LINKING RESOURCE AND CONSUMER DIVERSITY TO ECOSYSTEM FUNCTION IN A DETRITUS-BASED WATERSHED

by

JOHN STEPHEN KOMINOSKI

(Under the Direction of Catherine M. Pringle)

ABSTRACT

Global species declines have prompted research exploring the relationship between biodiversity and ecosystem function. Earlier studies focused on terrestrial plant species richness effects on primary productivity. More recently, attention has focused on effects of leaf litter species diversity on decomposition in terrestrial and aquatic ecosystems. Using a full-factorial design of litter from four dominant riparian tree species, we tested for effects of nonrandom species loss on breakdown dynamics (litter mass loss, litter chemistry, microbes and invertebrates) in a detritus-based stream and compared results with data from a riparian study. Data were analyzed using statistical analyses that tested for additive effects of individual litter species presence/absence and nonadditive effects of species richness and species composition. We found nonadditive effects of litter species diversity on litter breakdown rates that were explained by litter species richness and composition. We observed nonadditive effects of litter species diversity on litter nutrients and secondary compounds and additive effects on structural compounds. Nonadditive effects of litter species diversity on bacterial and fungal biomass were seen during early stages of breakdown, and additive effects on microbes during intermediate and later stages of breakdown were explained by the presence/absence of high- and low-quality litter species. We found both

nonadditive effects of litter species diversity and additive effects of species identity on macroinvertebrates that varied with time and litter chemistry. Mixing higher-quality litter with low-quality litter resulted in shifts in microbial community diversity and altered processing dynamics of individual litter species. Using an information-theoretic approach to compare stream and riparian datasets, we found that although litter species traits persisted during processing in both ecosystems, the relative importance of specific traits and species composition on litter processing varied between terrestrial and aquatic ecosystems. Inputs of terrestrially derived litter to stream ecosystems can be influenced by invasive plant pests. The hemlock woolly adelgid appeared to drive seasonal hemlock and carcass inputs to our study stream. Our results suggest that predicted changes in tree species composition in riparian forests will likely alter invertebrate and microbial communities that interact with litter quality and diversity to differentially affect detrital processing in terrestrial and aquatic ecosystems.

INDEX WORDS: biodiversity, ecosystem function, additive, nonadditive, nonrandom species loss, leaf litter, southern Appalachian stream, riparian

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DEDICATION

I dedicate this dissertation to the memory of Frank B. Golley, my friend, colleague, mentor, and inspiration.

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TABLE OF CONTENTS

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Increasing global species declines have stimulated research exploring the relationship between biodiversity and ecosystem function (Schulze and Mooney 1993, Kinzig et al. 2002, Loreau et al. 2002). Environmental differences between terrestrial and aquatic ecosystems make it difficult to generalize about the functional importance of species diversity in both systems (Giller et al. 2004). The relationship between species diversity and ecosystem function is likely dependent on ambient conditions, suggesting that species contributions to ecological processes may change over heterogeneous spatial and temporal environments (Cardinale et al. 2000, Swan and Palmer 2004). Interest in the functional importance of resource diversity in detritus-based ecosystems has led to studies of leaf litter (hereafter litter) species diversity on breakdown dynamics in both terrestrial (Gartner and Cardon 2004, Hättenschwiler and Gasser 2005, Hättenschwiler et al. 2005, Wardle et al. 2006, Ball et al. 2008) and aquatic ecosystems (Swan and Palmer 2004, LeRoy and Marks 2006, Kominoski et al. 2007, Lecerf et al. 2007). Since both riparian and stream food webs use detritus as a source of energy, nutrients, and habitat (Wallace et al. 1997, Hall et al. 2001, Wardle 2002, Moore et al. 2004), comparing effects of litter species diversity on breakdown dynamics in both system types is essential to advance predictability of litter species losses on ecosystem function at multiple temporal and spatial scales.

Nonrandom species loss and additivity versus nonadditivity

Species losses are predicted to be nonrandom (Huston et al. 2000, Loreau et al. 2001, Tilman and Lehman 2001), and scenarios based on random versus nonrandom species losses

yield different functional responses (Gross and Cardinale 2005). Models that test effects of random species loss focus on nonadditive (species interactions) effects of species diversity because each species has an equal probability of extinction, whereas tests of nonrandom species loss can examine additive (predictable from individual species) and nonadditive effects of species identity and diversity (Kominoski et al. 2007). Many earlier studies testing litter species diversity effects on breakdown tested random species loss yet have found nonadditive effects explained by species composition (Wardle et al. 1997, Hector et al. 2000, Swan and Palmer 2004).

Nonadditive effects of litter species diversity on breakdown are generally not explained by litter species richness (but see LeRoy and Marks 2006, Kominoski et al. 2007), rather by species composition, or the interactions among individual litter species in mixtures (Gartner and Cardon 2004, Swan and Palmer 2004, Hättenschwiler et al. 2005, LeRoy and Marks 2006, Kominoski et al. 2007, Lecerf et al. 2007). In terrestrial ecosystems, litter species identity (i.e., presence/absence) and composition tend to be stronger determinants of litter breakdown rates (Wardle et al. 1997, Hooper et al. 2005, Wardle et al. 2006, Ball et al. 2008) and invertebrate composition and diversity (Wardle et al. 1997, Wardle et al. 2006) than litter species diversity, per se. In contrast, litter species richness and composition have stronger effects on in-stream breakdown rates than species identity (Swan and Palmer 2004, LeRoy and Marks 2006, Kominoski et al. 2007, Lecerf et al. 2007), and less is known about the relationships between litter species diversity and stream invertebrate assemblages (but see LeRoy and Marks 2006). In order to explain differences between additive and nonadditive effects of litter species diversity on breakdown in terrestrial and aquatic ecosystems, concomitant tests of litter species diversity in both systems are necessary.

Litter breakdown in terrestrial and aquatic ecosystems

Although litter processing in terrestrial and aquatic ecosystems is thought to follow similar patterns (Wagener et al. 1998), breakdown in both systems occurs over different temporal and spatial scales and under different physical, chemical, and biological conditions, which interactively influence breakdown. Examining the distinct environmental conditions between terrestrial and aquatic environments may explain differential effects of litter diversity on breakdown in these ecosystems. Although many studies have compared various aspects of breakdown dynamics (e.g., breakdown rate, litter chemistry, and biotic communities) in single- and mixed-species litter, few have analyzed these parameters concomitantly, and none have synthesized results across terrestrial and aquatic ecosystems. The lack of an integrated perspective of litter species diversity on breakdown dynamics for various types of detritus-based ecosystems limits our ability to predict functional implications of plant species declines across landscapes in which connections between terrestrial and aquatic habitats are ecologically important (sensu Grimm et al. 2003).

Species' traits (functional characteristics) are known to influence ecosystem processes (Chapin et al. 2000) and have challenged species diversity-ecosystem function relationships (Loreau et al. 2001, Hooper et al. 2005). For example, changes in plant species diversity may alter the diversity of plant species traits (e.g., nitrogen-fixing, phenology) that are responsible for driving ecosystem processes rather than species diversity, per se (Diaz and Cabido 2001, Lavorel and Garnier 2002). Similarly, traits of plant species litter (dead organic matter), such as litter quality (chemical composition), associated decomposer biota, and resistance to decomposition, could be used to assess the effects of litter species composition on litter processing.

Study site, objectives, hypotheses

We conducted research at Coweeta Hydrologic Laboratory, Macon County, NC, USA (35º00'N, 83º30' W). Coweeta is a 2,185 ha forested basin in the Blue Ridge physiographic province of the southern Appalachian Mountains (Swank and Crossley 1988). Vegetation at Coweeta is mixed hardwood (dominated by *Quercus* spp., *Acer* spp., and *Liriodendron* spp.), with a dense understory of *Rhododendron maximum* that provides year-round shading of streams. Mean monthly air temperature ranges from 3 to 22°C, and mean annual precipitation ranges from 180 cm at low elevations to 250 cm at high elevations (Swift et al. 1988). Our study site was along a second-order reach of Ball Creek, which drains the southern portion of the Coweeta basin before joining Coweeta Creek, a tributary of the Little Tennessee River.

We collected litter from four dominant riparian tree species tulip poplar (*Liriodendron tulipifera*, L), red maple (*Acer rubrum*, A), chestnut oak (*Quercus prinus*, Q), and rhododendron (*Rhododendron maximum*, R), representing a range of initial chemistries and breakdown rates (Webster and Benfield 1986, Kominoski et al. 2007, Ball et al., 2008), and incubated litterbags in stream and riparian habitats along Ball Creek. We used a full-factorial design (Kominoski et al. 2007), which separates the confounding effects of litter species richness and composition (Huston 1997, Drake 2003), to test for functional effects of nonrandom species loss on breakdown dynamics (litter mass loss, changes in litter chemistry, changes in microbial and invertebrate consumers) in both terrestrial and aquatic systems.

Our objectives were to: 1) test for additive and nonadditive effects of litter species diversity on breakdown, litter chemistry, and biota (microbes and invertebrates) in litter incubated in stream habitats (Chapter 2); 2) understand the relationships between litter resource

heterogeneity and invertebrate (Chapter 3) and microbial community dynamics (Chapter 4); 3) compare litter processing in terrestrial and aquatic ecosystems to assess the relative importance of litter species' traits (chemical and biological) and species composition (Chapter 5); and 4) quantify the effects of an invasive pest species on the timing, quantity and quality of terrestrial organic matter inputs to a detritus-based, headwater stream.

The following hypotheses and/or questions are explored in these chapters:

Chapter 2. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream.

(1) Are effects of litter species diversity on breakdown dynamics additive?

(2) If nonadditive effects (interactions above and beyond main effects of species presence or absence) exist, are they explained by species richness or composition?

(3) If species composition effects exist, which species interactions are driving nonadditive effects?

Chapter 3. Litter species diversity and identity alter macroinvertebrate communities during breakdown in a detritus-based stream.

(1) Litter species diversity would have both additive and nonadditive effects on macroinvertebrate community dynamics and that effects would vary with time.

(2) Litter chemistry (i.e. quality) and mass remaining would explain variation in macroinvertebrate response to litter species diversity.

Chapter 4. Resource heterogeneity alters microbial diversity and stream organic matter processing.

(1) High-quality litter species (lower C:N ratio) would have higher rates of microbial respiration and litter mass loss than low-quality litter species (higher C:N ratio) but lower

microbial diversity due to greater resource availability (Tilman 1982).

(2) Mixing high-and low-quality litter would decrease rates of litter mass loss and microbial respiration of the high-quality species as compared to when it was incubated alone.

(3) Mixing high-and low-quality litter would increase microbial community diversity on the high-quality species as compared to when it was incubated alone.

Chapter 5. Litter processing in terrestrial and aquatic ecosystems: importance of species composition and trait persistence

(1) Due to persistence of autecological (individual species) traits among labile and recalcitrant species, litter species presence/absence (additive) will explain litter processing (e.g., litter mass remaining) in riparian habitats; whereas rapid changes in species traits of labile (readily changing) versus recalcitrant (resistant to change) litter within the connective matrix of water will generate species interactive effects on litter processing in stream habitats.

(2) Processing of riparian litter will be strongly influenced by various aspects of litter chemistry (e.g., nutrient content, structural and secondary compounds), and processing of in-stream litter will be most influenced by structural chemical compounds.

(3) Although microbial (bacteria and fungi) and invertebrate decomposers are important biological contributors to litter processing in both riparian and stream habitats, biotic processes likely better explain litter processing in riparian than stream habitats due to greater physical stability in terrestrial litter that supports biota.

Chapter 6. Invasive woolly adelgid appears to drive seasonal hemlock and carcass inputs to a detritus-based stream.

(1) What are the contributions of eastern hemlock (*Tsuga canadensis*) to direct litterfall and lateral inputs to a detritus-based stream?

(2) How do the quality, quantity, and timing of hemlock litter inputs change during infestation by the hemlock woolly adelgid (*Adelges tsugae*)?

(3) How might woolly adelgid carcasses serve as allochthonous subsidies to detritus-based streams?

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CHAPTER 2

NONADDITIVE EFFECTS OF LEAF LITTER SPECIES DIVERSITY ON BREAKDOWN DYNAMICS IN A DETRITUS-BASED STREAM[1]

[1]Kominoski, J.S., C.M. Pringle, B.A. Ball, M.A. Bradford, D.C. Coleman, D.B. Hall, and M.D. Hunter. *Ecology* 88: 1167-1176. Reprinted here with permission of publisher.

Abstract. Since species loss is predicted to be non-random, it is important to understand how those species that we anticipate losing interact with other species to affect ecosystem function. We tested whether litter species diversity, measured as richness and composition, affects breakdown dynamics in a detrital-based stream. Using full-factorial analyses of single- and mixed-species leaf packs [15 possible combinations of four dominant litter species; red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), chestnut oak (*Quercus prinus*), rhododendron (*Rhododendron maximum*)], we tested for single-species presence/absence (additive) or species interaction (nonadditive) effects on leaf pack breakdown rates, changes in litter chemistry, and microbial and macroinvertebrate biomass. Overall, we found significant nonadditive effects of litter species diversity on leaf pack breakdown rates, which were explained both by richness and composition. Leaf packs containing higher litter species richness had faster breakdown rates, and antagonistic effects of litter species composition were observed when any two or three of the four litter species were mixed. Less-consistent results were obtained with respect to changes in litter chemistry and microbial and macroinvertebrate biomass. Our results suggest that loss of litter species diversity will decrease species interactions involved in regulating ecosystem function. To that end, loss of species such as eastern hemlock (*Tsuga canadensis*) accompanied by predicted changes in riparian tree species composition in the southeastern US could have nonadditive effects on litter breakdown at the landscape-scale.

Key words: species diversity; richness; composition; nonadditive; ecosystem functioning; detrital-based ecosystem; streams.

INTRODUCTION

Increasing global species declines have stimulated research exploring the relationship between biodiversity and ecosystem function (Schulze and Mooney 1993, Kinzig et al. 2002, Loreau et al. 2002). Most of these studies have been conducted in terrestrial ecosystems and have focused primarily on effects of plant species diversity on net primary production (Naeem et al. 1996, Tilman et al. 1996, Hooper and Vitousek 1997, Hector et al. 1999, Tilman 1999) and effects of litter species diversity on breakdown dynamics (Taylor et al. 1989, Blair et al. 1990, Wardle et al. 1997, Kaneko and Salamanca 1999, Hector et al. 2000, Hättenschwiler et al. 2005). Similar research in aquatic ecosystems is lacking (Gessner et al. 2004, Giller et al. 2004). For example, only a few studies (Leff and McArthur 1989, McArthur et al. 1994, Swan and Palmer 2004, LeRoy and Marks 2006) have investigated the relationship between litter species diversity and breakdown dynamics in streams. Given that many stream food webs are dependent upon allochthonous litter as a source of energy, nutrients, and habitat (Vannote et al. 1980, Wallace et al. 1997, 1999), understanding the relationship between litter species diversity and breakdown dynamics in streams draining forested watersheds is of considerable ecological importance.

