DETRITIVORE DIVERSITY OR DOMINANT SPECIES: WHAT DRIVES DETRITAL
PROCESSING?

A Thesis
by
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ABSTRACT

DETRITIVORE DIVERSITY OR DOMINANT SPECIES: WHAT DRIVES DETRITAL
PROCESSING?
(August 2010)

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Researchers have been assessing the role that biodiversity plays in maintaining
ecosystem functioning for almost two decades. Previous research suggested that a dominant
species (the caddisfly *Pycnopsyche gentilis*) and not detritivore diversity determined leaf
breakdown in a southern Appalachian stream. However, in these previous studies the effects
of other large detritivores (the stonefly *Tallaperla* and the crane fly *Tipula*) could not be
directly compared to that of *Pycnopsyche*. Here I report the results of a field experiment in
which I created monocultures of these three species as well as 2- and 3-species combinations
and examined their effect on leaf breakdown. This experimental design allowed me to
determine if these other taxa facilitated the effect of *Pycnopsyche*, inhibited it, or had no
effect whatsoever. Treatments containing *Pycnopsyche*, regardless of presence or absence of
other taxa, exhibited the highest levels of leaf breakdown. Leaf mass lost (LML) in the
three-species polyculture was not significantly different from that in the *Pycnopsyche*
monoculture, i.e., there was no significant positive effect of diversity on LML. LML in the
Tallaperla monocultures was indistinguishable from controls in which only microbial

breakdown occurred. LML in the *Tipula* monocultures was intermediate between those of *Pycnopsyche* and *Tallaperla*. Neither *Tallaperla* nor *Tipula* facilitated or inhibited *Pycnopsyche*. However, *Tallaperla* inhibited leaf breakdown by *Tipula* in the treatments in which both were present. My results confirm that *Pycnopsyche* is the functionally dominant detritivore in this system. They also suggest a novel mechanism that can influence diversity-function relationships. Inhibitory interactions among functionally subordinate species may result in reduced ecosystem function despite increases in species richness.

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DEDICATION

I would like to dedicate this thesis to my parents, my advisor, and to my closest friends.

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INTRODUCTION

The importance of biodiversity for ecosystem function (BEF) has been evaluated and debated for the last fifteen years (Naeem et al. 1994, Tilman and Downing 1994, Huston 1997, Wardle 1999, Cardinale et al. 2006, Duffy 2009, 2010, Wardle and Jonsson 2010). Early BEF studies reported a positive relationship between biodiversity and various ecosystem functions, e.g. productivity (Naeem et al. 1994, Tilman et al. 1996) and decomposition (Jonsson and Malmqvist 2000, 2003). Hypothesized biological mechanisms that produce positive BEF relationships include niche complementarity and facilitation (Naeem et al. 1994, Jonsson and Malmqvist 2000). Niche complementarity should result in more efficient resource use when different species use a resource in diverse ways (Naeem et al. 1994, Fridley 2001, Tilman et al. 2001, Boyero et al. 2007). Facilitation promotes efficiency when one species facilitates the use of a resource by another species (Fridley 2001, Boyero et al. 2007).

Huston (1997) argued that positive diversity-function relationships might simply be an experimental artifact (i.e., the sampling effect). As species are randomly drawn from a potential species pool, the probability of including a species that has a greater effect on function (i.e., a functionally dominant species) also increases (Huston 1997, Wardle 1999). However, dominant species may create a positive relationship between diversity and ecosystem function even when experimental communities are not randomly assembled. This

effect may be especially important when there is considerable variation in species functional abilities (Figure 1a). The mean performance for the monocultures will undoubtedly be much lower than that of the highest performing monoculture. A regression line fit to these data gives the impression that function increases with increasing species richness (Figure 1a). However, when the performance of a multispecies treatment does not significantly differ from the highest functioning monoculture, a dominant species may be driving the perceived positive BEF relationship (Figure 1b). The positive relationship between richness and function in Figure 1a is an experimental artifact resulting from the increasing number of treatments containing the dominant species. Also, low mean performance of the monocultures may be due to one or more poorly performing species. To evaluate whether the positive relationship may be due to a single dominant species regression analyses should also be performed only on treatments containing the dominant species. If there is no relationship between species richness and function, then positive relationships between diversity and function are likely due to a dominant species. Only when the polyculture performance is significantly greater than the highest performing monoculture would a positive effect of biodiversity on function be demonstrated (Figure 1c). This approach is similar to the effect ratio generated by Cardinale et al. (2006).

In small, forested headwater streams a major ecosystem function performed by many taxa (e.g., larvae of stoneflies, caddisflies and mayflies, as well as crustaceans) is the decomposition of allochthonous leaf material, specifically the comminuting of large detrital particles (Petersen and Cummins 1974, Benfield et al. 1979, Herbst 1982, Webster and Benfield 1986, Cummins et al. 1989, Creed and Reed 2004). In streams of the southern Appalachian mountains, three large detritivorous insect species frequently coexist in

headwater streams. These species are *Pycnopsyche gentilis* (Trichoptera:Limnephilidae), *Tallaperla maria* (Plecoptera:Peltoperlidae) and *Tipula abdominalis* (Diptera:Tipulidae), hereafter *Pycnopsyche*, *Tallaperla* and *Tipula*, respectively. All three taxa are considered important detritivores (Wallace et al. 1970, Mackay and Kalff 1973, Eggert and Wallace 2007, Creed et al. 2009). These three species can comprise over 95% of detritivore biomass (Stout et al. 1993) and can account for 54-77% of the annual detritivore production in southern Appalachian headwater streams (Wallace et al. 1999).

More recent research suggests that *Pycnopsyche* is the dominant detritivore in these systems (Cherry 2000, Eggert and Wallace 2007, Creed et al. 2009). Cherry (2000) and Creed et al. (2009) conducted leaf pack breakdown experiments in two streams, Greene Creek and Sims Creek. Highest breakdown rates were observed in stream habitats in which *Pycnopsyche* was abundant. When *Pycnopsyche* was absent, leaf breakdown rates appeared to be driven by leaching and microbial breakdown, i.e., invertebrate detritivores (including various stoneflies such as *Tallaperla* and the crane fly *Tipula*, both of which were present) other than *Pycnopsyche* appeared to have little impact on detrital processing. In field experiments conducted by Creed et al. (2009), both correlative and experimental results pointed to *Pycnopsyche* being a functionally dominant detritivore. Additionally, Creed et al. (2009) determined that *Pycnopsyche* was a competitive dominant as it was able to displace other detritivore taxa from leaf packs it occupied. As a result, there was a negative relationship between detritivore diversity and leaf breakdown (Creed et al. 2009). However, the methods used by Creed et al. (2009) did not allow them to explicitly compare the effects of *Pycnopsyche* to the two other large detritivores in the system, *Tallaperla* and *Tipula*, as

large individuals of these taxa were frequently excluded from cages. Moreover, the
experimental designs they used were not the standard BEF design.

