drying the leaves to take initial biomass readings affected the accuracy of the data somewhat, as samples removed from the stream on subsequent collection days were dried in an oven and thus had lower relative water content when weighed (Haapala 2001). However, as oven-drying is more destructive to leaves than air-drying, it is not a desirable method to use at the start of a study when the integrity of the leaves is still important (Boulton and Boon 1991).

An inconsistency in the initial air-drying of the leaves for the Japanese Knotweed leaf packs, however, made the biomass numbers difficult to compare. The leaves were not completely dry when they were weighed and put into the leaf packs, so their initial biomass was artificially inflated. However, the decomposition rates we got for the Knotweed leaves were already slower than expected, so using an initial biomass that was even lower than the ones we did use would have calculated even slower rates.

We expected a much greater difference between the three leaf types, but instead got very similar breakdown rates. Even Maple and Oak were significantly different only half of the days, and Japanese Knotweed was not significantly different from either of them. Stream invertebrate communities change throughout the season to utilize leaf litter at different stages of decomposition, some favoring the coarser material available in the fall and winter, others the more processed material available in the spring and summer (Cummins et al 1979, Haapala 2001). Seasonal variation also points to the need for a longer study period so that we can see if the leaf types diverge. More trials also may decrease standard deviation.

Japanese Knotweed Invasions

The conditions created by my experimental Japanese Knotweed leaf packs were not completely indicative of a true invasion. While individual leaf packs contained just one leaf type, they represented only small islands in the relatively vast stream, and were still subjected to all of the other inputs that were naturally occurring. Since this was a non-invaded site, Knotweed leaf packs were still surrounded by native vegetation, even sometimes piling up right on top of them as they remained tethered in the current. If they had been natural piles of leaves washed into the stream on an invaded site, there would have been no other vegetation around to affect the macroinvertebrate communities that colonized. In a site truly invaded by Knotweed, no native vegetation will be found at all

(Seiger 1997, Shaw and Seiger 2002, Maerz et al. 2005). The macroinvertebrate communities present on my Knotweed leaf packs were not subsisting solely on the Knotweed, as would have been the case if an invasion had excluded all of the native vegetation previously supplying leaf litter to the stream ecosystem. This fact likely skewed the data.

Maerz et al. (2005) found that Green Frogs (*Rana clamitans*) were less successful foraging in conditions where Japanese Knotweed had invaded. Their study suggested that the frogs were unable to locate and capture food behind the invasion front because the Knotweed had such a strong effect on the macroinvertebrate community as to render them an insufficient prey base. In North America no herbivores are known to be able to subsist on Knotweed alone (Shaw and Seiger 2002). Invertebrate community differences among leaf types found in the current study were weak, but a more controlled study which more accurately imitated true invasion conditions may lead to different results.

The mass ratio hypothesis states that plant species' effects on ecosystem function are proportional to its contribution to total plant biomass (Grime 1998). Vegetation is divided into three categories with respect to relationships between plant abundance and ecosystem properties. Dominant species are usually large in stature and contain the most biomass in the system. Subordinates are more numerous but make up less biomass overall, and often show fidelity to particular dominants. Transient species are generally not associated with dominants, make a small total contribution to the biomass of the system and vary in functional traits (Grime 1998, *also* Huston 1997, Aarssen 1997). For the purposes of this study, native vegetation still occupied the dominant positions, because Japanese Knotweed was restricted to a few small leaf packs.

To a large extent, the characteristics of the dominants dictate ecosystem properties, which are relatively insensitive to variations in richness of subordinate or transient species (Grime 1998). This would explain the lack of change seen in this study as a response to the Knotweed, as leaf type was extremely localized and did not affect the native dominants or even subordinates of the system. Knotweed can be considered a transient species in this system within the context of the mass ratio hypothesis.

However, while the dominants in a system have the most immediate control over ecosystem processes, subordinates and transients influence the recruitment of the dominant species, which may become more apparent only in the long term. Providing a pool of potential colonizers, minor vegetation components may move to a more influential position when conditions are favorable. The loss of diversity, therefore, even on a relatively small scale, may hinder the system's ability to adapt to disturbances (Grime 1998). When an invasive can find a way to move up in influence to the exclusion of subordinates and even dominants, then we see the large-scale effects on native species that were expected here. Cascade effects on higher trophic levels are still an issue, but perhaps they are more likely to occur only when the invasive reaches dominant status, following a disturbance or successful takeover by aggressive growth.

Demonstrating species interactions can prove difficult under field conditions, creating problems for field work and stream community ecology in general. Due to the high mobility of stream fauna, the expression of local effects can easily get lost (Malmqvist 1993). Studies involving species richness done in a laboratory can oversimplify the variety of species in the natural system and make too many generalizations. Field experiments, on the other hand, often give a more realistic view of ecosystem-level relationships, but their results can be either insignificant or too complex to reveal the answers to many questions about the function of species richness (Jonsson et al. 2003). All of these variables need to be considered when designing experiments and when analyzing outcomes.

A more controlled study would probably need to utilize several study sites, including a stream that had actually been invaded by Knotweed to the exclusion of native vegetation. This would require leaf packs using native vegetation to be located in separate streams, meaning that other variables which were consistent in this study would change between sites (*e.g.* water temperature, discharge, bank and streambed chemistry). However, it would ensure that Knotweed leaf packs were not being affected by other allochthonous inputs to the stream, and would allow for a broader look at invertebrate colonization patterns in the context of the whole stream, rather than just localized effects. A longer data collection period would allow the entire season to be examined, including the halfway point of leaf breakdown, seasonal weather patterns, and subsequent changes in invertebrate communities.

CONCLUSION

As non-native species expand their reach year by year, concern for the biological integrity of invaded systems turns to scientific study to answer pressing questions. The effects of invasive species on pre-existing ecology involve complex variables and unexpected turns; anticipating the full impact of the changes they bring is difficult, when it is even possible. Still, predictions can be shaped by analyses of the various factors at play in order to create best management practices that seek to mitigate damage to the stability of the invaded habitats. Looking at similar habitats that already have been invaded is a good start, and controlled experiments that simulate one or more aspects of an invasion help to provide valuable information.

Recent studies have shown Japanese Knotweed to be a formidable invader, replacing native vegetation swiftly and thoroughly. Some research already is suggesting the negative impacts this could have on native ecology but the details remain largely unclear. Hypotheses of Knotweed providing an unsuitable environment for native fauna, starting at the invertebrate level, were not confirmed by this study. However, as a preliminary foray this study was obviously not conclusive. Looking at the invertebrate communities over a full-season would lend valuable insight into bottom-up effects on higher trophic levels and the ecosystem as a whole.

As more information becomes available about Japanese Knotweed invasions and the interrelationships between macroinvertebrates and the system at large, scientists and resource managers alike would be wise to look further into controlled studies which examine directly the effects of Knotweed on specific elements of invaded ecosystems to better understand these invasions and what can most effectively be done about them.

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