Differences in litter chemistry account for high interspecies variation in breakdown rates. Previous studies examining structural and chemical composition of decomposing litter found that species containing higher initial C:N (Melillo et al. 1982, Webster and Benfield 1986), tannin (Gallardo and Merino 1992, Ostrofsky 1997), and lignin concentrations (Meentemeyer 1978) had slower breakdown rates than less recalcitrant species. However, while several studies have examined changes in chemistry of single-species litter throughout decomposition (Petersen and Cummins 1974, Suberkropp et al. 1976, Chauvet 1987, Hunter et al. 2003), this information is lacking for mixed-species assemblages. Understanding changes in mixed-species litter chemistry

during breakdown may provide insights into mechanisms by which litter species interactions affect breakdown dynamics (Moore et al. 2004).

Microbial conditioning and subsequent invertebrate consumption of litter contribute to breakdown (Swift et al. 1979, Webster and Benfield 1986). Bacteria and fungi differ in their contribution to breakdown, with fungi being apparently more important than bacteria in both terrestrial (Hendrix et al. 1986, Blair et al. 1990, Bailey et al. 2002) and aquatic (Findlay and Arsuffi 1989, Gessner and Chauvet 1994, Baldy et al. 1995, Hieber and Gessner 2002) ecosystems. Invertebrates are dominant processors of litter in detrital-based ecosystems (Seastedt 1984, Cuffney et al. 1990), and litter species diversity can influence invertebrate composition, abundance, feeding activity, and growth rates (Hansen and Coleman 1998, Hansen 1999, Swan and Palmer 2006). Comparing the trophic dynamics of bacteria, fungi, and invertebrates in response to litter species diversity may help predict effects of changes in riparian tree species diversity on the functioning of detrital-based ecosystems.

Traditionally, studies investigating effects of species diversity on ecosystem function have measured species richness as a surrogate for species diversity; however, species diversity can be defined as species richness, evenness, functional traits, and composition or interactions among species (Chapin et al. 2000, Hooper et al. 2005). Yet, studies attempting to identify the causal mechanisms behind how species diversity affects ecosystem function have often not separated the confounding effects of species richness and composition (Huston 1997, Drake 2003). One solution is to investigate single-species presence/absence versus mixed-species richness and composition effects using full-factorial experimental designs to test additivity of litter species diversity. Here, we used full-factorial analyses of variance to test additivity of litter species diversity (richness and composition) on breakdown dynamics (leaf pack breakdown rates,

changes in litter chemistry, and effects on microbial and macroinvertebrate biomass) in a detrital-based stream. This design allowed us to address the following questions: (1) Are effects of litter species diversity on breakdown dynamics additive?; (2) If nonadditive effects (interactions above and beyond main effects of species presence or absence) exist, are they explained by species richness or composition?; (3) If species composition effects exist, which species interactions are driving nonadditive effects?

METHODS

Study Site

We conducted this study in a second-order reach of Ball Creek, a headwater stream at Coweeta Hydrologic Laboratory in Macon County, North Carolina, USA (35º00'N, 83º30' W). Coweeta is a 2,185 ha forested basin in the Blue Ridge physiographic province of the southern Appalachian Mountains (Swank and Crossley 1988). Vegetation at Coweeta is mixed hardwood (dominated by *Quercus* spp., *Acer* spp., and *Liriodendron* spp.), with a dense understory of *Rhododendron maximum* that provides year-round shading of streams. Mean monthly air temperature ranges from 3 to 22°C, and mean annual precipitation ranges from 180 cm at low elevations to 250 cm at high elevations (Swift et al. 1988). Mean daily stream temperature along the study reach of Ball Creek during this study ranged from 1.3 to 16.6°C.

Leaf packs and experimental design

We selected four dominant riparian tree species (Swank and Crossley 1988) in the Coweeta basin [tulip poplar, *Liriodendron tulipifera* (*L*); red maple, *Acer rubrum* (*A*); chestnut oak, *Quercus prinus* (*Q*); and rhododendron, *Rhododendron maximum* (*R*)] that represented a

range of initial litter chemistries (Table 2.1). Webster and Waide (1982) found the relative contribution (%) of annual litter fall at Coweeta for these species as follows: 9.1 (*L*), 4.8 (*A*), 19.0 (*Q*), 11.6 (*R*). Our experimental design was a randomized complete block. All 15 possible single- and mixed-species combinations (*L*, *A*, *Q*, *R, LA, LQ…LAQR*; *sensu* Jonsson and Malmqvist 2000) were crossed with nine levels of exposure time (i.e. nine sampling dates), and were replicated at four stream locations (blocks), giving a total of 540 experimental units (15 × 9 × 4). Note that although time was an experimental factor, this was not a repeated measures design. Because of the destructive nature of sampling leaf packs, distinct, individually randomized experimental units were used at each time point.

In autumn 2003 we collected freshly-abscised leaves and then air-dried them. Each leaf pack comprised approx. 15 g total litter, with individual species in mixed-species packs being represented in equal mass proportions; litter was encased in plastic, mesh pecan bags (19.1 cm × 38.1 cm, 5 × 5 mm mesh; Cady Industries Inc., Georgia) after initial dry mass determinations. On 10 January 2004 we deployed 480 leaf packs (15 treatments × 4 blocks × 8 sampling dates); the remaining 60 leaf packs were transported back to the laboratory the same day and were used to measure initial litter chemistry and handling loss. Packs within each experimental block were grouped in arrays of 15 treatments and secured to the stream bottom using plastic ties with galvanized gutter nails. Arrays were randomly retrieved from blocks 7, 14, 28, 70, 118, 169, 183 and 190 days after deployment. Packs were transported on ice to the laboratory and processed within 12 h of retrieval.

After retrieval, litter was rinsed over nested sieves (1 mm and 250 μm) to collect macroinvertebrates and remove sediments and debris. Five leaf disks (1.2 cm dia.) were sampled from a representative composite of litter species in each leaf pack for both fungal and bacterial

analyses (see below). An additional five leaf disks were taken to estimate mass of leaf discs removed for fungal and bacterial analyses. Remaining litter was oven-dried at 60ºC for 24 h, ground using a Wiley Mill, and then ball-milled using a Spex CertiPrep 8000-D Mixer Mill prior to litter chemistry analyses.

Litter mass loss and chemistry

Ash-free dry mass (AFDM) was determined as the difference between pre- and post-combustion (at 550°C for 1 h) mass of oven-dried (60ºC) litter. Mass loss was measured by dividing the retrieved AFDM by the initial (i.e. day 0) AFDM. Litter carbon and nitrogen concentrations were measured using a Carlo Erba 1500N CHN Analyzer, cellulose, hemicellulose, and lignin concentrations using an Ankom A200 Fiber Analyzer, and condensed tannins, hydrolysable tannins, and total phenolics using techniques described by Rossiter et al. (1988) and Hunter and Schultz (1995).

Biota

We measured biota biomass on sampling days 14, 70, and 118. We estimated bacterial cell density using epifluorescent microscopy (Porter and Feig 1980). Briefly, the five 1.2 cm dia. leaf disks from each replicate leaf pack were preserved at 4ºC in a 0.2 μm filtered solution of 5% formaldehyde (Velji and Albright 1986). Next, bacterial cells were separated from leaf disks by sonication (Weyers and Suberkropp 1996) and cells stained with 2 mL of 10 μg mL^{-1} DAPI solution for an incubation period of 10 min. Samples were filtered and mounted on glass microscope slides (Velji and Albright 1986), then kept in the dark and refrigerated until counted. We counted cells from ten random fields per slide using 1000× epifluorescent microscopy.

Bacterial cell biovolumes were estimated using geometric shapes (Bratbak 1985, Psenner 1993, Wetzel and Likens 2000), and total bacterial carbon was estimated by multiplying cell biovolumes by 5.6×10^{-13} g C μm^{-3} (Bratbak 1985).

Leaf disks for fungal biomass estimates were preserved at 4°C in 99.9% HPLC-grade methanol (Newell et al. 1988). Ergosterol, a surrogate for fungal biomass (Gessner and Chauvet 1993), was extracted by refluxing for 30 min at 80ºC in alcoholic base (5 mL of 4% KOH in methanol added to 25 mL methanol). Samples were partitioned into pentane and evaporated to dryness at 30ºC using N_2 gas. Dried samples were re-dissolved in 2 mL of methanol, sonicated, filtered (0.45 μm), and stored at 4ºC. Ergosterol was measured on a RP-10 column using an HPLC by comparing absorbance at 282 nm after separation from other lipids (Suberkropp and Weyers 1996). Ergosterol concentrations were converted to fungal biomass using the ratio of 5.5 μg ergosterol per 1 mg fungal dry mass (Gessner and Chauvet 1993).

Macroinvertebrates were separated into two size classes (> 1 mm and 250 μm – 1 mm) and preserved in 90% ethanol. Organisms were identified to lowest possible taxonomic level and were assigned to functional feeding groups (Merritt and Cummins 1996, Barbour et al. 1999, Wallace et al. 1999). Chironomidae were separated into Tanypodinae and non-Tanypodinae. Length-mass regressions (Benke et al. 1999) were used to estimate macroinvertebrate biomass.

Statistical analyses

To estimate leaf pack breakdown rates, we used an exponential model to incorporate litter mass remaining from all nine sampling dates into a single model. We assumed the relationship $E(AFDM_t) = \theta e^{-kt}$, where $E(AFDM_t)$ is the expected (i.e. population mean) proportion of ash-free dry mass (AFDM) on day t, k is the breakdown rate, and θ is the initial mean AFDM at time 0.

To simplify model fitting and statistical inference, we linearized this relationship and fit models of the form $\ln_e(AFDM_t) = \varphi - kt + \varepsilon_t$, where $\varphi = \log(\theta)$, and ε_t is a mean 0, constant variance error term. Note that we allow $\varphi \neq 0$ (i.e. $\theta \neq 1$) and also allow it to differ across experimental conditions to account for non-constant handling loss. In addition, the coefficient on time, k, which represents the breakdown rate, was also allowed to differ across experimental conditions to assess litter species diversity effects on this parameter. The effects of species diversity on the breakdown rate k (which appear as interactions between the continuous variable time and individual species presence/absence indicators in the linearized model) are of primary interest in the analysis rather than the species diversity effects on the initial mean AFDM parameter φ (which appear as main effects and interactions among the species presence/absence indicators not involving time in the linearized model). The model assumed that the error variance was proportional to the square of time and was therefore fit with weighted least squares. This assumption was made to account for non-constant variance observed in the residuals.

Litter chemistry variables were modeled similarly to AFDM. In each case, the chemical component and time were each transformed to make their relationship approximately linear so that a model similar to that used for AFDM could be used, whereby a constant (through time) rate of change parameter appeared as the slope on (transformed) time. That is, we fit models of the form $f_1(y) = \beta_0 + \beta_1 f_2(t) + \varepsilon$ and modeled species diversity effects on the rate of change parameter β_1. Here, f_1 and f_2 are transformations of the chemistry variable y and time t, respectively.

To test if leaf pack breakdown rates and rates of change in litter chemistry depended upon species diversity or single-species presence/absence, we used full-factorial models for the rate of change parameter (the coefficient on the continuous variable time - k in the models for AFDM

and β_1 in the litter chemistry models). That is, the rate parameter was modeled in terms of main effects *A*, *L*, *Q*, *R* and interactions *A*L*, *A*Q*, *A*R*, *L*Q*, *L*R*, *Q*R*, *A*L*Q*, *A*L*R*, *A*Q*R*, *L*Q*R*, *A*L*Q*R,* where here the main effects corresponded to dummy variables for presence/absence of the four single species. The influence of diversity on the rate of change was tested through a joint test of significance ($P < 0.05$) of the two- and higher-way interaction terms, which we refer to as the test for non-additivity. A significant non-additivity test means that individual species presence/absence in leaf packs is insufficient to explain differences in the rates of change, but it is the combinations of species that occur, or species diversity, that is crucial. Eight outliers (having external Studentized residuals > 3) were omitted from the analysis, and six leaf packs were lost during the study. This changed our total degrees of freedom to 525 of the 540 possible experimental units.

When species effects were additive, we reported marginal means for presence and absence of each species and whether the presence/absence effect was significant. To investigate whether this non-additivity was due to species richness (the number of species present in mixed-species packs, 2, 3, or 4) or species composition (which particular species are present together in mixed-species packs), we decomposed treatment effects (differences among the 15 different leaf pack types, corresponding to 14 degrees of freedom in the analysis of variance) into effects of individual species (4 df, 1 for each species), richness effects (accounting for 2 df), and composition effects (interactions among species not explained by richness, accounting for 8 df). When richness alone was insufficient to explain litter species diversity effects, we reported the particular species interactions that were found to be significant (see Results).

In contrast to AFDM and the litter chemistry variables, which were measured on 9 sampling dates, biota data were collected on only three sampling dates. This limited sampling

precluded the modeling of biota variables via a function of time. Therefore, biota data were analyzed at each sampling date using three separate models.

Data were transformed when necessary to meet assumptions of homoscedasticity. All analyses were conducted using PROC GLM or MIXED at $\alpha = 0.05$ in SAS version 9.1 (SAS Institute Inc., Cary, USA).

RESULTS

Litter breakdown and chemistry

In Fig. 2.1 we show observed breakdown rates for each leaf pack and, for mixed-species packs, the expected breakdown rates based on the monocultures (*sensu* Wardle et al. 1997). Differences in breakdown rates are apparent between the different litter species in monocultures; however, mixed-species packs appeared to behave idiosyncratically (Fig. 2.1). In contrast, using a full-factorial ANOVA we detected significant non-additivity of litter species diversity effects on leaf pack breakdown rates ($F_{10,490} = 1.93$, $P = 0.039$; Table 2.2), which was comprised of marginally significant species richness ($F_{2,490} = 2.86$, $P = 0.059$; Table 2.2) and composition effects ($F_{8,490} = 1.70$, $P = 0.096$; Table 2.2). This non-additivity could not be adequately explained by litter species richness alone. Although higher litter species richness was associated with faster breakdown rates (Fig. 2.2), there were also antagonistic interactions between certain species, whereby the combined presence of *A* with *L*, *A* with *Q*, and *L* with *Q* resulted in mean breakdown rates that were lower than those resulting from the combined additive effects of the two species (Fig. 2.3a-c).

Effects of litter species diversity on rates of change for C:N and phenolics were nonadditive (Time*Diversity terms: $F_{10,494} = 6.43$, $P < 0.0001$ and $F_{10,489} = 2.70$, $P = 0.003$,

respectively), whereas the effect of species diversity on rate of change for lignin was additive (Time*Diversity term: $F_{10,470} = 0.79$, $P = 0.640$). The significant litter species diversity effect for C:N was composed of both significant species richness and composition effects ($F_{2,494} = 3.72$, $P = 0.025$ and $F_{8,494} = 7.11$, $P < 0.001$, respectively), while composition, but not richness, accounted for the diversity effect on phenolics (composition term: $F_{8,489} = 3.03$, $P = 0.003$). Higher litter species richness (> 1 species) was associated with lower rates of change in C:N. A three-way interaction between *A*, *L*, and *Q* and a two-way interaction between *Q* and *R* were found ($F_{1,494} = 14.60$, $P < 0.001$ and $F_{1,494} = 7.68$, $P = 0.006$, respectively) in which *Q* and *R* had positive, but antagonistic effects on the C:N rate of change through time. In addition, *L* and *Q* had positive effects on C:N rate of change that were additive in the absence of *A*, but antagonistic when species *A* was present. Species *A* had a positive effect on this parameter only when both *L* and *Q* were absent; otherwise, the presence of *A* reduced the rate of change in the C:N ratio. For phenolics, three-way interactions among *A*, *L*, and *Q* and among *L*, *Q*, and *R* were found to affect the rate of change ($F_{1,489} = 4.12$, $P = 0.043$ and $F_{1,489} = 5.28$, $P = 0.022$, respectively). Essentially, there is no simple pattern to describe how the rate of change in phenolics depended upon the presence/absence of the four species. The presence of *Q. prinus* significantly increased the rate of change in lignin concentrations ($F_{1,470} = 9.02$, $P = 0.003$).