The purpose of this experiment was to directly compare the effect of *Pycnopsyche* to
large *Tallaperla* and *Tipula,* as well as determine if there was a positive effect of increased
detritivore diversity on leaf breakdown. An additional benefit of using the standard BEF
experimental design is that it allowed me to assess if any interspecific interactions (i.e.,
facilitation or inhibition) occur among these three large detritivore species. Specifically, I
was interested in determining if either *Tipula* or *Tallaperla* inhibited or facilitated the effect
of *Pycnopsyche* on detrital processing. The null hypothesis for this experiment is that there
would be no difference between observed and predicted leaf mass loss in the polyculture.
Any significant deviation from these predicted values for species-combination treatments
would therefore suggest facilitation (if greater than predicted values) or inhibition (if lower
than predicted values). An additional hypothesis was that if there was no significant
difference between the *Pycnopsyche* monoculture and the 3-species polyculture, this would
indicate a functionally dominant species effect (Figure 1b).

METHODS

Greene Creek is a first-order stream located in the headwaters of the South Fork of the New River in North Carolina, USA ($36^{o}14'2"$N, $81^{o}65'8"$W). This stream originates in an undisturbed forest of the Blue Ridge Mountains where dominant riparian tree species include yellow birch (*Betula allegheniensis*), red maple (*Acer rubrum*), oak (*Quercus* spp.) and hemlock (*Tsuga canadensis* and *T. caroliniana*) (Creed et al. 2009). The study reach was ~ 50 m long and was situated in a transitional zone (the intermediate section in Creed et al. 2009) between the undisturbed forested section and the pasture section of the stream. This section of Greene Creek is 0.5-1.0 m wide with an average depth of 8-9 cm and the substrate consists primarily of cobble, gravel and bedrock, with some patches of sand and silt. The stream water temperature during my experiment averaged 2.67^{o} C and ranged from 0.11-7.09^{o} C. The average water temperature change over the course of a day was 1.24^{o}C. The most dramatic change in water temperature over a single day was 2.69^{o} C.

Three months prior to the start of the experiment, yellow birch leaves were collected (after the abscission layer had formed, but prior to falling) from trees in the study watershed and air dried in the lab. Leaf packs (5.0 g initial air dried mass) were constructed after soaking overnight in deionized water by clamping the petiole ends of the leaves in a binder clip. On 23 January 2009 the leaf packs were secured inside 32 small, plastic flow-through enclosures (35 x 20 x 20 cm). Leaf packs were conditioned for 14 d inside the enclosures,

the ends of which were covered with 243 μm mesh to exclude macroinvertebrates but allowed microbial colonization. The enclosures were secured in the stream by attaching a brick to each side.

Pycnopsyche gentilis, Tallaperla maria and Tipula abdominalis were collected from Greene Creek on 7 February 2009 and placed into the treatment enclosures the same day. There were three levels of species richness (1-species, 2-species combination and 3-species combination) with four replicates of all seven species treatments (3 single-species monocultures, 3 two-species combinations and 1 three-species polyculture) for a total of 28 enclosures. Four additional enclosures containing only leaves served as controls to assess mass loss attributable to leaching and microbial breakdown in the absence of macroinvertebrate detritivores. The animals were visually sorted into groups of similar sized individuals. While I was able to directly determine the sizes of Tipula and Tallaperla, I used the case size as a surrogate for the size of Pycnopsyche larvae. Pycnopsyche gentilis larvae cut circular discs out of leaves and attach them together to create a triangular shaped leaf case, which they carry around throughout their larval life (Mackay and Kalff 1973). A subsample of individuals (n = 10) of each species was collected in order to estimate initial lengths and masses of each species. Initial mean total length and initial oven-dried mass for individuals of each species is as follows: Pycnopsyche (13.59 ± 0.38 mm; 2.28 ± 0.29 mg), Tallaperla (9.08 ± 0.35 mm; 6.37 ± 0.52 mg), Tipula (32.5 ± 1.99 mm; 20.94 ± 1.58 mg).

The number of individuals per leaf pack for each species in a treatment was 3 Pycnopsyche, 5 Tallaperla and 1 Tipula, which translates to 0.6, 1, and 0.2 individuals per g leaf pack air-dried mass, respectively. These densities for Tipula and Tallaperla are comparable to natural densities observed in Greene Creek (Creed et al. 2009) and other

southern Appalachian streams (Stout et al. 1993). Densities in these other studies are based on all individuals whereas I used large *Tallaperla* and *Tipula* in my study. Therefore, my densities for large individuals of these two taxa are probably higher than those normally encountered. *Pycnopsyche* densities were lower than natural densities observed in Greene Creek (Creed et al. 2009), but comparable to those reported by Stout et al. (1993) for streams at Coweeta, NC.

The experiment was terminated on 7 March 2009. All leaf material, invertebrates and sediment were placed in sealable plastic bags and transported to the lab. Leaves were then gently cleaned of sediment and invertebrates. Invertebrates were preserved in 70% ethanol. Leaves were dried at 60° C for 4 d, then weighed and ashed at 550° C for 3 h to determine ash-free dry mass (AFDM). To calculate leaf mass lost (LML) that was solely attributable to macroinvertebrates for certain analyses, I subtracted the average LML in leaching and microbial controls from treatments containing macroinvertebrates; this provided me with LML (corrected). Total length of all macroinvertebrates was determined and then the animals were oven-dried at 60° C for 4 d and weighed to the nearest tenth of a milligram to determine their final biomass. Due to the mortality of a *Tipula* in a monoculture enclosure and a *Pycnopsyche* in a 2-species enclosure (*Pycnopsyche-Tipula*) I excluded these treatments from the analyses.

Data were analyzed using analysis of variance (ANOVA) and regression analysis. The ANOVA was performed to check for any significant differences in LML among the species treatments. I also performed a linear regression on the full data set to see if there was a relationship between detritivore richness and LML (corrected). Regression analysis was also used to compare richness effects versus dominant species effects. Mean leaf mass lost

attributable to microbial breakdown was 0.24 g; this was factored out to obtain LML

(corrected) for the treatments containing the three insect species. A one-sample t-test

allowed me to test whether or not LML observed in the multispecies treatments were equal to

the predicted LML (calculated using values obtained from the monocultures of each species).