Biota

For bacterial biomass we detected non-additivity of litter species diversity on day 14 ($F_{10,42} = 2.05$, $P = 0.052$) and additivity on days 70 and 118 (diversity terms: $F_{10,34} = 0.71$, $P = 0.710$ and $F_{10,41} = 1.36$, $P = 0.230$, respectively). The nonadditive litter species diversity effect on day 14 was explained by composition ($F_{8,42} = 2.09$, $P = 0.06$) rather than richness. A significant

three-way interaction between *A*, *L*, and *Q* ($F_{1,42} = 3.72$, $P = 0.06$) occurred, which resulted in lower bacterial biomass than would have been expected under additivity. When diversity effects were simply additive, there were clear effects of species presence or absence on bacterial biomass. That is, on days 70 and 118 presence of *R* inhibited bacterial biomass ($F_{1,34.3} = 18.74$, $P < 0.001$; $F_{1,41.2} = 46.36$, $P < 0.001$, respectively); (Fig. 2.4a), while presence of *L* enhanced bacterial biomass on day 70 ($F_{1,34.2} = 6.77$, $P = 0.014$; Fig. 2.4a).

As for bacteria, there was a nonadditive effect of litter species diversity on fungal biomass at day 14 ($F_{10,21.1} = 2.82$, $P = 0.022$) and additive effects on days 70 and 118 ($F_{10,23} = 1.99$, $P = 0.084$ and $F_{10,30.5} = 0.36$, $P = 0.950$, respectively). The nonadditive diversity effect on day 14 was the result of composition ($F_{8,17.3} = 3.15$, $P = 0.022$) rather than richness. Significant two-way interactions between *A* and *R* ($F_{1,3.25} = 9.85$, $P = 0.046$) and *L* and *R* ($F_{1,7.15} = 5.80$, $P = 0.046$) were found, whereby interactions resulted in lower fungal biomass than would have been expected under conditions of additivity. For day 70, the presence of *L* enhanced fungal biomass ($F_{1,14} = 5.59$, $P = 0.032$), while presence of *Q* and *R* inhibited fungal biomass ($F_{1,14} = 5.17$, $P = 0.051$ and $F_{1,14} = 34.52$, $P = 0.0003$, respectively); (Fig. 2.4b). Presence of *R* also inhibited fungal biomass on day 118 ($F_{1,14} = 30.23$, $P < 0.001$).

In contrast to bacteria and fungi, there was neither significant litter species diversity nor litter species presence/absence effects on macroinvertebrate shredder biomass. Mean (± 1 SE) shredder biomass (mg g^{-1} litter AFDM) values, across all leaf packs, were 19.7 (± 3.3), 99.6 (± 21.7), and 83.7 (± 16.0) for days 14, 70, and 118, respectively.

DISCUSSION

We observed overall significant nonadditive effects of litter species diversity (both richness and composition) on leaf pack breakdown rates. Less-consistent results were obtained with respect to changes in litter chemistry and microbial and macroinvertebrate biomass. Both leaf pack breakdown rates and changes in litter C:N were affected by species richness; however, leaf pack breakdown rates increased with increasing species richness, whereas rates of change in litter C:N were not different among leaf packs containing > 1 species. Interactions between *L. tulipifera* and *A. rubrum* and each with either *Q. prinus* or *R. maximum* resulted in decreased rates of change of litter C:N and phenolics concentrations and slower breakdown rates than expected under additivity. However, *R. maximum* did not have a significant effect on leaf pack breakdown rates. The presence of *L. tulipifera* was also associated with higher bacterial and fungal biomass during intermediate stages of breakdown, while bacterial and fungal biomass were consistently lower in the presence of *R. maximum*, and the presence of *Q. prinus* increased the rate of change of litter lignin concentrations and inhibited fungal biomass during intermediate stages of breakdown. However, neither presence of *R. maximum* or *Q. prinus* (or low microbial biomass) explained breakdown rates *per se*. Finally, it is possible that nonadditive effects of litter species diversity on bacterial and fungal biomass on day 14 could be due to low macroinvertebrate shredder biomass, whereas higher macroinvertebrate shredder biomass on days 70 and 118 may have resulted in top-down control of microbial biomass.

Results suggest that complex litter species interactions drive patterns of breakdown dynamics. Mixing litter of different chemical and physical properties alters the resource quality and physical habitat complexity within leaf packs, resulting in changes in breakdown rates and decomposer abundance and activity (Hansen and Coleman 1998, Hansen 1999, Hector et al.

2000, Swan and Palmer 2006). More recalcitrant litter, such as *R. maximum*, may alter the physical structure and subsequent breakdown of the entire leaf pack, however, we did not observe a significant effect of *R. maximum* presence/absence or species interactions with *R. maximum* on leaf pack breakdown rates. In our study, mixed-species leaf packs were composed of chemically- and structurally-diverse litter, which affected changes in litter chemistry and microbial but not macroinvertebrate biomass. Presence of lower-quality (*Q. prinus* and *R. maximum*) and higher-quality (*L. tulipifera*) litter in leaf packs appeared to inhibit and stimulate microbial biomass, respectively. However, we observed both synergistic and antagonistic effects of litter mixing on breakdown rates due to litter species richness and composition, respectively. It is possible that microbial and shredder activity or diversity, rather than biomass, are better explanatory variables of nonadditive effects of litter species diversity on observed breakdown rates (Jonsson et al. 2001). However, shredder diversity in our study stream was dominated by only two taxa *Tallaperla* sp. and *Lepidostoma* sp.; all other shredder taxa were rare. It is also possible that macroinvertebrate shredders mediated the observed effects of presence of low-quality litter on microbial biomass. Macroinvertebrate shredders may have selectively consumed the high-quality, and presumably microbially conditioned, litter in mixed-species packs when low-quality litter was present (Arsuffi and Suberkropp 1985), which could explain the apparent inhibition of low quality litter on microbial biomass but lack of subsequent inhibition on breakdown rates.

Our results expand on existing datasets that have related litter species diversity to breakdown dynamics. One study in a mid-Atlantic (Maryland, U.S.A.) stream found additive effects of litter species diversity on breakdown rates during autumn (Swan and Palmer 2004), whereas we observed nonadditive effects of litter species diversity on breakdown rates. Aside

from explanations provided by Swan and Palmer (2004) (e.g., temperature), differences between the two studies may be explained by differences in litter species assemblages. Swan and Palmer (2004) assembled leaf packs using litter from eight common riparian tree species, such as slippery elm and black willow, which are not common to Coweeta watersheds. McArthur et al. (1994) suggested that the presence of a recalcitrant litter species inhibited microbial activity and subsequent breakdown of a fast-decomposing species. Although we observed inhibitory effects of recalcitrant species, such as *Q. prinus* and *R. maximum* on microbial biomass, *R.maximum* did not contribute to antagonistic, nonadditive effects of litter species diversity on leaf pack breakdown rates. In addition, we found significant effects of litter species diversity (specifically composition) and litter species presence/absence on bacterial and fungal biomass, which have not been reported previously for litter mixtures. Fungal diversity has been linked to litter diversity (Bärlocher and Graça 2002, Laitung and Chauvet 2005), and although fungal diversity and litter breakdown rates are not directly related (Bärlocher and Graça 2002, Dang et al. 2005), there is evidence of indirect effects of fungal diversity on litter breakdown rates via macroinvertebrate consumers (Lecerf et al. 2005). However, while fungal biomass and breakdown rates are positively correlated for single-species leaf packs in streams (Gessner and Chauvet 1994), the mechanisms linking litter species diversity, bacterial and fungal biomasses, and mixed-species leaf pack breakdown rates remain unclear and will be investigated further. Lastly, a recent laboratory study found that feeding activity and secondary production of the macroinvertebrate shredder, *Tallaperla maria*, was affected by litter species composition and not richness *per se* (Swan and Palmer 2006). *Tallaperla* sp. and *Lepidostoma* sp. were dominant shredders in our study stream (Kominoski, unpublished data); however, our *in situ* study found no effects of litter species presence/absence or species interactions on total shredder biomass. The absence of an

effect of litter species diversity on shredder biomass could be explained by the absence of crayfish from leaf packs. Crayfish are important shredders in Ball Creek (Schofield et al. 2001), but were likely excluded from our leaf packs due to the mesh size of our litterbags.

Our results suggest that loss of riparian tree species diversity will affect stream ecosystem functioning by reducing dynamic interactions that naturally occur during breakdown of mixed-species leaf packs. Of current concern in North American forests is the loss of eastern hemlock (*Tsuga canadensis*) due to introduction of the hemlock woolly adelgid (*Adelges tsugae*), a rapidly infesting insect from which the hemlock is undefended (Orwig et al. 2002). Another plant pathogen concern is "sudden oak death," which has recently been found in non-oak hosts, such as rhododendron (Garboletto et al. 2003). In southeastern U.S. forests, eastern hemlock and rhododendron are dominant, low quality riparian species (Webster and Benfield 1986). In the absence of rhododendron, eastern hemlock is predicted to be replaced by tulip poplar (Ellison et al. 2005), a high quality species (Webster and Benfield 1986). Also, a loss of rhododendron could be followed by an increase in red maple, which exhibits high understory tolerance and is predicted to increase in dominance over the next century (Abrams 1998). Results from our study suggest that decreases tree species diversity and changes in species composition in riparian forests of the southeastern U.S. could have nonadditive effects on litter breakdown in streams at the landscape-scale.

Species losses and extinctions are predicted to be non-random (Huston et al. 2000, Tilman and Lehman 2001). Therefore, experimental designs that randomly select mixed-species interactions at different levels of richness do not completely test effects of biodiversity loss on ecosystem function. If we can predict which species we expect to lose given specific environmental changes, knowing how those species interact with other species to influence

ecosystem function is of paramount importance. Our results suggest that litter species diversity drives species interactions involved in regulating ecosystem functioning. Given that riparian ecosystems on a global scale are subject to environmental changes, there is a need for additional studies to test the effects of declines in litter species diversity on in-stream breakdown dynamics using dominant riparian tree species assemblages in other regions of the world.

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TABLE 2.1. Mean initial chemistry (± 1 SE) of single-species litter. Values represent concentrations (% g AFDM). CT = condensed tannins, HT = hydrolysable tannins.

Species	C:N	Lignin	CT	HT	Phenolics
L. tulipifera	56.3 ± 0.4	12.5 ± 0.4	11.4 ± 2.0	19.5 ± 0.3	23.8 ± 1.0
A. rubrum	93.7 ± 1.8	9.8 ± 0.2	12.6 ± 1.6	19.3 ± 4.1	16.3 ± 5.2
Q. prinus	61.6 ± 1.3	14.4 ± 0.5	4.7 ± 1.4	13.7 ± 1.4	18.9 ± 3.3
R. maximum	162.7 ± 4.8	10.6 ± 0.1	10.5 ± 3.6	14.1 ± 3.2	20.3 ± 3.6

TABLE 2.2. ANOVA results for test of litter species diversity effects [Time*Diversity; composed of effects of species richness (Time*Rich) and species composition (Time*Comp) effects] above and beyond the main effects of species presence/absence (Time*A, Time*L, Time*Q, Time*R) on leaf pack breakdown rates. Significant ($\alpha = 0.05$) Time*Diversity effect indicates non-additivity of litter species interactions. ‡Note that a Type I (sequential) F test is used here, so this effect represents treatment differences in k above and beyond those already accounted for in the model; that is, above and beyond main effects of Time*A, Time*L, Time*Q, and Time*R on k.

Source	Interpretation	df	Type I SS	MS	F	*P*
Block	Variability in θ due to blocks	3	0.001	< 0.001	0.120	0.951
Trt	Variability in θ due to treatments	14	0.031	0.002	0.780	0.687
Time	Constant term in the factorial model for *k*	1	4.148	4.148	1473.030	< 0.001
Time*Block	Variability in *k* due to blocks	3	0.005	0.002	0.600	0.618
Time * *A*	Variability in *k* due to presence/absence of species *A*	1	0.043	0.043	15.330	< 0.001
Time * *L*	Variability in *k* due to presence/absence of species *L*	1	0.077	0.077	27.240	< 0.001
Time * *Q*	Variability in *k* due to presence/absence of species *Q*	1	0.001	0.001	0.490	0.486
Time * *R*	Variability in *k* due to presence/absence of species *R*	1	0.080	0.080	28.420	< 0.001
Time*Diversity‡		10	0.054	0.005	1.930	0.039
Time*Rich	Non-additivity of species effects on *k* decomposed into species richness and species composition effects	2	0.016	0.008	2.860	0.058
Time*Comp		8	0.038	0.005	1.700	0.096
Error		490	1.379	0.003		
Total		525	5.821			

FIGURE LEGENDS

FIG. 2.1. Single- and mixed-species leaf pack breakdown rates (*k*). Expected values for mixed-species are the means of monocultures. Error bars represent ± 1 SE.

FIG. 2.2. Mean leaf pack breakdown rates (*k*) for each level of litter species richness. Richness levels 1 (n = 16), 2 (n = 24), 3 (n = 16), 4 (n = 4). Error bars represent ± 1 SE.

FIG. 2.3. Profile plots (interaction plots) of nonadditive effects of litter species interactions on mean breakdown rates: (a) A*L (*A. rubrum* * *L. tulipifera*); (b) A*Q (*A. rubrum* * *Q. prinus*); and (c) L*Q (*L. tulipifera* * *Q. prinus*). Convergent (antagonism) as opposed to divergent (synergism) lines are indicated, whereas additivity would be represented by parallel lines.

FIG. 2.4. Main effects of litter species presence/absence on: (a) mean bacterial biomass (mg C g^{-1} litter AFDM) on day 70; and (b) mean fungal biomass (mg C g^{-1} litter AFDM) on day 70. Error bars represent ± 1 SE. * denotes significant differences ($P < 0.05$) between bars.

Fig. 2.1.