This allowed me to assess inter-specific interactions (facilitation or inhibition) among

detritivores. A regression analysis was used to assess if detritivore final biomass was related

to LML in my experiment. Additionally, a Leaf-Mass-Lost:Animal-Biomass ratio was

calculated to evaluate how LML was related to the increase in species biomass as diversity

increased. The effect of treatment on this ratio was also analyzed using regression analysis.

RESULTS

I found a significant effect of treatment on leaf mass lost ($F_{7,22} = 24.56$, $p < 0.001$; Figure 2). Mean leaf mass lost (LML) from the microbial controls on average was 0.24 g. The amounts of LML in the *Pycnopsyche* and the *Tipula* monocultures were significantly greater than the microbial control (Figure 2). LML in the *Tallaperla* monoculture and the *Tallaperla-Tipula* treatments were not significantly different from the microbial control (Figure 2). LML in the *Pycnopsyche-Tipula* and *Pycnopsyche-Tallaperla* treatments were not significantly different from either the *Pycnopsyche* monoculture or the 3-species polyculture (Figure 2).

My null hypothesis for the experiment was that observed values for LML would not be different from predicted values for the 2- and 3-species treatment, based on the monocultures. There were significant differences between observed and predicted LML values for two of the four polycultures (Figure 3). LML from the *Tipula-Tallaperla* treatment was significantly lower than that predicted (one-sample t-test, $t_{3,0.05} = -9.24$, $p = 0.003$; Figure 3). The 3-species polyculture was also significantly lower than the predicted values for LML (one-sample t-test, $t_{3,0.05} = -3.58$, $p = 0.037$; Figure 3). The LML in the *Pycnopsyche-Tipula* and *Pycnopsyche-Tallaperla* treatments were not significantly different from predicted LML based on the monocultures.

The higher LML values in the *Pycnopsyche-Tipula* and *Pycnopsyche-Tallaperla* treatments may have been due to these treatments containing larger *Pycnopsyche* and not as a result of the other detritivores being present. Regression analysis comparing final *Pycnopsyche* biomass to LML from all replicates containing *Pycnopsyche* found that LML was positively related to *Pycnopsyche* final biomass ($F_{1,13} = 21.51$, $p < 0.001$, $r^2 = 0.594$; Figure 4). No relationship between final animal biomass and LML was observed for either *Tipula* ($F_{1,12} = 1.27$, $p = 0.282$, $r^2 = 0.02$) or *Tallaperla* ($F_{1,14} = 1.49$, $p = 0.242$, $r^2 = 0.032$).

Regression analysis is frequently used to test for a relationship between increasing species richness and a particular ecosystem function. Using this approach I found a slight increase in LML as species richness increased, although the effect was not significant ($F_{1,24} = 3.1$, $p = 0.091$, $r^2 = 0.077$; Figure 5a). When I performed a regression analysis of only treatments containing *Pycnopsyche* the positive relationship between species richness and leaf breakdown disappeared ($F_{1,13} = .01$, $p = 0.905$, $r^2 = 0.000$; Figure 5b). LML in the 3-species polyculture was not significantly different from LML in the *Pycnopsyche* monocultures.

Mass of *Tallaperla* was consistently the highest across all treatments (mean: 26.5 mg, range: 17.6-37.8 mg, Table 1). Mass of *Tipula* was intermediate (mean: 17.1 mg, range: 11-34.2 mg), while mass of *Pycnopsyche* was usually the lowest (mean: 15.8 mg, range: 9.6-22.1 mg). There was no relationship between the final mass of detritivores from the various treatments and LML (corrected) (Figure 6). As consumption may be influenced by body size I standardized leaf consumption (mg) by detritivore mass (mg), which produced a unitless ratio: leaf-mass-lost:animal-mass (Figure 7a). The ratios for the three taxa were significantly different ($F_{2,8} = 30.24$, $p < 0.001$). The ratio for *Pycnopsyche* in monoculture was

significantly higher than the ratio for both *Tipula* (p = 0.007) and *Tallaperla* (p < 0.001). *Tipula*'s ratio was also significantly higher than the ratio for *Tallaperla* (p = 0.05). I expected to see higher LML in species-rich polycultures due to the increase in total detritivore biomass. Nevertheless, when I calculated ratio values for the 2- and 3-species treatments there was a negative relationship between the ratio and species richness (i.e., even though detritivore biomass was increasing, LML per unit detritivore mass was declining) although the relationship was not significant ($F_{1,24}$ = 1.59, p = 0.219, r^2 = 0.023; Figure 7a). However, I noticed that the ratio for *Pycnopsyche* became increasingly lower with increasing species richness, possibly due *Tallaperla* and *Tipula* having a lower ratio. Therefore, the same analysis was performed on just the treatments containing *Pycnopsyche*. Due to the addition of poor performing species, the ratio decreased significantly as species richness was increased ($F_{1,13}$ = 37.51, p < 0.001, r^2 = 0.723; Figure 7b).

DISCUSSION

Pycnopsyche gentilis is a functionally dominant detritivore. The leaf-mass-lost:animal-biomass ratio, which illustrates the amount of leaf mass lost per unit detritivore biomass, showed that *Pycnopsyche* had a ratio that was ~2.3 times that of Tipula and ~23 times that of *Tallaperla*. *Pycnopsyche*'s higher overall ingestion rate of leaf material relative to other species (see also Eggert and Wallace 2007), as well as the fact that it uses discs cut from leaves for case construction (Mackay and Kalff 1973, Creed et al. 2009) results in *Pycnopsyche*'s greater effect on leaf breakdown. My results are consistent with those of Eggert and Wallace (2007) and Creed et al. (2009). They are also consistent with Herbst's (1980, 1982) conclusions that members of the genus *Pycnopsyche* are functionally dominant detritivores in streams they inhabit.

The effect of *Tallaperla* on leaf breakdown was not significantly different from the controls in which only leaching and microbial breakdown occurred. This is an interesting finding because it contradicts previous reports that *Tallaperla* was important for detrital processing (Wallace et al. 1970, Hutchens and Wallace 2002). In the *Tipula* monoculture leaf mass lost was significantly greater than the microbial control and the *Tallaperla* monoculture, which supports the idea that this taxon is an important shredder (Cummins et al. 1973, Herbst 1980, 1982). However, when placed in containers with *Tallaperla*, *Tipula*'s effect on leaf mass lost was negligible. As a consequence of this inhibition of *Tipula* by

Tallaperla there was a reduction in leaf mass lost relative to predicted values as species richness increased. I believe that this is the first evidence for a mechanism where inhibitory interactions among functionally subordinate species can prevent an increase in ecosystem functioning despite increases in species richness.

There are at least two possible mechanisms by which *Tallaperla* inhibits *Tipula*. First, detritivorous stonefly species have been reported to remove much of microbial material from the leaf surface (Lieske and Zwick 2007). *Tallaperla* may in fact be removing the microbes, thus creating less palatable leaves for *Tipula*. *Tipula* may feed less as a consequence which in turn could lead to reduced growth by this species (Lawson et al. 1984). Since I only measured final detritivore biomass and did not evaluate detritivore growth, I cannot be certain that *Tipula*'s growth was affected by *Tallaperla*'s feeding. Alternatively, the inhibition of *Tipula* by *Tallaperla* may simply be due to *Tallaperla*'s movement in the leaf pack. *Tipula* is easily agitated if touched and it begins swimming, possibly to avoid further contact (M. Rollins, personal observations). *Tallaperla* may come into physical contact with *Tipula* causing *Tipula* to stop feeding. *Tipula*'s response to these encounters when not confined inside an enclosure may be to move to another leaf pack where *Tallaperla* is not present. In the enclosures, from which *Tipula* could not emigrate, *Tipula*'s reduced feeding rate on leaves might have been due to them being restricted to a single leaf pack. As these two species often coexist in the same southern Appalachian headwater streams (Wallace et al. 1970, Stout et al. 1993, Eggert and Wallace 2007, Creed et al. 2009) it is possible that *Tipula* routinely encounters *Tallaperla* and thus only has a limited effect on leaf breakdown. My results suggest that *Tipula* would only have a strong effect on leaf

breakdown in streams in which *Tallaperla*, or a species that has an effect similar to *Tallaperla*, is absent. Note that *Tipula* was not inhibited by the presence of *Pycnopsyche*.

I used leaves from a single tree species (yellow birch) in my experiment. Leaf consumption by detritivores is often a function of the kind of leaves that are present (Wallace et al. 1970, Mackay and Kalff 1973, Herbst 1982). It is possible that different results may have been obtained if leaves from a different tree species were used or if leaves from multiple tree species were present in the leaf packs. However, the consumption rates of these three macroinvertebrates on other leaves have been assessed (see Wallace et al. 1970, Mackay and Kalff 1973, Herbst 1982, Swan and Palmer 2006, Eggert and Wallace 2007) and the consumption rates for these taxa in my experiment are similar to the consumption rates on other types of leaves with similar breakdown rates. As similar BEF experiments with these three detritivore species have not been conducted using other types of leaves it is not clear at present if similar results would be obtained.

It was intriguing that across species monocultures, the enclosures with *Tallaperla*, which had the highest biomass, actually had the lowest amount of leaf mass lost, while enclosures with the lowest detritivore biomass (i.e., *Pycnopsyche*) had the greatest amount of leaf mass lost. Moreover, only *Pycnopsyche* final biomass was correlated with leaf mass lost. This suggests that species identity and not detritivore biomass is more important in determining detrital breakdown. Also, it is important to note that the density of *Pycnopsyche* used in this experiment was very low relative to densities that can occur in these streams (see Creed et al. 2009). Using *Pycnopsyche* abundances similar to those that occur when it is abundant could have provided an even more dramatic result with respect to leaf mass lost. Thus, in future BEF studies it is vital to assess the impact that a species has at densities

commonly observed in nature (Dangles and Malmqvist 2004, Hillebrand and Matthiesen 2009). This will provide a baseline that experimentally manipulated densities can be compared to when assessing the effects of changing species abundances.

Although this study was performed in a single stream (Greene Creek), it is important to recognize that these results may be applicable to other streams and other systems. *Pycnopsyche*, *Tipula* and *Tallaperla* can account for much of the detritivore biomass and the majority of annual detritivore production in southern Appalachian headwater streams (Stout et al. 1993, Wallace et al. 1999). So it appears that these results may not be limited to Greene Creek; *Pycnopsyche* may be the functionally dominant detritivore in many other southern Appalachian headwater streams. Moreover, both *Pycnopsyche* (Mackay and Kalff 1973) and *Tallaperla* (Stark 1983) are distributed throughout the Appalachian mountain chain, while *Tipula* can be found in small to intermediate size streams throughout North America (Vannote and Sweeney 1985). Therefore, it appears that *Pycnopsyche* may be a functionally dominant detritivore throughout much of the Appalachian Mountains. Moreover, *Tallaperla* may inhibit the effect of *Tipula* in many of these streams.

Functionally dominant detritivores may drive detrital processing in other streams as well. Dangles and Malmqvist (2004) found that streams which were strongly dominated by a few species had higher rates of decomposition compared to streams where there was an even distribution of species. Encalada et al. (2010) compared leaf breakdown in two sections (forest and pasture) of a tropical montane stream. They reported that the abundance of a detritivorous caddisfly (*Phylloicus* sp.) was the best predictor of percentage of litter remaining. This result suggests that *Phylloicus* sp. may be the functionally dominant detritivore in tropical montane streams of Ecuador. Their finding is similar to that of Creed

et al. (2009) who reported the highest breakdown rate in a stream section (forest) with the highest density of *Pycnopsyche gentilis*.

Although early stream biodiversity-ecosystem function studies reported positive relationships between species richness and function (Jonsson and Malmqvist 2000, Jonsson et al. 2001), more recent studies have reported that function is not related to detritivore diversity (Boyero et al. 2007, Creed et al. 2009, McKie et al. 2009, Encalada et al. 2010). Laboratory experiments are not always good predictors of field experiments (McKie et al. 2009), and many of the initial BEF studies were performed in laboratory settings. It appears that in some streams biodiversity is not important for leaf breakdown, but rather a single species performs the majority of leaf breakdown (Creed et al. 2009, Encalada et al. 2010).

Are functionally dominant species only important for detrital processing in stream ecosystems? Results from a meta-analysis of 111 BEF studies that evaluated diversity effects on various ecosystem functions suggest that resource depletion by a single functionally dominant species in monoculture tends to be no different than that of the most species-rich polyculture (Cardinale et al. 2006). Many of these studies analyzed in this meta-analysis reported a positive BEF relationship. This result from the meta-analysis suggests that functionally dominant species drive many functions in many systems.