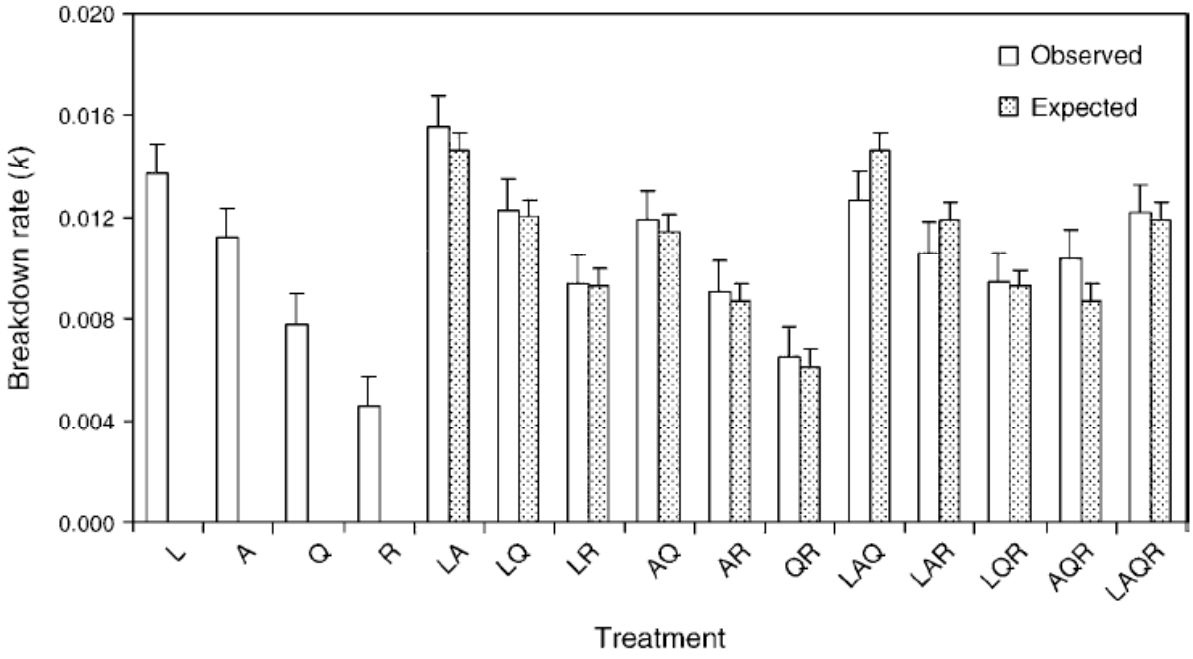

0.020
0.016
0.012
0.008
0.004
0.000
Breakdown rate (k)
Observed
Expected
L
A
Q
R
LA
LQ
LR
AQ
AR
QR
LAQ
LAR
LQR
AQR
LAQR
Treatment

Fig. 2.2.

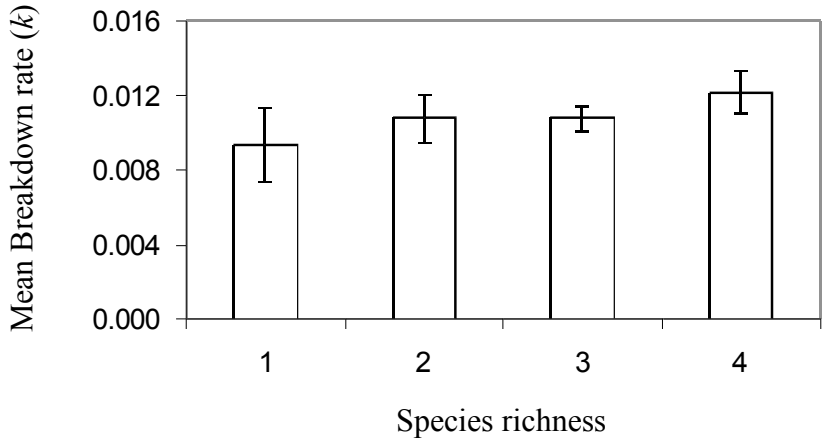

Mean Breakdown rate (k)
0.016
0.012
0.008
0.004
0.000
1
2
3
4
Species richness

Fig. 2.3

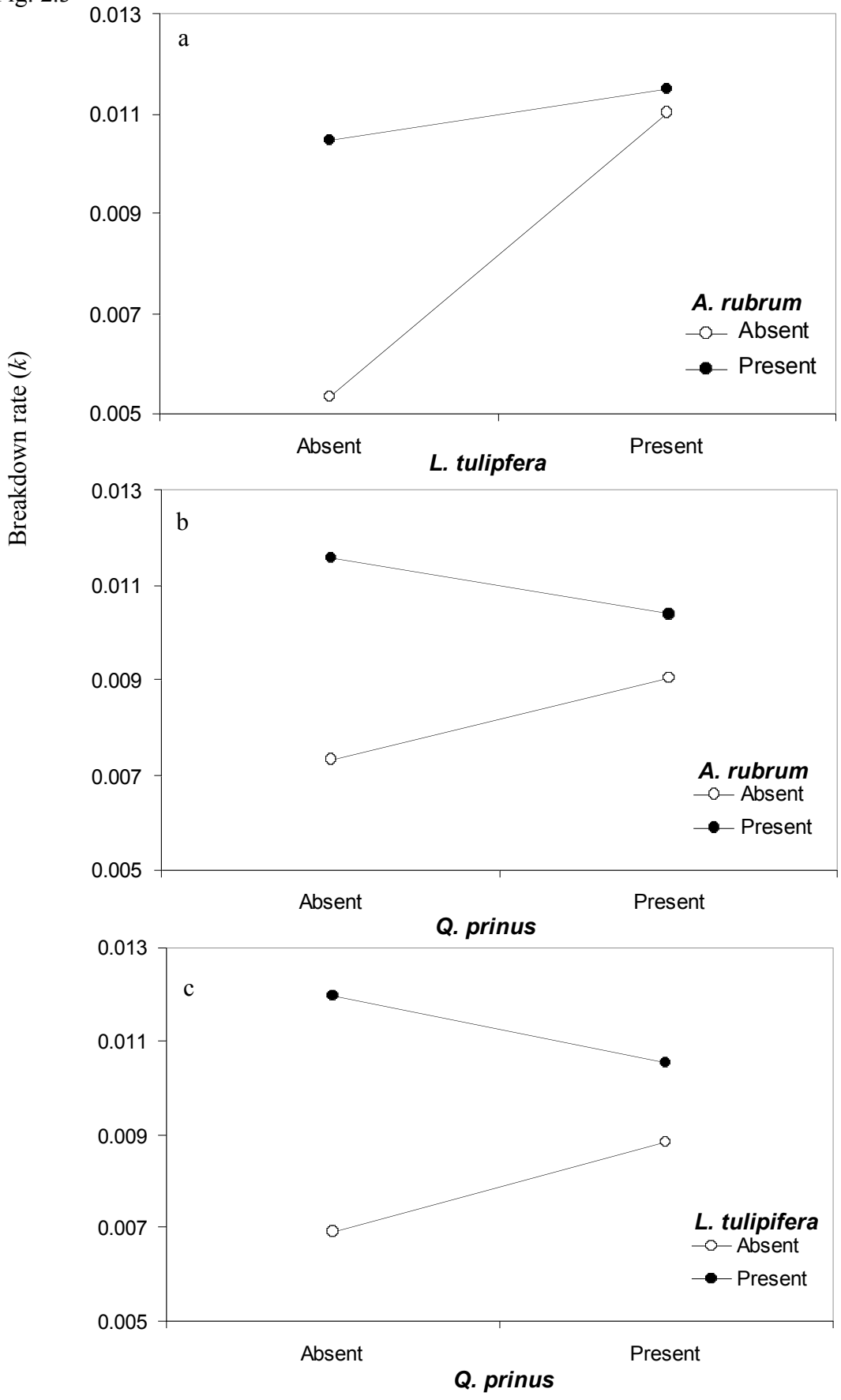
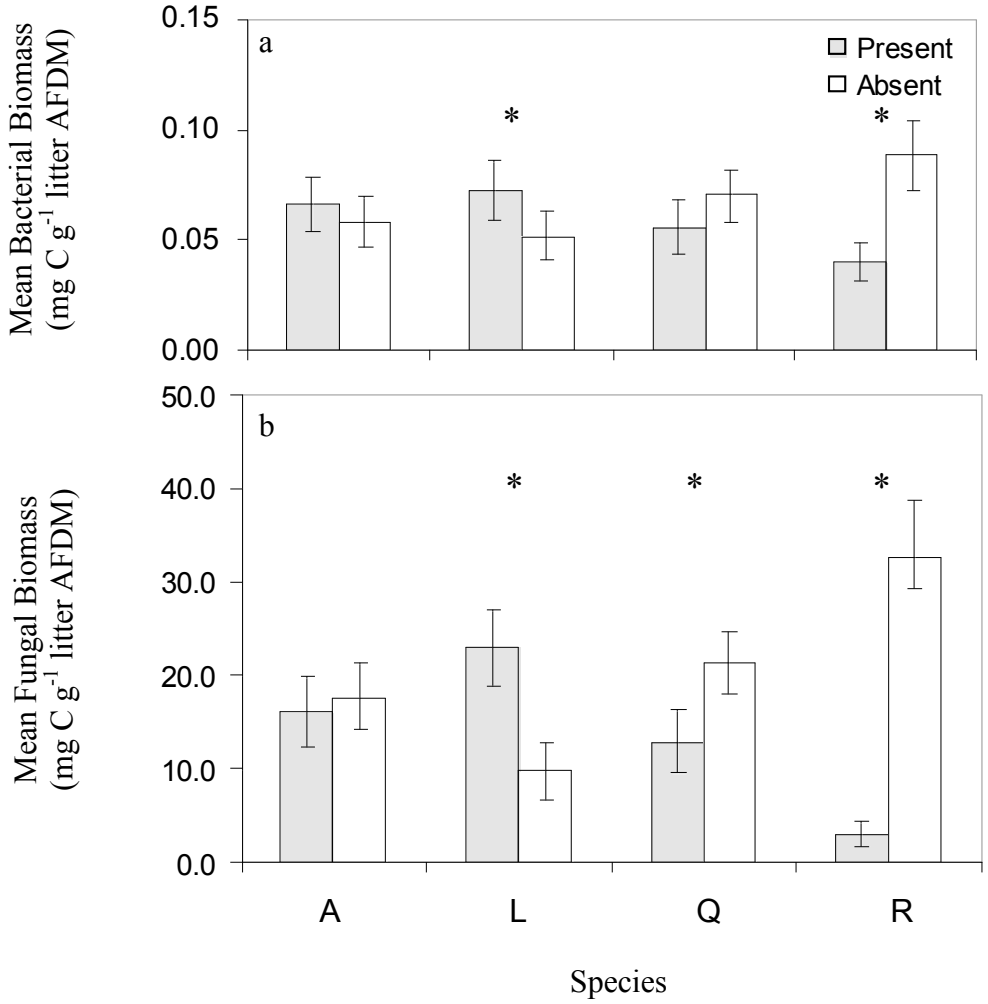

Breakdown rate (k)
a
0.013
0.011
0.009
0.007
0.005
Absent
Present
A. rubrum
Absent
Present
L. tulipfera
b
0.013
0.011
0.009
0.007
0.005
Absent
Present
A. rubrum
Absent
Present
Q. prinus
c
0.013
0.011
0.009
0.007
0.005
Absent
Present
L. tulipifera
Absent
Present
Q. prinus

Fig. 2.4.


Mean Bacterial Biomass
(mg C g-1 litter AFDM)
0.15
0.10
0.05
0.00
a
Present
Absent
*
*
Mean Fungal Biomass
(mg C g-1 litter AFDM)
50.0
40.0
30.0
20.0
10.0
0.0
b
*
*
*
A
L
Q
R
Species

CHAPTER 3

LITTER SPECIES IDENTITY AND DIVERSITY AFFECT MACROINVERTEBRATE COMMUNITIES DURING BREAKDOWN IN A DETRITUS-BASED STREAM[2]

[2]Kominoski, J.S. and C.M Pringle. To be submitted to *Oecologia*

Abstract Understanding relationships between resource and consumer diversity is essential to predicting how changes in resource heterogeneity might affect multiple trophic levels. Using full-factorial analyses of single- and mixed-species litter from dominant riparian tree species with distinct litter chemistries (red maple [*Acer rubrum*], tulip poplar [*Liriodendron tulipifera*], chestnut oak [*Quercus prinus*], and rhododendron [*Rhododendron maximum*]), we tested for effects of single-species presence/absence (additive) and species interactions (nonadditive) on macroinvertebrate community dynamics (assemblage structure, diversity, abundance, and biomass) during breakdown in a detritus-based, headwater stream (North Carolina, USA). We found significant nonadditive effects of litter species diversity and additive effects of species identity on macroinvertebrates that varied with time and litter chemistry. For example, differences in litter species richness resulted in different macroinvertebrate assemblages during early and later stages of breakdown, and macroinvertebrate taxa colonizing litter were predictable for mixed- but not single-species litter, regardless of litter species composition. Presence/absence of high- (e.g., *L. tulipifera*) and low-quality (e.g., *R. maximum*) litter species altered macroinvertebrate diversity, abundance, and biomass. Specifically, both *L. tulipifera* and *R. maximum* had stimulatory and inhibitory effects on taxa richness and evenness that varied during breakdown but were not related to litter chemistry. In addition, presence/absence of *R. maximum* reduced total macroinvertebrate abundance, which was positively related to litter lignin and negatively related to litter nutrients, condensed tannins, hydrolysable tannins, and total phenolics. Presence/absence of *L. tulipifera* reduced total macroinvertebrate biomass, which was negatively related to condensed and hydrolysable tannins as well as remaining litter mass. Our results suggest that complex relationships between macroinvertebrates and litter species diversity and identity are time-dependent and partially explained by litter quality. Broad-scale shifts in riparian

tree species composition and subsequent effects on litter inputs to streams could alter the dynamics of stream macroinvertebrate communities, potentially affecting higher trophic levels.

Keywords*:* Nonrandom species loss; Additive and nonadditive effects; Leaf litter chemistry; southern Appalachians; Riparian tree species composition

Introduction

Global species declines have prompted research exploring the relationship between biodiversity and ecosystem functioning (Schulze and Mooney 1993; Kinzig et al. 2002; Loreau et al. 2002; Hooper et al. 2005). Earlier studies focused on effects of terrestrial plant species richness on primary productivity (Naeem et al. 1996; Tilman et al. 1996; Hector et al. 1999). More recently, attention has focused on effects of terrestrial plant species diversity on leaf litter decomposition (e.g., detrital breakdown) in both terrestrial (Gartner and Cardon 2004; Hättenschwiler et al. 2005; Ball et al. 2008) and aquatic ecosystems (Swan and Palmer 2004; LeRoy and Marks 2006; Kominoski et al. 2007; Lecerf et al. 2007). Since the majority of primary production in temperate ecosystems enters food webs as detritus (McNaughton et al. 1989; Cebrian 1999), and the slow processing of detritus inherently stabilizes ecosystem energetics (Wetzel 1995; Moore et al. 2004), detrital resource heterogeneity may play an important role in structuring food webs that utilize detritus as a dominant energy source.

In many aquatic ecosystems, detritus is a dominant basal resource that provides energy essential to maintain diverse food webs (Wetzel 1995; Hall et al. 2000). Allochthonous leaf litter entering forested, headwater streams supports multiple trophic levels and feeding guilds of

macroinvertebrates (Wallace et al. 1997; 1999; Hall et al. 2001), which are dominant biological contributors to litter breakdown (Hieber and Gessner 2002) and themselves support higher trophic levels in aquatic and terrestrial systems. Although nonadditive effects of litter species diversity on in-stream breakdown rates have been consistently observed (Swan and Palmer 2004; LeRoy and Marks 2006; Kominoski et al. 2007; Lecerf et al. 2007), effects of litter species diversity on macroinvertebrate community dynamics are less clear (Swan and Palmer 2006 a,b; LeRoy and Marks 2006; Kominoski et al. 2007). Further investigation into the effects of litter species diversity on macroinvertebrate communities is needed to better predict structural and functional consequences of changes in riparian tree species composition on adjacent stream ecosystems.

Although environmental changes will likely affect biodiversity through nonrandom species losses and compositional shifts (Vitousek et al. 1997; Huston et al. 2000; Loreau et al. 2001; Tilman and Lehman 2001; Ellison et al. 2005), most experiments are designed to test for effects of random species loss. Such designs do not conclusively test effects of the loss of a particular species and cannot separate the effects of species richness and composition (Huston 1997; Drake 2003). Therefore, the need to understand the effects of nonrandom plant species losses (e.g., Ellison et al. 2005) on litter breakdown dynamics requires experimental designs and statistical analyses that can identify additive (species identity) and nonadditive effects (species interactions) of litter species diversity (e.g., Kominoski et al. 2007; Ball et al. 2008). Understanding how nonrandom species loss will affect detritus-based, stream ecosystems is vital as we continue to lose foundation species and shift riparian forest tree composition (Orwig et al. 2002; Ellison et al. 2005).

In our previous study (Kominoski et al. 2007), we used a full-factorial experimental design to test for effects of litter species diversity on breakdown dynamics in a headwater stream. Overall, we found significant nonadditive effects of litter species diversity on breakdown rates that were explained by both species richness and composition. However, effects of litter species diversity on changes in litter chemistry and microbial and shredder biomass were less consistent. We observed nonadditive effects of litter species diversity on litter nutrients and secondary compounds and additive effects on structural compounds. Nonadditive effects of litter species diversity on bacterial and fungal biomass were seen during early stages of breakdown, and additive effects on microbes during intermediate and later stages of breakdown were explained by the presence/absence of high- and low-quality litter species. There were no clear effects of litter species diversity on shredder biomass. Building on our previous study (Kominoski et al. 2007), here we conduct a comprehensive analysis of total macroinvertebrate community dynamics (diversity, abundance, biomass) in response to litter species diversity during breakdown to test effects of nonrandom species loss. We predicted that (1) litter species diversity would have both additive and nonadditive effects on macroinvertebrate community dynamics and that effects would vary with time; (2) litter quality (i.e. chemistry) and mass remaining would explain variation in macroinvertebrate response to litter species diversity. Our study allows us to test if resource heterogeneity, achieved by mixing litter species of different physical, chemical, and biological properties, affects consumer communities and whether that effect is explained by litter species identity (additive effects) or species interactions (nonadditive effects).

Materials and methods

Study site

Research was conducted in a second-order reach of Ball Creek, a headwater stream at Coweeta Hydrologic Laboratory, Macon County, NC, USA (35º00'N, 83º30'W). Coweeta is a 2,185 ha forested basin in the Blue Ridge physiographic province of the southern Appalachian Mountains (Swank and Crossley 1988). Vegetation is mixed hardwood (dominated by *Quercus* spp., *Acer* spp., and *Liriodendron* spp.), with a dense understory of *Rhododendron maximum* that contributes to year-round shading of streams, causing low in-stream autotrophic production (Webster et al. 1997). Mean monthly air temperature ranges from 3 to 22°C, and mean annual precipitation ranges from 180 cm at low elevations to 250 cm at high elevations (Swift et al. 1988). Mean daily stream temperature along the study reach of Ball Creek during this experiment ranged from 1.3 to 16.6°C.

Litterbags and experimental design

We selected four riparian tree species that are dominant and abundant at Coweeta [red maple, *Acer rubrum* (A); tulip poplar, *Liriodendron tulipifera* (L); chestnut oak, *Quercus prinus* (Q); and rhododendron, *Rhododendron maximum* (R)]. These species represent a range in initial litter chemistries and breakdown rates (Webster and Benfield 1986; Kominoski et al. 2007). All 15 possible single- (richness level = 1) and mixed-species (richness level = 2 - 4) combinations were crossed with three harvest dates and replicated at four locations (blocks) within a 75 m reach of Ball Creek, for a total of 180 experimental units in a randomized complete block design.

Freshly abscised leaves were collected and air-dried in the laboratory for two months during autumn 2003. Approximately 15 g of single- and mixed-species litter in equal mass proportions were placed in plastic mesh bags (19.1 × 38.1 cm, 5 × 5 mm mesh) after initial dry mass determinations. On 10 January 2004, 180 litterbags were deployed in Ball Creek; an additional 60 litterbags were transported back to the laboratory the same day and were used to estimate handling loss and initial litter chemistry. Litterbags within each experimental block were grouped in arrays of 15 treatments and secured to the stream bottom by using plastic ties with galvanized gutter nails. Arrays were randomly retrieved from blocks on harvest days 14, 70, and 118. Litterbags were transported to the laboratory on ice and processed within 12 h of retrieval.

Retrieved litter was rinsed over nested sieves (1 mm and 250 μm) to collect macroinvertebrates and remove sediments and debris. Leaf disks were sampled from a representative composite of litter species in each litterbag for both fungal and bacterial analyses. Litter was oven-dried at 60ºC for 24 h, and weighed. Ash-free dry mass (AFDM) was determined as the difference between pre- and post-combustion (at 550°C for 1 h). Remaining litter in each litterbag was milled with a Spex CertiPrep 8000-D Mixer Mill (Spex, Metuchen, NJ, USA) prior to chemical analyses.

Litter chemistry

Litter chemistry for single- and mixed-species litter was analyzed on all harvest dates (Appendix A). Litter nutrient content, carbon (C), nitrogen (N), and phosphorus (P), were measured as a percentage of litter mass (g AFDM). Litter C and N were measured with a Carlo Erba 1500N CHN Analyzer (Carlo Erba, Milan, Italy). Litter for P analysis was weighed into acid-washed,

pre-ashed ceramic crucibles, combusted at 500°C, acid-digested, and analyzed spectrophotometrically (ascorbic acid method; APHA 1998). Cellulose, hemicellulose, and lignin concentrations were analyzed with an Ankom A200 Fiber Analyzer (Ankom, Macedon, NY, USA). Condensed tannins, hydrolysable tannins, and total phenolics were analyzed with techniques described by Rossiter et al. (1988) and Hunter and Schultz (1995).

Aquatic macroinvertebrates

Macroinvertebrates were removed from all litterbags and preserved in 95% ethanol. Individuals were counted and identified to the lowest possible taxonomic level and assigned to a functional feeding group (Merritt and Cummins 1996; Wallace et al. 1999). Chironomidae were identified as Tanypodinae and non-Tanypodinae. A total of 118 genera from 50 families and 13 orders were identified (Appendix B). Length-mass regressions (Benke et al. 1999) were used to estimate total macroinvertebrate biomass per litterbag. Macroinvertebrate diversity was analyzed as taxa richness, taxa evenness, Shannon's diversity index (*H*'), and Simpson's diversity index (*D*') for each litterbag on harvest days 14, 70, and 118.

Statistical analyses

To examine overall macroinvertebrate community responses to single- and mixed-species litter, we used a nonmetric multidimensional scaling (NMDS) ordination method relativized to species maximum with a Bray-Curtis distance measure in PC-ORD (Version 4.10, MjM Software, Gleneden Beach, OR, USA). We used a multi-response permutation procedure (MRPP) to test

community-wide differences in macroinvertebrate assemblages attributed to harvest date and litter species diversity. Indicator taxa analysis (Dufrêne and Legendre 1997) was used to determine specific macroinvertebrate taxa responses to litter species diversity during breakdown. An indicator value (0 – 100) was generated for each taxon based on the product of its relative frequency and relative abundance. Monte Carlo tests (1000 randomizations) determined if indicator values were greater than expected by chance. Indicator taxa have both an indicator value > 20 and a $P \leq 0.05$ (Dufrêne and Legendre 1997).

To test for additive and nonadditive effects of litter species diversity on macroinvertebrate diversity, abundance, and biomass, we used full-factorial analysis of variance (ANOVA) with Type I sums of squares (SS) (Kominoski et al. 2007). Time was treated as a discrete variable (e.g., Ball et al. 2008), and block, time, the presence/absence of the four single-species litter (A, L, Q, R) to test for additive effects, and a diversity term to test for nonadditive effects were added sequentially to the model. Interactions between time and block, time and species presence/absence, and time and diversity were added to the model. Each species presence/absence represented main effects, and the diversity term (i.e. interaction) corresponded to either mixed-species richness (2 – 4) and/or composition effects (A × L, A × Q, A × R, L × Q, L × R, Q × R, A × L × Q, A × L × R, A × Q × R, L × Q × R, A × L × Q × R). A significant additive effect of diversity indicates that species presence/absence was significant. Since Type I SS were used, species terms are sensitive to the order in which they are added to the model. Therefore, the model was re-run with each species presence/absence term added first to test for a significant additive effect of each species. A significant nonadditive effect of diversity means that litter species diversity, not species presence/absence, was significant. In this case, we re-ran the full-factorial analysis replacing diversity with richness. If species richness was significant we

added a composition term to test for effects of richness and composition. If richness was not significant, nonadditive effects were explained by species composition. Macroinvertebrate abundance and biomass were analyzed per litterbag and per gram AFDM litter remaining; however, effects of litter species diversity on macroinvertebrates per litterbag and per gram AFDM litter remaining were similar. Therefore, we chose to report macroinvertebrate abundance and biomass per litterbag, which is a conservative normalization of litter species diversity effects on macroinvertebrates.

Simple linear regressions to compare relatedness of macroinvertebrates to litter chemistry and mass remaining were conducted using PROC REG in SAS version 9.1 (SAS Institute Inc., Cary, NC, USA). Full-factorial ANOVAs were carried out using PROC GLM in SAS with an alpha (type I error rate) of 0.10. Assumptions of normality of residuals were met for all analyses (Shapiro-Wilkes test) through data transformations when necessary.

Results

Macroinvertebrate assemblage structure

Macroinvertebrate assemblage structure varied over time and in response to litter species richness levels, not litter species presence/absence or composition. The MRPP procedure with NMDS visualization indicated that macroinvertebrate assemblages differed by time (MRPP A = 0.04, $P < 0.001$; Fig. 3.1). Macroinvertebrate assemblages on day 14 were influenced by concentrations of total phenolics, hydrolysable tannins, condensed tannins, and percent litter AFDM remaining (Fig. 3.1). The A statistic estimates the effect size of a parameter on

assemblage structure. Therefore, an A of 0.04 shows a relatively strong effect of time on macroinvertebrate assemblages (McCune and Grace 2002). Subsequent MRPP analyses on each harvest day showed significant effects of litter species richness levels on macroinvertebrate assemblages on days 14 (MRPP A = 0.01, $P = 0.02$), and 118 (MRPP A = 0.01, $P = 0.04$). On day 14, two-species litter had significantly different macroinvertebrate assemblages than single- (A = 0.01, $P = 0.01$) or three-species litter (A = 0.02, $P = 0.001$). Similarly, on day 118, single- and two-species litter had significantly different macroinvertebrate assemblages than three-species litter (A = 0.01, $P = 0.02$ and A = 0.01, $P = 0.02$, respectively).

Indicator taxa analyses showed an effect of litter species richness on macroinvertebrate taxa presence within litterbags. Several taxa of shredders, including the dominant *Tallaperla* sp., were associated with two- and three- species litter on days 14 and 70; whereas several predator taxa were associated with three- and four-species litter on day 118 (with the exception of the predator *Suwallia* sp., which was associated with two-species litter on day 14; Table 3.1).

Macroinvertebrate community diversity

Litter mixing had additive effects on macroinvertebrate community diversity that varied with time. Presence/absence of *L. tulipifera* in litter mixtures had significant effects on taxa richness (Table 3.2), and presence/absence of *R. maximum* significantly affected taxa evenness (Table 3.2). Richness generally increased during breakdown and was greater in the presence of *L. tulipifera* during early stages of breakdown. By intermediate stages of breakdown, richness was greater in litterbags that lacked *L. tulipifera* (Fig. 3.2a). Evenness generally declined during breakdown. Litterbags containing *R. maximum* had higher taxa evenness during early and intermediate stages of breakdown, and evenness was greater in the absence of *R. maximum*

during the later stages of breakdown (Fig. 3.2b). Presence/absence effects of *L. tulipifera* and *R. maximum* on taxa richness and taxa evenness, respectively, were not related ($r^2 < 0.20$, $P > 0.05$) to litter chemistry or mass remaining of single- and mixed-species litter where *L. tulipifera* and *R. maximum* were present or absent. Litter diversity had no effect on Shannon's and Simpson's diversity during breakdown.

Macroinvertebrate abundance and biomass

We detected additive effects of litter species identity on total macroinvertebrate abundance and biomass. *Rhododendron maximum* had significant additive effects on macroinvertebrate abundance throughout breakdown (Table 3.3), resulting in consistently lower macroinvertebrate abundance in single- and mixed-species litterbags when it was present (Fig. 3.3a). Presence/absence of *L. tulipifera* had significant time-dependent effects on total macroinvertebrate biomass (Table 3.3). Specifically, total macroinvertebrate biomass was significantly lower in *L. tulipifera* litter during intermediate and later stages of breakdown (Fig. 3.3b). Presence/absence effects of *R. maximum* on macroinvertebrate abundance were partially explained litter nutrient content (C:N, C:P), structural compounds (lignin), and secondary compounds (condensed tannins, hydrolysable tannins, total phenolics; Table 3.4a). Presence/absence effects of *L. tulipifera* on macroinvertebrate biomass were partially explained by litter secondary compounds (condensed tannins, hydrolysable tannins) and mass remainig (Table 3.4b).

Discussion

Macroinvertebrate communities responded to litter species presence/absence and richness during breakdown. Additive effects of litter species presence/absence on total macroinvertebrate diversity, abundance, and biomass were explained by litter quality; presence of high- (e.g., *L. tulipifera*) and low-quality (e.g., *R. maximum*) litter species both inhibited and stimulated community dynamics during breakdown. In addition, macroinvertebrate taxa colonizing litter were predictable for mixed- but not single-species litter, regardless of litter species composition (Table 3.1). As most naturally forming leaf packs in streams are comprised of multiple litter species, our results suggest that certain macroinvertebrate taxa are responding to litter resource heterogeneity (i.e., species richness) rather than litter chemistry of individual litter species.

Although litter quality and mass remaining partially explained additive effects on macroinvertebrate communities, this appeared to be driven by *changes in* rather than *persistence of* litter chemistry. Variation in initial litter chemistry among species has often been suggested to be a good predictor of litter breakdown dynamics (Webster and Benfield 1986; LeRoy and Marks 2006; LeRoy et al. 2007). However, secondary compounds rapidly leach from litter during in-stream breakdown (Ostrofsky 1997; Rier et al. 2005; Ardón and Pringle 2008). In this study, declines in secondary compounds occurred in all litter regardless of species identity and were associated with a subsequent increase in macroinvertebrate abundance and biomass during breakdown (Table 3.4a, b). Given that detritus generally becomes more homogeneous during breakdown (sensu Moore et al. 2004), due to physical, chemical, and biological processing, initial chemistry of single- and mixed-species litter is likely inadequate to explain litter species diversity effects on macroinvertebrates throughout breakdown. Indeed, presence of *R. maximum* and absence of *L. tulipifera* in our litter treatments resulted in both higher and lower

macroinvertebrate diversity (Figs. 3.2a, b) and biomass (Fig. 3.3b) during certain stages of breakdown, despite the long-held belief that fast-decomposing species are a higher quality resource than slow-decomposing species (Webster and Benfield 1986). Since initial concentrations of secondary defense compounds were similar among species and followed similar trends during breakdown, it is likely that time-dependent, additive responses of macroinvertebrates to litter species diversity are explained by dynamic physical and chemical properties of litter, and resource competition among detritivores.