Although declines in biodiversity may have significant consequences for organisms that rely on those species being lost (e.g., predators, parasites), the results from this study, in addition to the results from the meta-analysis performed by Cardinale et al. (2006), do not support the idea that biodiversity drives ecosystem functioning. Rather, in the majority of cases, regardless of system or function, a functionally dominant species appears to be controlling particular functions. In no way do these results suggest that preserving

biodiversity is not an important goal of conservation biology. Rather, they suggest the idea of biodiversity being an important driver of ecosystem function (e.g., primary production, nutrient cycling and organic matter processing) is not well supported by the experimental data and thus not an appropriate rationale for the conservation of biodiversity.

In conclusion, my results suggest that a functionally dominant species (i.e., *Pycnopsyche gentilis*) is performing the majority of leaf breakdown in Greene Creek, North Carolina. My results support the conclusions of Creed et al. (2009). Moreover, the meta-analysis of Cardinale et al. (2006) suggests that this may not be a unique result. In addition to this, my study is the first to show that one functionally subordinate species (i.e., *Tallaperla maria*) can inhibit feeding by another functionally subordinate species (i.e., *Tipula abdominalis*). Such inhibitory interactions between functionally subordinate species may prevent a positive biodiversity-ecosystem function relationship from occurring.

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Table 1. Final detritivore dry mass (mean +/- 1 SE) for all treatments. Units are mg. N = 4 for all detritivore treatments unless noted with an (*) where N = 3. Treatment abbreviations: (P) *Pycnopsyche*, (C) *Tipula*, (S) *Tallaperla*, (PC) *Pycnopsyche-Tipula*, (PS) *Pycnopsyche-Tallaperla*, (CS) *Tipula-Tallaperla*, (PCS) *Pycnopsyche-Tipula-Tallaperla*.

| | | | Treatment | | | | | |
Species	P	C	S	PC	PS	CS	PCS	Mean
P	15.1	-----	-----	19.2*	12.8	-----	15.9	15.8
	(1.3)			(1.5)	(2.2)		(2.4)	
C	------	19.2*	-----	16.4	-----	14.9	18.0	17.1
		(3.5)		(1.7)		(1.8)	(5.4)	
S	------	-----	29.8	-----	31.1	24.2	20.9	26.5
			(4.4)		(4.0)	(2.5)	(1.6)	
Total	15.1	19.2	29.8	35.6	43.9	39.0	54.8	

FIGURE LEGENDS

Figure 1. Hypothetical biodiversity-ecosystem function relationships. A. Hypothetical BEF regression of all treatments, showing a positive relationship. B. Hypothetical BEF regression of only treatments containing the most productive species, showing no significant difference between the most productive species monoculture and the three-species polyculture (evidence for dominant species effect). C. Hypothetical BEF regression of only treatments containing the most productive species, showing that the three-species polyculture is significantly different than the most productive species monoculture (evidence for positive BEF relationship).

Figure 2. Average leaf mass lost for each treatment. Units are grams (g) and bars denote $+1$ SE. Letters above the bars represent results of a Tukey's test; bars with the same letter are not significantly different. Treatment abbreviations are the same as in Table 1 except (M) Microbial Control.

Figure 3. Comparison of observed (black) and predicted (gray) leaf mass lost (corrected) values for species combination treatments. Leaf mass lost has been corrected for loss attributed to leaching and microbial breakdown. Predicted values were obtained by adding values from monocultures of species included in the combination treatment. '*' represents a significant difference between observed and predicted values ($p < 0.05$) and 'NS' represents no significant difference ($p > 0.05$). Treatment abbreviations are the same as in Table 1.

Figure 4. Relationship between leaf mass lost (corrected) (g) and final *Pycnopsyche* biomass (mg) in treatments containing *Pycnopsyche* ($r^2 = 0.594$, $p < 0.01$).

Figure 5. A. The relationship between leaf mass lost (corrected) and detritivore species richness for the full data set ($r^2 = 0.075$, $p = 0.094$). B. The relationship between leaf mass lost (corrected) and detritivore species richness for only treatments containing *Pycnopsyche* ($r^2 = 0.000$, $p = 0.905$). Data points are values from individual replicates.

Figure 6. The relationship between leaf mass lost (corrected) (g) and final detritivore biomass (mg) across all treatments ($r^2 = 0.020$, $p = 0.489$).