Detritus containing multiple litter species can provide heterogeneous microhabitats structured by a mixture of labile and recalcitrant materials that support different communities of consumers (Hansen and Coleman 1998; Kaneko and Salamanca 1999). Although most studies have found that nonadditive effects of litter diversity on breakdown rates are due to species composition and not richness (Swan and Palmer 2004; LeRoy and Marks 2006; Kominoski et al. 2007; Lecerf et al. 2007), explanations in support of litter species richness effects have also been suggested (Hector et al. 2000; Kominoski et al. 2007). Although there does not appear to be a monotonic relationship between litter species richness and macroinvertebrate communities (LeRoy and Marks 2006; this study), results from this study indicate that litter species richness partially explains differences in assemblage (Fig. 3.1) and indicator taxa (Table 3.1). The lack of a clear litter diversity effect on macroinvertebrates is likely explained by differential resource utilization of litter among stream invertebrate functional feeding groups. For example, dominant functional feeding group taxa responded to litter species richness differently during breakdown (Table 3.1). Increased dominance of the shredder, *Tallaperla* sp., in two-species litter during early and intermediate stages of breakdown and predator taxa in three- and four-species litter during later stages of breakdown (Fig. 3.1) likely explain differences in macroinvertebrate

assemblages attributed to litter species richness. Preferential feeding by dominant shredders is one mechanism suggested to explain nonadditive effects of litter species diversity on breakdown rates in experimental chambers (Swan and Palmer 2006b). However, results from our *in situ* study suggest that additional mechanisms may be operating.

We observed nonadditive effects of litter species diversity on breakdown rates (Kominoski et al. 2007), additive and nonadditive effects on changes in litter chemistry, additive and nonadditive effects on microbial biomass (Kominoski et al. 2007), and additive and nonadditive effects on macroinvertebrates (this study). There are several plausible explanations for these apparently inconsistent patterns: (1) litter breakdown rates are driven more by physical processes of flow and structural integrity of litter than chemical or biological processes; (2) resource requirements (food, habitat, and refuge) of macroinvertebrates change throughout breakdown depending on their life histories, resource supply, and competition; and (3) functional identity of litter (e.g., labile versus recalcitrant) fulfill different resource roles throughout breakdown.

If macroinvertebrates preferentially feed on high-quality litter, what mechanism explains inhibitory effects of *L. tulipifera* on macroinvertebrate biomass? It is possible that highly labile litter with low structural content, such as *L. tulipifera*, supports less macroinvertebrate abundance and biomass during intermediate and later stages of breakdown due to insufficient substrate to maintain stable habitat and refuge. In contrast, highly-recalcitrant litter, which provides stable substrate for colonizing macroinvertebrates, offer less palatable resources and likely increases competition among consumers that require food and refuge. This could explain why total macroinvertebrate abundance and biomass were lower in litter containing *L. tulipifera* and *R. maximum* (Figs. 3.3a, b) as compared to litter where either species was absent. Both

species of litter are at opposite ends of the quality spectrum and have different resource capacities. For example, our previous study found that the presence of *R. maximum* in single- and mixed-species litter appeared to inhibit bacterial and fungal biomass (Kominoski et al. 2007). However, we also observed consistently higher bacterial and fungal biomass in single- and mixed-species litter containing *L. tulipifera*. Perhaps lower macroinvertebrate biomass associated with *L. tulipifera* litter during intermediate and later stages of breakdown (Fig. 3.3b) facilitated higher microbial biomass. During advanced stages of decomposition, labile species, such as *L. tulipifera*, are likely not structurally supportive of macroinvertebrates, which may explain its apparent inhibitory effects. Our results suggest that dynamic chemical and physical properties of mixed-species litter support stream macroinvertebrate communities in a complex manner and that litter species identity and quality partially explain these dynamic patterns.

Riparian ecosystems help maintain regional biodiversity (Naiman et al. 1993) and support ecosystem function and stability in adjacent streams through litter inputs (Wallace et al. 1997; 1999). Whiles and Wallace (1997) suggested that riparian tree species composition could influence taxonomic composition of stream macroinvertebrates. We have shown here that the richness and identity of riparian tree species may have bottom-up effects on adjacent stream macroinvertebrate communities during breakdown. Changes in riparian tree species composition could potentially alter stream food web dynamics and ecosystem functioning. For example, in eastern U.S. forests, current declines in eastern hemlock (*Tsuga canadensis*) resulting from infestation of the woolly adelgid (*Adelges tsugae*) are altering riparian tree species composition (Orwig et al. 2002). Loss of eastern hemlock is also predicted to result in an overall decrease in riparian tree species diversity (Ellison et al. 2005). Ecological implications of shifts in riparian tree species composition on stream ecosystems are largely unknown and illustrate the need to

further understand relationships between resource and consumer diversity, as well as how both affect ecosystem functioning. Stream macroinvertebrates appear to be linked to both litter species identity and richness during breakdown.

Conclusions

We found significant nonadditive effects of litter species diversity and additive effects of species identity on macroinvertebrates that varied with time and litter chemistry. Differences in litter species richness resulted in different macroinvertebrate assemblages during early and later stages of breakdown, and macroinvertebrate taxa colonizing litter were predictable for mixed- but not single-species litter, regardless of litter species composition. These results indicate that shifts in riparian tree species composition may have bottom-up effects on stream macroinvertebrate communities through alterations in the heterogeneity of litter inputs. As species declines and composition shifts are predicted to be nonrandom (Huston et al. 2000; Tilman and Lehman 2001), full-factorial experimental designs that test for species identity and interaction effects are needed to understand the functional implications of nonrandom species compositional changes. Detrital resource heterogeneity in streams reflects the species composition of riparian plant communities, and our results suggest that stream macroinvertebrate dynamics are partially explained litter species identity and diversity. Given that global environmental change is affecting tree species composition in riparian ecosystems, further investigation into the functional consequences of these nonrandom species shifts on adjacent stream ecosystems is needed.

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Table 3.1 Indicator taxa analysis results for macroinvertebrates unique to different litter species richness levels and harvest days during breakdown in Ball Creek, Coweeta Hydrologic Laboratory, NC, USA. Values represent indicator values (I-value), Monte Carlo *P*-values, litter species richness, and harvest day (Day). Functional feeding groups (FFG) were identified for each indicator taxon (C-G = collector-gatherer, P = predator, SC = scraper, SH = shredder).

Indicator taxon	FFG	I-value	*P*-value	Litter species richness	Day
Baetis sp.	SC	35.3	0.02	4	14
Ephemerella sp.	C-G	23.1	0.03	4	14
Suwallia sp.	P	33.5	0.04	2	14
Tallaperla sp.	SH	43.4	0.02	2	14
Pycnopsyche sp.	SH	21.4	0.05	3	70
Tallaperla sp.	SH	45.0	0.05	2	70
Araneae	P	44.8	0.01	4	118
Dicranota sp.	P	37.4	0.03	4	118
Hexatoma sp.	P	41.5	0.01	4	118
Isopoda sp.	SH	25.0	0.03	3	118
Stenus sp.	P	18.7	0.05	3	118

Table 3.2 ANOVA results of tests for additive (i.e. main effects; species presence/absence terms) and nonadditive (i.e. Diversity term; species interactions) effects of litter species diversity on macroinvertebrate taxa richness (litterbag^{-1}) and evenness (litterbag^{-1}) using Type I SS. *Acer rubrum* (A), *Liriodendron tulipifera* (L), *Quercus prinus* (Q), *Rhododendron maximum* (R). Species terms were affected by the order in which they were added to the model. Therefore, when results were additive, we re-ran analyses placing each species first in the order. Significant *P*-values are bolded.

Taxa richness	df	SS	MS	F	*P*
Block	3	18.9	6.3	0.31	0.82
Time	2	311.3	155.7	7.66	<0.01
A	1	9.6	9.6	0.47	0.49
L	1	0.3	0.3	0.01	0.91
Q	1	9.5	9.5	0.47	0.50
R	1	0.1	0.1	0.01	0.94
Diversity	10	134.0	13.4	0.66	0.76
Time*Block	6	266.3	44.4	2.18	0.05
Time*A	2	12.8	6.4	0.32	0.73
Time*L	2	130.2	65.1	3.20	**0.04**
Time*Q	2	0.7	0.4	0.02	0.98
Time*R	2	51.4	25.7	1.26	0.29
Time*Diversity	20	494.1	24.7	1.22	0.25
Error	120	2438.4	20.3		
Total	173	3877.6	381.9		
Taxa evenness					
Block	3	0.03	0.01	0.32	0.81
Time	2	0.24	0.12	4.55	0.01
A	1	<0.01	<0.01	0.11	0.74
L	1	<0.01	<0.01	0.10	0.76
Q	1	0.01	0.01	0.34	0.56
R	1	<0.01	<0.01	0.06	0.81
Diversity	10	0.24	0.02	0.90	0.53
Time*Block	6	0.22	0.04	1.34	0.25
Time*A	2	0.01	0.01	0.23	0.80
Time*L	2	0.04	0.02	0.66	0.52
Time*Q	2	0.01	0.01	0.27	0.77
Time*R	2	0.15	0.08	2.80	**0.07**
Time*Diversity	20	0.60	0.03	1.12	0.34
Error	120	3.21	0.03		
Total	173	4.76	0.37		

Table 3.3 ANOVA results of tests of additive (i.e. main effects; species presence/absence) and nonadditive (i.e. Diversity term; species interactions) effects of litter species diversity on total macroinvertebrate abundance (individuals litterbag^{-1}) and biomass (mg litterbag^{-1}) using Type I SS. *Acer rubrum* (A), *Liriodendron tulipifera* (L), *Quercus prinus* (Q), *Rhododendron maximum* (R). Species terms were affected by the order in which they were added to the model. Therefore, when results were additive, we re-ran analyses placing each species first in the order. Significant values ($P \leq 0.10$) are bolded.

Abundance	df	SS	MS	F	*P*
Block	3	25282	8427	0.73	0.53
Time	2	803918	401959	35.00	<0.01
A	1	1855	1855	0.16	0.69
L	1	1038	1038	0.09	0.76
Q	1	11921	11921	1.04	0.31
R	1	48549	48549	4.23	**0.04**
Diversity	10	124201	12420	1.08	0.38
Time*Block	6	44189	7364	0.64	0.70
Time*A	2	3967	1983	0.17	0.84
Time*L	2	5706	2853	0.25	0.78
Time * Q	2	22909	11454	1.00	0.37
Time * R	2	26880	13440	1.17	0.31
Time*Diversity	20	289092	14454	1.26	0.22
Error	120	1378202	11485		
Total	173	2787715	549208		
Biomass					
Block	3	3.94	1.31	3.41	0.02
Time	2	8.27	4.14	10.75	<0.01
A	1	0.05	0.05	0.12	0.73
L	1	0.09	0.09	0.25	0.62
Q	1	0.27	0.27	0.69	0.41
R	1	0.13	0.13	0.35	0.56
Diversity	10	6.07	0.61	1.58	0.12
Time*Block	6	17.79	2.97	7.71	<0.01
Time*A	2	0.41	0.20	0.53	0.59
Time*L	2	2.98	1.49	3.87	**0.02**
Time * Q	2	0.46	0.23	0.59	0.55
Time * R	2	0.36	0.18	0.46	0.63
Time*Diversity	20	9.58	0.48	1.25	0.23
Error	120	46.17	0.38		
Total	173	96.56	12.52		

Table 3.4 Simple linear regressions relating effects of litter chemistry and ash-free dry mass (AFDM) remaining to species identity effects of (**a**) rhododendron, *Rhododendron maximum* (R) on total macroinvertebrate abundance (individuals litterbag^{-1}) and (**b**) tulip poplar, *Liriodendron tulipifera* (L) on total macroinvertebrate biomass (mg litterbag^{-1}) during breakdown. Comparisons were made for all single- and mixed-species litter where R and L were present. Relationships explaining at least 20% ($r^2 \geq 0.20$) of the variation in macroinvertebrate abundance and biomass are bolded and followed by a + or – to indicate the direction of the relationship. Carbon to nitrogen mass ratio (C:N), carbon to phosphorus (C:P) were calculated as mass ratios, and all litter chemistry values were calculated per g AFDM. "NS" = not significant ($P > 0.05$).

A	R present		R absent	
Abundance	r^2	*P*	r^2	*P*
C:N	0.12	<0.01	**0.27 -**	<0.01
C:P	0.04	0.04	**0.28 -**	<0.01
% Cellulose	NS	NS	0.05	0.04
% Hemicellulose	0.07	0.01	NS	NS
% Lignin	**0.27 +**	<0.01	NS	NS
% Condensed tannins	**0.42 -**	<0.01	**0.25 -**	<0.01
% Hydrolysable tannins	**0.35 -**	<0.01	**0.27 -**	<0.01
% Total phenolics	**0.35 -**	<0.01	**0.27 -**	<0.01
AFDM (g)	0.15	<0.01	0.17	<0.01

B	L present		L absent	
Biomass	r^2	*P*	r^2	*P*
C:N	0.09	<0.01	0.09	<0.01
C:P	0.05	0.03	0.07	0.02
% Cellulose	0.10	<0.01	NS	NS
% Hemicellulose	NS	NS	NS	NS
% Lignin	NS	NS	0.09	<0.01
% Condensed tannins	0.12	<0.01	**0.20 -**	<0.01
% Hydrolysable tannins	0.06	0.01	**0.21 -**	<0.01
% Total phenolics	0.13	<0.01	0.19	<0.01
AFDM (g)	**0.25 -**	<0.01	**0.21 -**	<0.01

Figure legends

Fig. 3.1 Nonmetric multidimensional scaling (NMDS) ordination of stream macroinvertebrate community assemblages in n-dimensional space using whole-model multiple response permutation procedure (MRPP). Different symbols represent macroinvertebrate assemblages on different harvest days. Contrasts indicate that macroinvertebrate assemblages were significantly different on harvest days during breakdown (A = 0.07, $P < 0.001$). Bi-plot vectors show correlations of the matrix with concentrations of total phenolics (r = 0.39), hydrolysable tannins (r = 0.36), condensed tannins (r = 0.39), and proportion of litter ash-free dry mass remaining (AFDM; r = 0.38).

Fig. 3.2 Main effects of litter species presence/absence on macroinvertebrate (**a**) taxa richness, and (**b**) taxa evenness (means ± 1 SE; $n = 8$ for "present" and $n = 7$ for "absent"). Species abbreviations are: L, tulip poplar, *Liriodendron tulipifera*; R, rhododendron, *Rhododendon maximum*. An asterisk denotes significant differences between open and closed symbols on the same day.

Fig. 3.3 Main effects of litter species presence/absence on macroinvertebrate (**a**) macroinvertebrate total biomass, and (**b**) total abundance (means ± 1 SE; $n = 8$ for "present" and $n = 7$ for "absent"). Species abbreviations are: A, red maple, *Acer rubrum*; L, tulip poplar, *Liriodendron tulipifera*; Q, chestnut oak, *Quercus prinus*; R, rhododendron, *Rhododendon maximum*. An asterisk denotes significant differences between open and closed symbols or open and shaded bars on the same day.