Figure 7. A. The relationship between the ratio of leaf mass lost-animal dry mass and detritivore species richness ($r^2 = 0.0231$, $p = 0.219$). B. The relationship between leaf mass lost-animal dry mass ratio and detritivore species richness of treatments containing *Pycnopsyche* ($r^2 = 0.723$, $p < 0.001$). Points are values from individual replicates. One *Tipula* replicate and one *Pycnopsyche-Tipula* replicate were omitted due to mortality of individuals (see text). There is one hidden value for *Pycnopsyche-Tipula* in the two-species treatment.
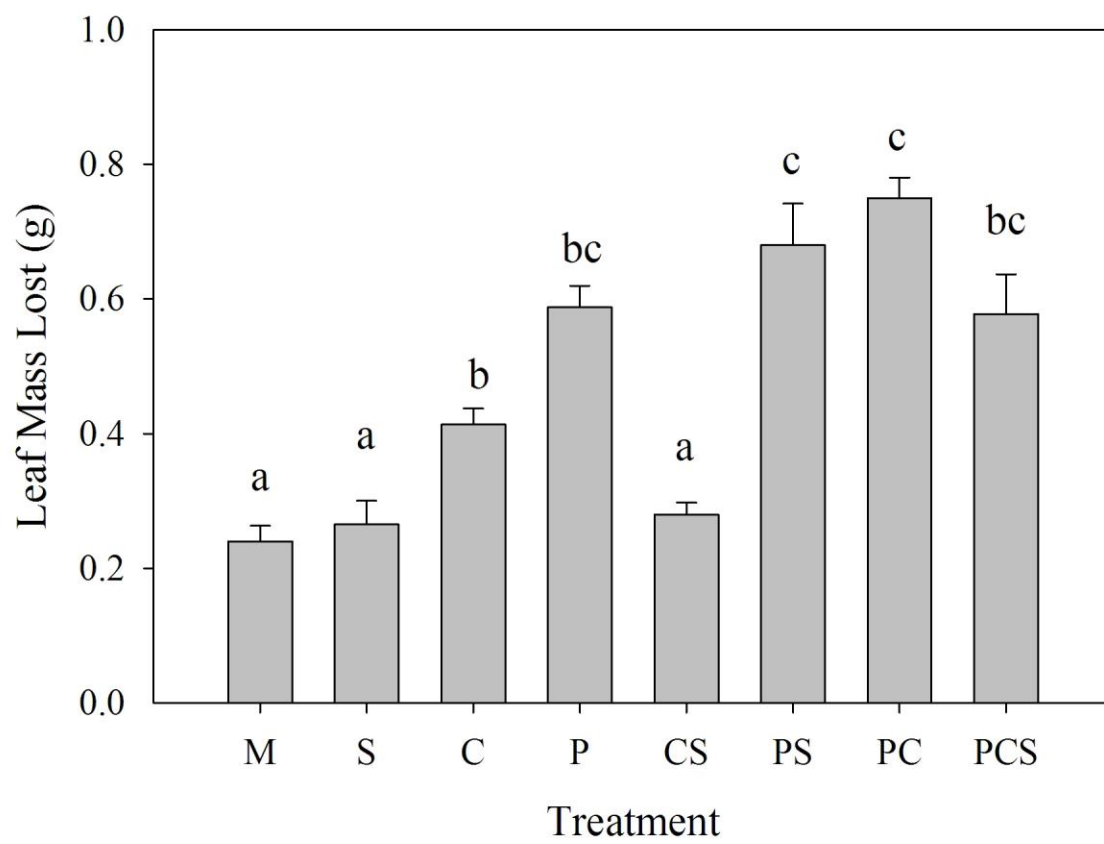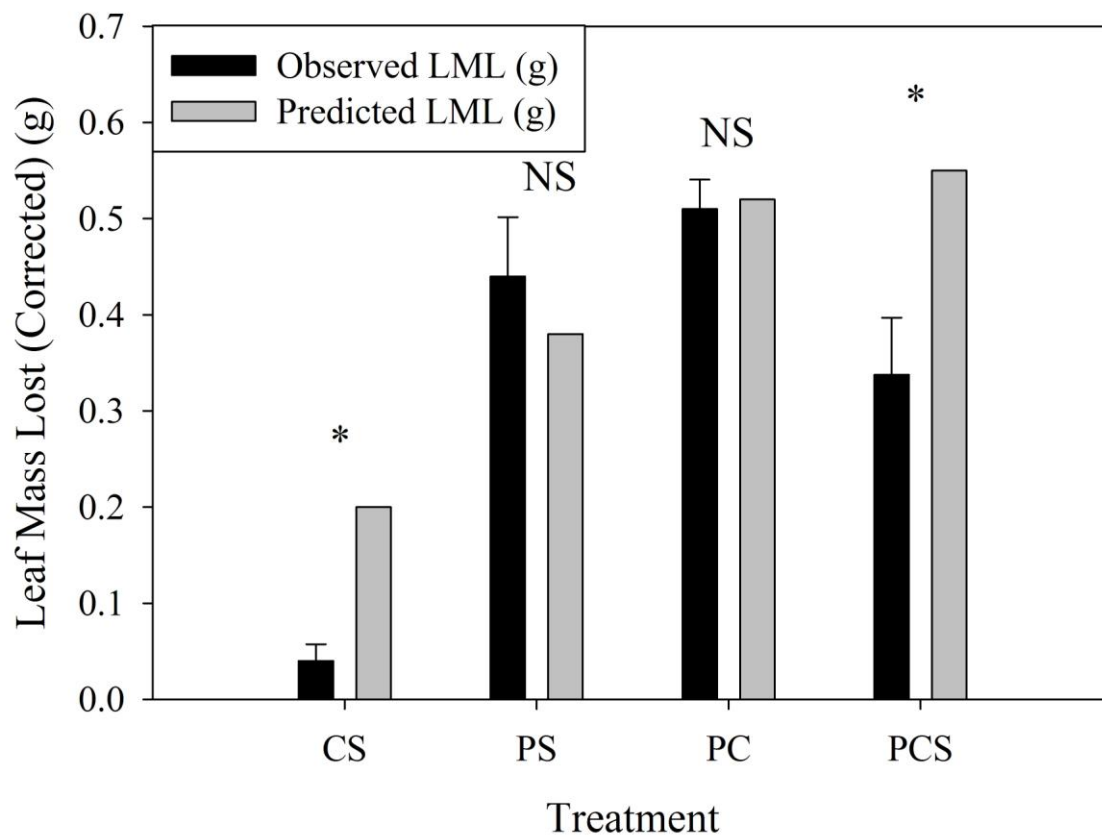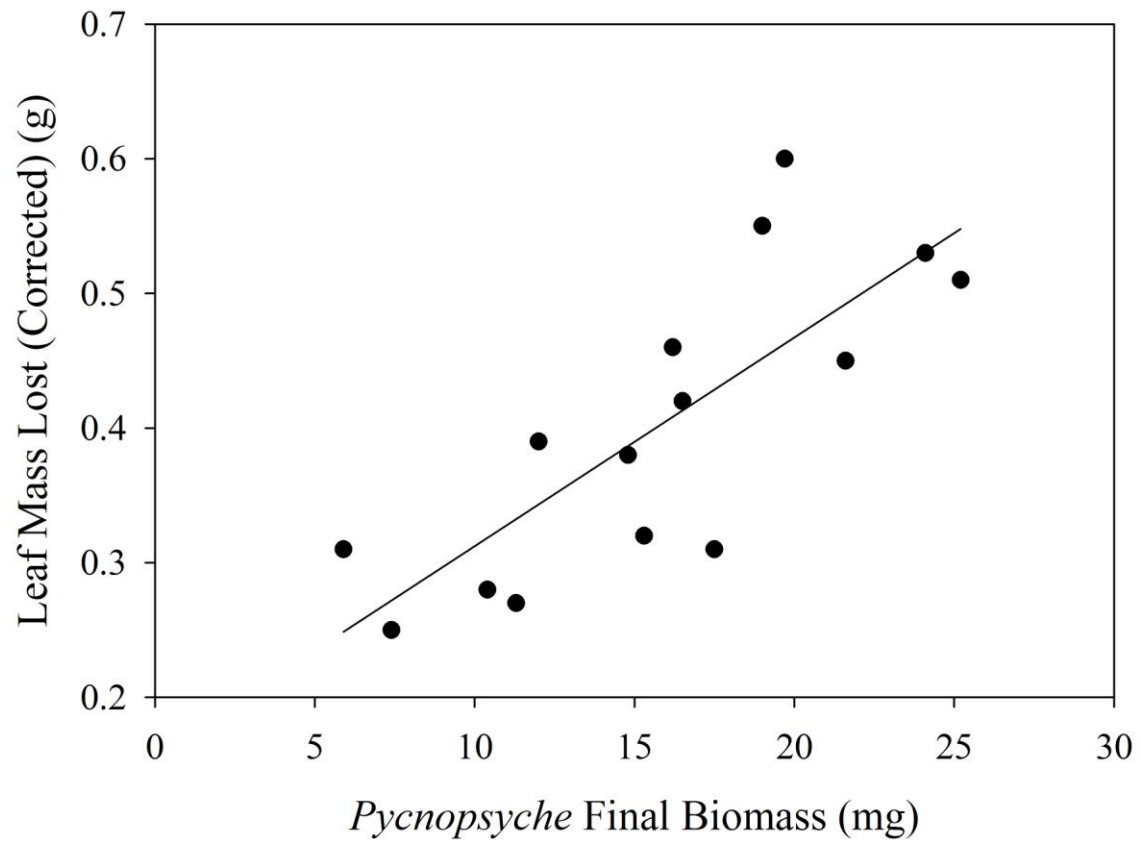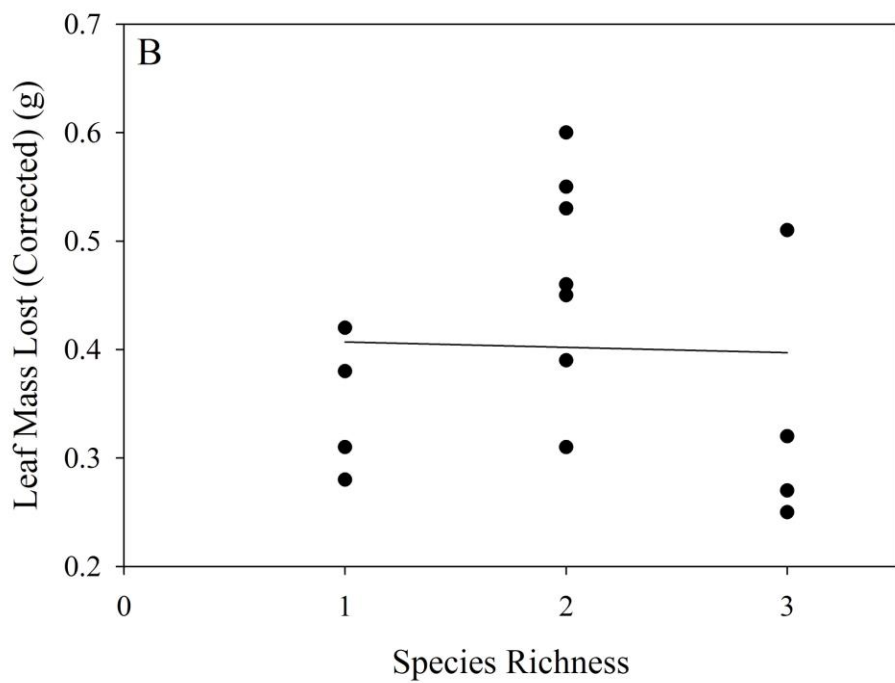
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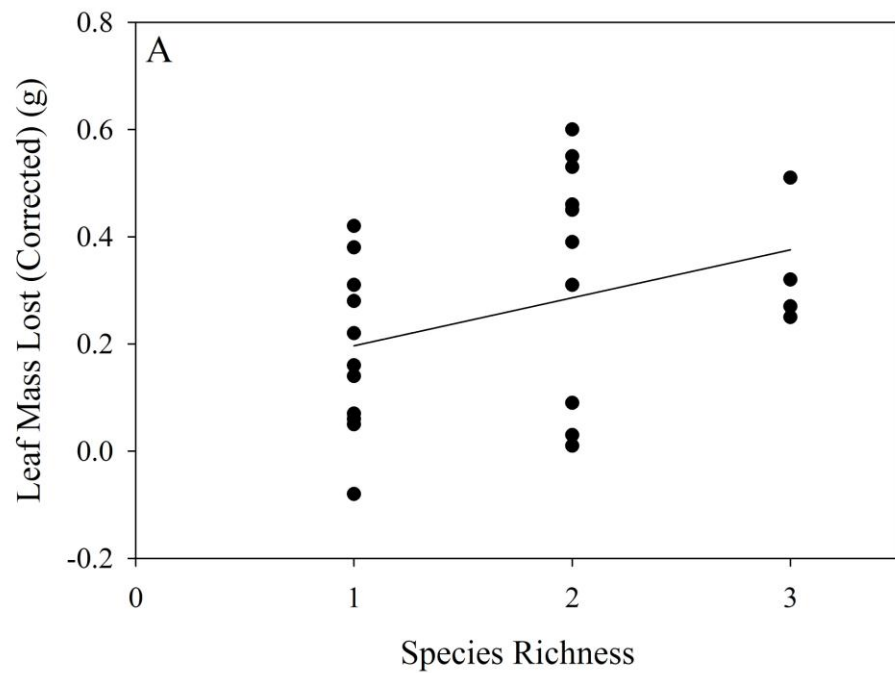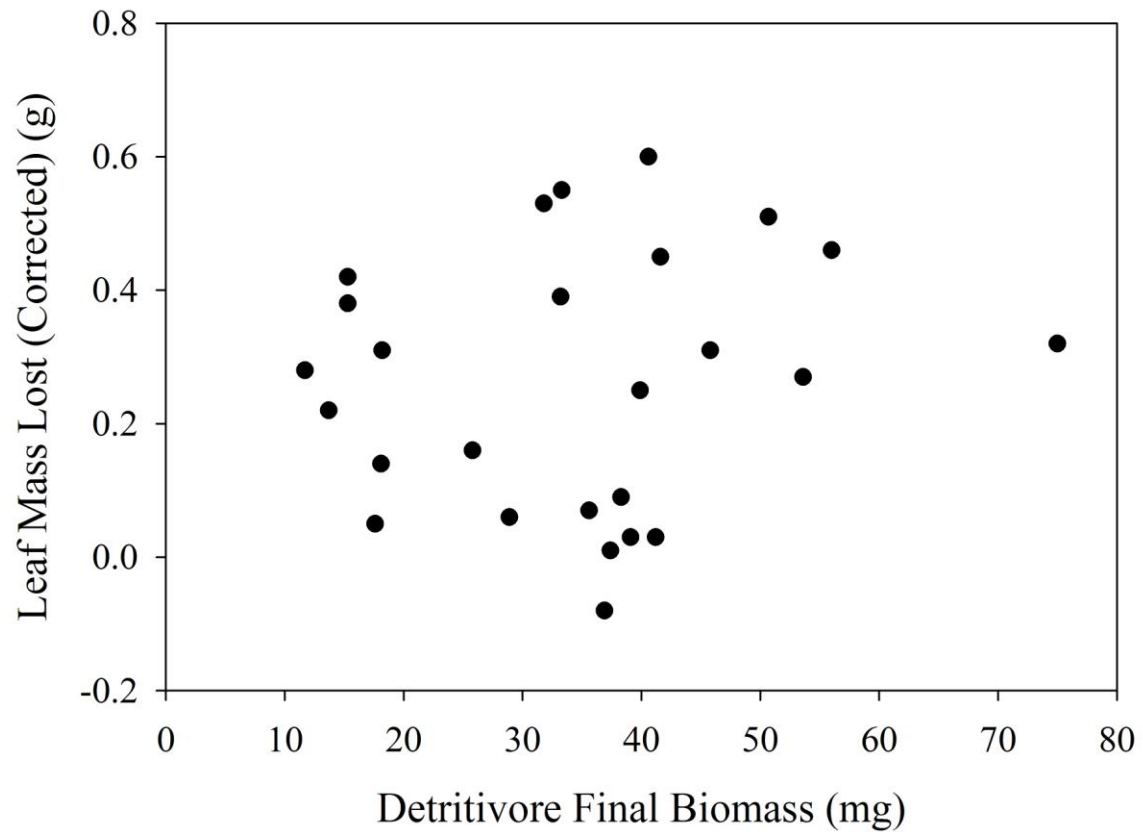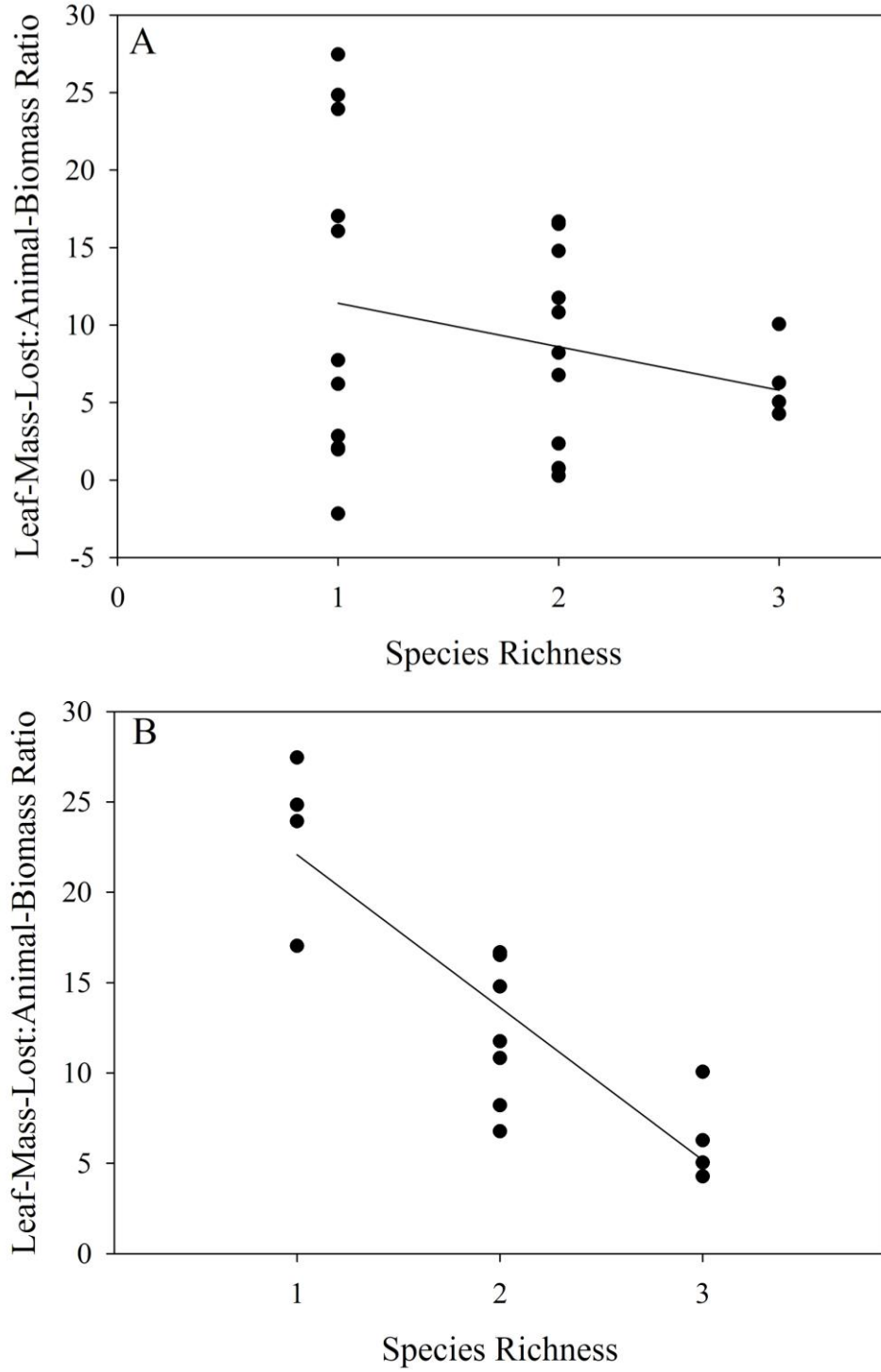
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VITA

Mark Alan Rollins was born in Charlotte, North Carolina, on August 9, 1985. He attended Knollwood Elementary and West Rowan Middle School in Salisbury, North Carolina, and graduated from West Rowan High School in Mt. Ulla, North Carolina in June 2003. The following autumn, he entered Wingate University to study biology, and in May 2007 he was awarded the Bachelor of Science degree. In the fall of 2007 he began study toward a Master of Science degree in Biology at Appalachian State University. The Master of Science degree was awarded in August 2010. His parents are Russell Rollins and Patricia Wilhite.