Fig. 3.1

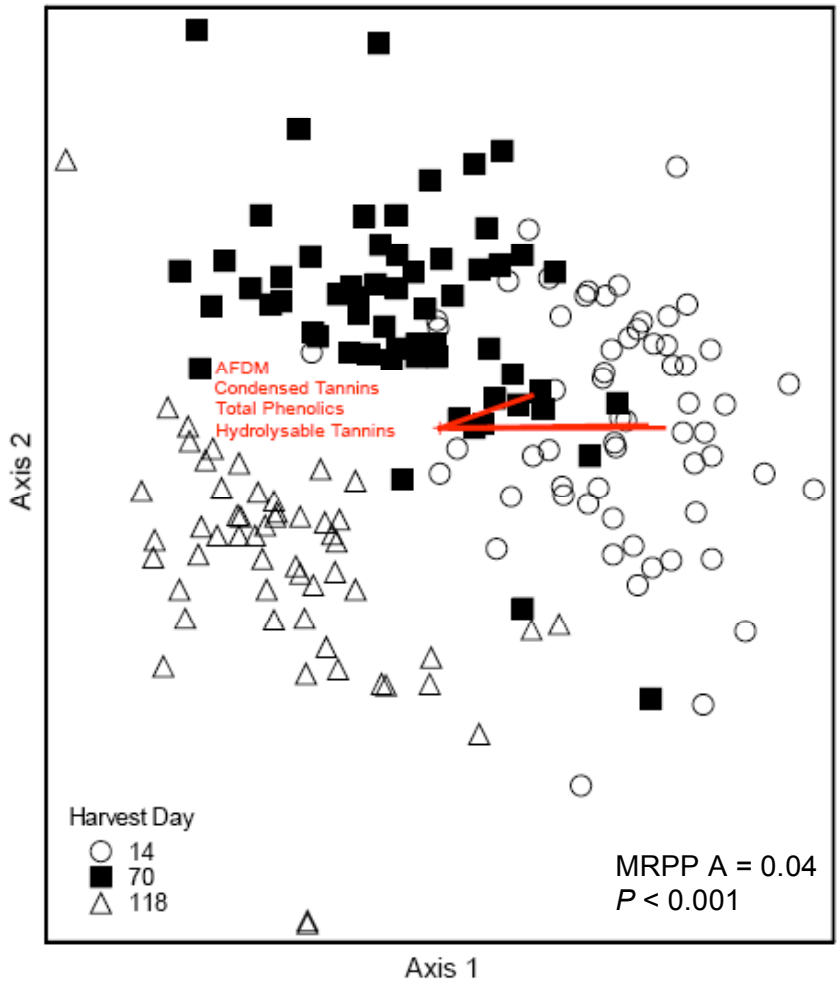

AFDM
Condensed Tannins
Total Phenolics
Hydrolysable Tannins
Axis 2
Axis 1
Harvest Day
14
70
118
MRPP A = 0.04
P < 0.001

Fig. 3.2

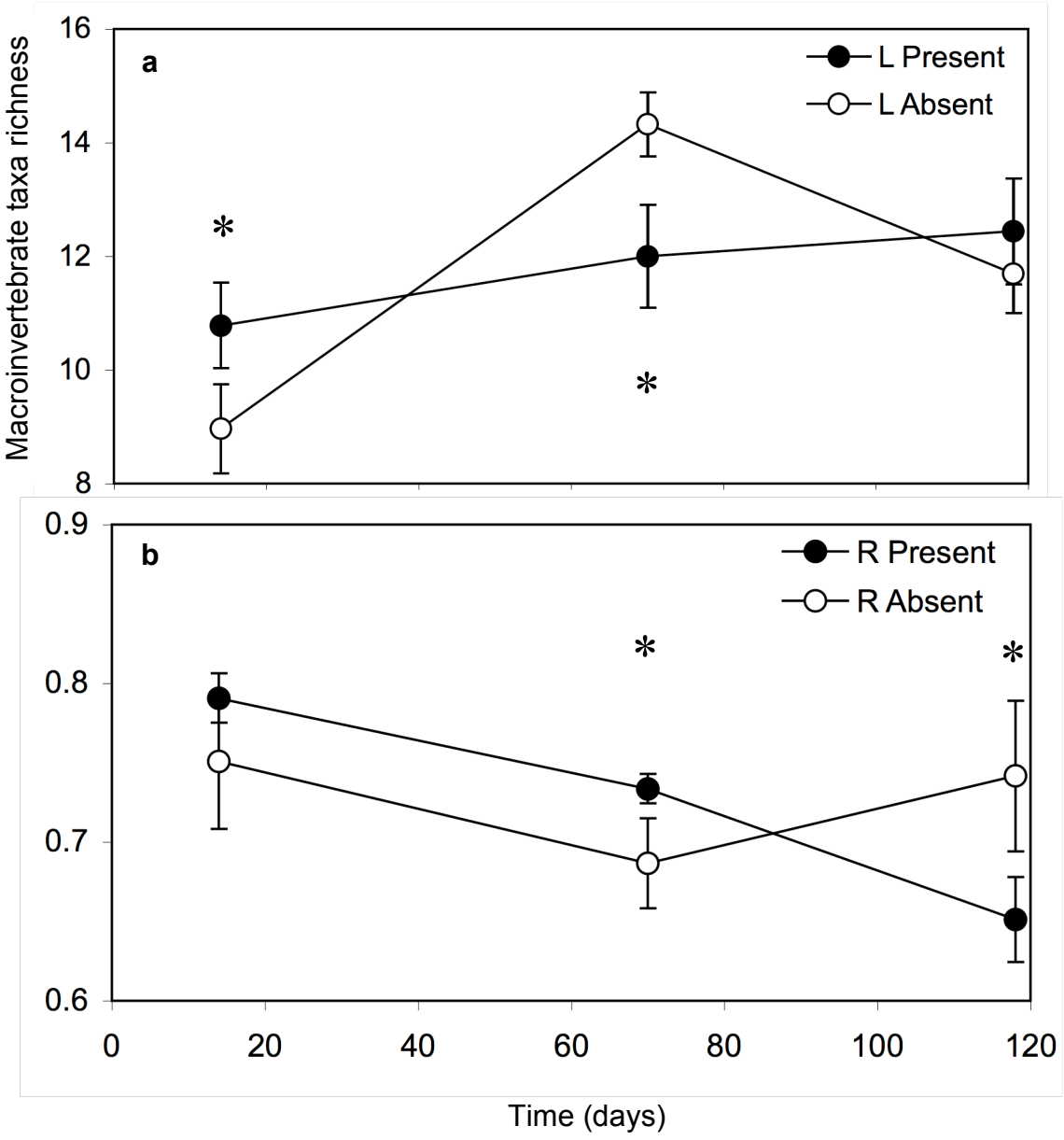
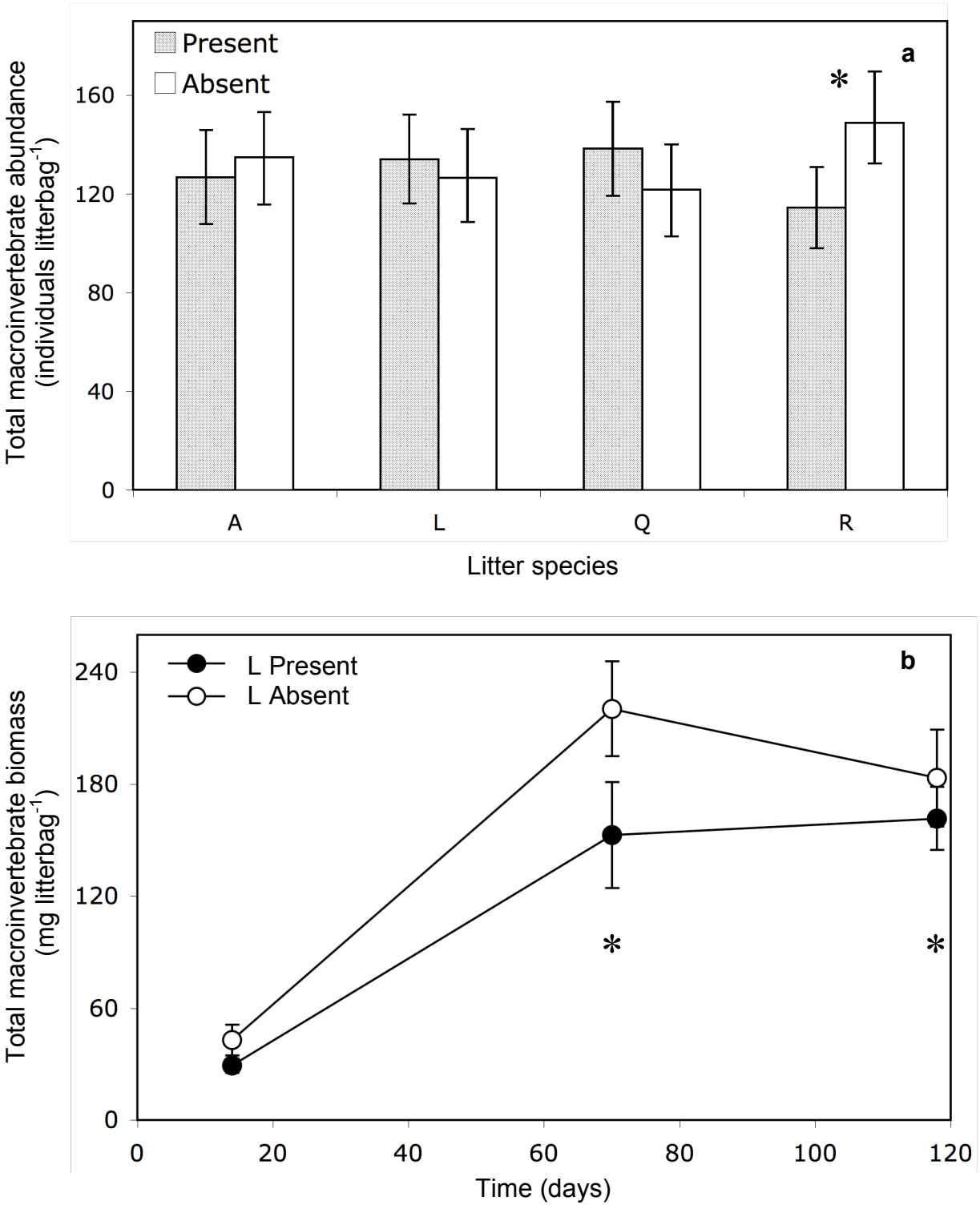

a
L Present
L Absent
Macroinvertebrate taxa richness
16
14
12
10
8
*
*
b
R Present
R Absent
0.9
0.8
0.7
0.6
*
*
0
20
40
60
80
100
120
Time (days)

Fig. 3.3


Present
Absent
a
*
160
120
80
40
0
Total macroinvertebrate abundance
(individuals litterbag-1)
A
L
Q
R
Litter species
L Present
L Absent
b
240
180
120
60
0
*
*
0
20
40
60
80
100
120
Time (days)
Total macroinvertebrate biomass
(mg litterbag-1)

CHAPTER 4

LITTER RESOURCE HETEROGENEITY ALTERS STREAM MICROBIAL DIVERSITY AND FUNCTIONING[3]

[3]Kominoski, J.S., T.J. Hoellein, J.J. Kelly, C.M. Pringle. To be submitted to *Ecology Letters*

Abstract Relationships between resource and consumer diversity and feedbacks with ecosystem function have received little attention in detritus-based ecosystems. Here, we examined effects of litter quality and species heterogeneity on microbial community diversity and litter processing in a forested headwater stream. Major chemical differences among low- and high-quality litter species persisted throughout the 50-day incubation period. The carbon-to-nitrogen ratio of some individual species changed when mixed with other litter species. Although litter mass loss was generally unaffected by mixing, microbial respiration increased on some litter species in response to resource heterogeneity. Enhanced resource heterogeneity, which was experimentally achieved by litter mixing, resulted in shifts in microbial community diversity on individual litter species. Bacterial and fungal community diversity increased and decreased, respectively, with litter mixing but varied among individual litter species. Our results suggest that predicted changes in tree species composition in riparian forests could alter stream microbial communities and detrital processing.

Keywords: bacteria; biodiversity; DGGE; DNA; ecosystem function; fungi; respiration; streams

Rapid losses of species worldwide have elevated concerns about how ecosystems will function as biodiversity declines (Tilman *et al.* 2001, Loreau *et al.* 2002, Hooper *et al.* 2005). Changes in biodiversity can affect fundamental ecosystem processes, such as, primary productivity (Tilman *et al.* 2001, Hooper *et al.* 2005) and organic matter decomposition (Gartner & Cardon 2004, Hättenschwiler *et al.* 2005). Biodiversity effects on decomposition have been shown empirically though resource manipulations of plant leaf litter (Gartner & Cardon 2004, Swan & Palmer 2004, Hättenschwiler *et al.* 2005, Kominoski *et al.* 2007), as well as consumer-level manipulations of invertebrates (Jonsson & Malmqvist 2000, Dangles & Malmqvist 2004, Hättenschwiler & Gasser 2005) and microorganisms (Bärlocher & Corkum 2003, Dang *et al.* 2005, Duarte *et al.* 2005, Lecerf et al. 2005, Tiunov & Scheu 2005).

Forested, headwater streams are ideal environments to test effects of litter resource heterogeneity on invertebrate detritivores and microbial decomposers and subsequent litter decomposition. Terrestrially derived litter is the dominant organic matter resource (Wallace *et al.* 1997, 1999, Webster *et al.* 1997, Hall *et al.* 2001), and consumers in these donor-controlled ecosystems do not directly affect the heterogeneity of allochthonous organic matter resources. In addition, litter species heterogeneity is especially relevant to stream ecosystems because global-scale processes such as climate change, species invasions, and the spread of pathogens are nonrandomly altering plant species composition within riparian communities (Ellison *et al.* 2005). Shifts in riparian tree species composition will alter litter inputs to streams, which may affect the structure of microbial communities and overall organic matter processing in these ecosystems.

Forested watersheds in the eastern United States provide an excellent example of these phenomena. Current declines in eastern hemlock (*Tsuga canadensis* L.) resulting from the

invasive woolly adelgid (*Adelges tsugae* L.) are altering forest communities along the Appalachian Mountains (Orwig *et al.* 2002). In the southern Appalachians, declines in eastern hemlock could increase the dominance of rhododendron (*Rhododendron maximum* L.), which is known to inhibit canopy tree seedling establishment (Nilsen *et al.* 1999, Walker *et al.* 1999). Since *R. maximum* is an abundant, low-quality litter species (Webster & Benfield 1986), potential increases in *R. maximum* litter could have structural and functional implications for forested, headwater streams.

Although composition and diversity of riparian tree species influences species diversity of aquatic hyphomycetes (Bärlocher & Graça 2002, Laitung & Chauvet 2005, Lecerf *et al.* 2005), mechanistic explanations remain largely unexplored. Several studies have used molecular techniques to more comprehensively characterize microbial communities associated with single-species litter (Das *et al.* 2007, Nikolcheva *et al.* 2003, Nikolcheva *et al.* 2005), but no study has tested effects of litter species heterogeneity on microbial community diversity associated with individual litter species, which would enhance our understanding of synergistic and antagonistic effects of litter species diversity on microbial communities. Our previous research showed that bacterial and fungal biomass were lower in mixtures containing *R. maximum* (Kominoski *et al.* 2007). In contrast, we recorded stimulatory effects of *Liriodendron tulipifera* L. (tulip poplar) on bacterial and fungal biomass when it was present in mixtures (Kominoski *et al.* 2007). However, since we measured microbial biomass on composite samples from litter mixtures, we do not know how litter heterogeneity affected microbial communities on individual litter species within a mixture.

Our primary objective was to test the effect of litter species heterogeneity on microbial community diversity and litter processing of individual litter species. We used molecular

techniques to assess bacterial and fungal community diversity. We hypothesized that breakdown dynamics of individual litter species would differ when incubated individually versus in mixtures. Specifically, we predicted that: 1) high-quality litter species (lower C:N ratio) would have higher rates of microbial respiration and litter mass loss than low-quality litter species (higher C:N ratio) but lower microbial diversity due to greater resource availability (Tilman 1982); 2) mixing high-and low-quality litter would decrease rates of litter mass loss and microbial respiration of the high-quality species as compared to when it was incubated alone; and 3) mixing high-and low-quality litter would increase microbial community diversity on the high-quality species as compared to when it was incubated alone.

METHODS

Study site

Research was conducted in a second-order reach of Ball Creek at Coweeta Hydrologic Laboratory Long-term Ecological Research facility (Coweeta) located in Macon County, North Carolina, USA. Coweeta is a 2,185 ha forested basin in the Blue Ridge physiographic province of the southern Appalachian Mountains (Swank & Crossley 1988). Vegetation is mixed hardwood (dominated by *Quercus* spp., *Acer* spp., and *Liriodendron* spp.), with a dense understory of *R. maximum* that provides year-round shading of streams. Mean monthly air temperature ranges from 3 to 22°C, and mean annual precipitation ranges from 180 cm at low elevations to 250 cm at high elevations (Swift et al. 1988). Mean stream temperature during the study was 9.7°C (range: 4.7 – 16.4°C).

We collected litter from four dominant riparian tree species that differ in litter quality [red maple, *Acer rubrum* L. (A); tulip poplar, *Liriodendron tulipifera* L. (L); chestnut oak,

Quercus prinus L. (Q); rhododendron, *Rhododendron maximum* L. (R)]. After initial dry mass was measured, approximately five grams total of single- (A, L, Q, R) and mixed-species (A+R, L+R, Q+R) litter were placed in plastic mesh litterbags (19.1 × 38.1 cm, 5 × 5 mm mesh) in equal mass proportions. On 17 September 2006, corresponding with peak litterfall, 35 litterbags (7 single- and mixed-species treatments × 5 replicates) were randomly deployed in replicate blocks of the stream channel along a 75-m reach, and additional litterbags were used to estimate handling loss and measure initial litter chemistry. We retrieved litterbags after 50 d, and transported them to the laboratory on ice for processing, which was completed within 12 h. Litter was rinsed over sieves to remove sediment and debris. Individual litter species within mixtures were removed and analyzed separately, enabling us to analyze effects of litter mixing on breakdown dynamics of individual litter species. Leaf disks (17-mm diameter) were removed for microbial respiration and microbial community analyses. Remaining litter was oven-dried at 60 °C for 48 h and ball-milled with a Spex CertiPrep 8000-D Mixer Mill (Spex, Metuchen, NJ, USA) prior to litter chemistry and mass loss analyses.

Litter chemistry and mass loss

Litter carbon and nitrogen ratios (C:N) were measured with a Carlo Erba 1500N CHN Analyzer (Carlo Erba, Milan, Italy). Oven-dried litter was weighed and combusted at 500 °C for four hours to estimate ash-free dry mass (AFDM) remaining. Litter AFDM was measured by subtracting ash weight from dry weight.

Microbial respiration

We measured microbial respiration in the laboratory as oxygen uptake of incubated litter. Ten leaf disks (17 mm diameter) were taken from single-species litter, and 20 leaf disks (10 per species) were excised from litter mixtures. Leaf disks were placed in darkened respiration chambers (30 mL) containing unfiltered stream water, and oxygen concentrations were measured every five minutes with YSI 5100 Dissolved Oxygen Meters (Yellow Springs, OH, USA) for 30 min (Gulis & Suberkropp 2003). Controls contained only unfiltered stream water. Oxygen consumption was determined as the slope of the regression of oxygen concentration over time, adjusted for unfiltered stream water controls and temperature, and expressed per gram litter AFDM per hour (Gulis & Suberkropp 2003).

DNA extraction and PCR

Microbial DNA was isolated from two frozen (-80 °C) leaf disks (17 mm diameter) of individual litter species using an Ultraclean Soil DNA extraction kit (MoBio Laboratories, Carlsbad, CA, USA). Extracted DNA and DNA of bacterial (*Pseudomonas aeruginosa* PAO1) and fungal (*Cortinarius multiformis*) reference cultures were amplified with polymerase chain reaction (PCR). Universal primers (Integrated DNA Technologies, Inc., Coralville, IA, USA) were used to amplify a fragment of 16S rRNA gene of bacteria and the intergenic transcribed spacer (ITS) region of fungal 18S rRNA gene. Bacterial primer pairs 341F+GC and 534R were used to amplify a 200bp fragment of of the 16S rRNA gene (Muyzer *et al.* 1993). The ITS region of fungi was amplified with primer pairs ITS3GC at the 5' end (May *et al.* 2001, Nikolcheva *et al.* 2005) and ITS4 (White *et al.* 1990, Nikolcheva & Bärlocher 2005, Nikolcheva *et al.* 2005). Both forward primers contained GC-clamps at the 5' end, which ensured separation during denaturing

gradient gel electrophoresis (DGGE; Muyzer *et al.* 1993). Each 50 μL PCR reaction contained 0.4 uM forward primer, 0.4 uM reverse primer, 2.5 mM $MgCl_2$ (Promega, Madison, WI, USA), 0.2 mg ml^{-1} bovine serum albumin (Amersham Biosciences, Piscataway, NJ, USA), 160 uM dNTP, 1X GoTaq buffer (Promega), 3 units GoTaq DNA polymerase (Promega), and 3 μL of sample DNA. A 1:1000 and 1:1 dilution of DNA extract was optimal for amplification of bacterial and fungal DNA, respectively. All PCR reactions were performed using a DNA thermocycler (PTC-100, MJ Research, Waltham, MA, USA) and included an initial denaturing step at 94°C for 2 min, followed by 40 cycles of denaturing at 94°C for 1 min, annealing at 56.4 °C for 1 min, and extension at 72°C for 1 min. A final extension cycle was run at 72°C for 5 min. Additional extension times have been suggested to eliminate artifactual double bands in DGGE (Janse *et al.* 2004).

Denaturing gradient gel electrophoresis (DGGE) analysis

Microbial community diversity was assessed with DGGE (Muyzer & Smalla 1998), using Bio-Rad D Code Universal Mutation Detection System (Bio-Rad Laboratories, Hercules, CA, USA). PCR products were loaded onto 6% (fungi) or 8% (bacteria) polyacrylamide gels with 20 to 60% urea-formamide denaturing gradients and electrophoresed at 60V for 14 h. After electrophoresis, gels were removed and stained with GelStar® nucleic acid stain (1:10,000 dilution; Lonza Inc., Allendale, NJ, USA), and imaged with Gel Doc 2000 digital gel imaging system (Bio-Rad). Bacterial and fungal ribotypes, corresponding to distinct DNA base sequences, were represented as bands along the polyacrylamide gel (Nikolcheva *et al.* 2003, Das *et al.* 2007). Bands were identified across lanes and band intensity values for each band were recorded using Gel Doc

imaging software (Bio-Rad). Indices of bacterial and fungal community diversity were measured from the number of bands (i.e. DNA ribotypes).

Statistical analyses

Initial C:N was compared among individual litter species using one-way analysis of variance (ANOVA) and post hoc comparisons (Tukey's HSD). Linear regressions were used to assess relationships among litter mass loss, litter C:N, and microbial respiration after 50 d incubation. Litter C:N, mass loss, and microbial respiration rates of individual litter species, incubated alone and in mixtures, were compared with t-tests and one-way ANOVA with Tukey's HSD. Analyses were conducted with SAS version 9.1 (SAS Institute Inc., Cary, NC, USA) with an alpha (type I error rate) of 0.10. Data were either log- or arcsine-square root transformed to meet assumptions of homoscedasticity. Assumptions of normality of residuals were met for all analyses (Shapiro-Wilkes test).

RESULTS

Litter species incubated individually

Litter C:N was significantly different among individual species both initially ($F_{3,4} = 37.6$, $P = 0.002$) and after 50 days of incubation ($F_{3,16} = 62.7$, $P < 0.001$). Among all four tree species, leaf litter C:N ratios decreased after 50 days of individual incubation in Ball Creek (Table 4.1), but C:N of *R. maximum* litter remained significantly higher than all other litter species ($P < 0.05$; Table 4.1). For leaf species incubated individually, there was a significant negative relationship between day 50 litter C:N and percent AFDM lost ($r^2 = 0.34$, $P < 0.01$). However, there were no

significant relationships between microbial respiration and day 50 litter C:N ($r^2 = 0.05$, $P > 0.10$) or percent AFDM lost ($r^2 = 0.15$, $P > 0.10$).

Litter species incubated in mixtures

Mass loss from *Q. prinus* ($t_{8, 0.10} = -2.15$, $P = 0.064$) mixed with *R. maximum* was significantly greater than for *Q. prinus* incubated alone (Fig. 4.1). However, litter mixing did not have an effect on *A. rubrum* ($t_{8, 0.10} = -0.99$, $P = 0.35$) or *L. tulipifera* ($t_{8, 0.10} = -0.34$, $P = 0.75$) mass loss (Fig. 4.2). In addition, *R. maximum* mass loss was unaffected by mixing with higher-quality litter species ($F_{3,16} = 0.45$, $P = 0.72$; Fig. 4.1).

Litter quality of some individual species was significantly affected by litter mixing. Litter C:N of *A. rubrum* was higher when mixed with *R. maximum* ($t_{8, 0.10} = -1.85$, $P = 0.10$), and *R. maximum* was higher when incubated in mixtures with some high quality litter species ($F_{3,16} = 3.77$, $P = 0.03$). Specifically, a mixture of *R. maximum* with *L. tulipifera* had higher C:N than *R. maximum* alone ($P < 0.05$; Fig. 4.2). However, C:N of *L. tulipifera* ($t_{8, 0.10} = -1.30$, $P < 0.23$) and *Q. prinus* ($t_{8, 0.10} = 1.67$, $P = 0.16$) were unaffected by incubation with *R. maximum* (Fig. 4.2).

Litter mixing also had some significant effects on rates of microbial respiration associated with individual litter species. Specifically, respiration rates were higher on *A. rubrum* ($t_{5.33, 0.10} = -1.92$, $P = 0.10$) and *Q. prinus* ($t_{8, 0.10} = -4.28$, $P = 0.003$) litter incubated in mixtures with *R. maximum* litter when compared to either incubated individually (Fig. 4.3). In contrast, respiration rates associated with *L. tulipifera* litter were not affected by mixing with *R. maximum* ($t_{1.13, 0.10} = 0.56$, $P = 0.66$; Fig. 4.3), and mixing higher quality litter with *R. maximum* had no effect on its associated microbial respiration ($F_{3,11} = 2.42$, $P = 0.12$; Fig. 4.3).

Bacterial and fungal communities

DGGE analyses detected differences in bacterial and fungal communities on individual litter species from single- and mixed-species treatments (Appendix C). The highest number of bacterial DNA ribotypes (e.g. DNA bands) was observed on *L. tulipifera* and *R. maximum* when both were in mixture (Fig. 4.4a); however, *L. tulipifera* and *R. maximum* from single-species contained the lowest bacterial diversity (Fig. 4.4a). Bacterial diversity on *R. maximum* also increased when it was incubated with *A. rubrum* and *Q. prinus* (Fig. 4.4a). When incubated with *R. maximum*, bacterial diversity decreased on *A. rubrum*, but increased on *L. tulipifera* and *Q. prinus* (Fig. 4.4a). Among single species, fungal DNA bands were greatest on *R. maximum* (Fig. 4.4b), and fungal diversity increased on *R. maximum* when it was incubated with *L. tulipifera* (Fig. 4.4b). Fungal diversity on *A. rubrum* and *Q. prinus* litter were not affected by mixing with *R. maximum*, and fungal diversity on *L. tulipifera* litter decreased when incubated with *R. maximum* (Fig. 4.4b). Fungal diversity on *R. maximum* was slightly inhibited by the presence of *A. rubrum* and *Q. prinus* in litter mixtures (Fig. 4.4b).

Although no significant differences were detected, litter heterogeneity appeared to increase overall bacterial community diversity ($t_{8,\ 0.10} = 1.64$, $P = 0.14$) and decrease overall fungal community diversity ($t_{8,\ 0.10} = 0.35$, $P = 0.72$; Fig. 4.5).

DISCUSSION

Enhanced resource heterogeneity, achieved by mixing litter of different litter qualities, resulted in variable effects on microbial communities associated with individual litter species. For leaf litter incubated individually, there was a clear relationship between litter quality, defined here as C:N ratio, and litter mass loss. High-quality litter (lower C:N ratio) showed higher rates of mass

loss (Fig. 4.1). We observed higher microbial respiration on some high-quality litter species that were mixed with low-quality *R. maximum*, suggesting that the presence of highly structured, recalcitrant litter increased oxygen availability within mixed-species litter, which allowed for increased oxygen consumption by aerobic microbes colonizing higher-quality litter. However, mixing with *R. maximum* only decreased mass loss in one litter species (*Q. prinus*). Presence of *R. maximum* in mixed-litter changed litter quality, mass loss, and microbial respiration of high-quality litter relative to single-species leaf packs, although the effects were variable among species. Similarly, *R. maximum* quality, mass loss, and associated microbial respiration were affected by other litter species present in mixtures. In general, presence of high-quality litter species decreased *R. maximum* litter quality but had no effects on its mass loss or associated microbial respiration. Despite the lack of a strong effect of litter mixing on mass loss of individual species, our results partially support our hypotheses of increased microbial respiration and shifts in microbial community diversity on individual litter species associated with heterogeneous, mixed-species litter.

Mixing low-quality litter (e.g., *R. maximum*) with high-quality litter from different tree species resulted in patterns contrary to our predictions. Our hypothesis was that mixing low- and high-quality litter would decrease rates of litter mass loss and microbial respiration on high-quality litter relative to it being incubated alone, which was developed from results of our previous study that found apparent microbial inhibition by *R. maximum* litter (Kominoski *et al.* 2007). However, when we examined individual species litter within mixtures, we found that *R. maximum* presence increased microbial respiration on two of the three high-quality litter species (Fig. 4.3) and increased the rate of litter mass loss for one litter species (Fig. 4.1). These results indicate that within a mixed-species leaf pack, the presence of a rigid, recalcitrant litter species

such as *R. maximum* may have a important structural contributions to the architecture of leaf packs that affect the resource utilization of individual litter species by microorganisms. For example, *R. maximum* may increase dissolved oxygen availability within leaf packs by permitting greater interstitial space between individual leaves. Higher oxygen availability, as determined by the architecture of leaf packs, may explain the higher microbial respiration rates we observed for mixed-species leaf packs containing *R. maximum*.

Detritus increases ecosystem stability and supports consumer biodiversity (Moore *et al.* 2004). Enhanced detrital heterogeneity, which we experimentally achieved through litter mixing, resulted in shifts in microbial community diversity on individual litter species. Bacterial and fungal community diversity was higher on *R. maximum* compared to higher-quality litter species, and microbial diversity on individual litter species in mixtures with *R. maximum* responded variably (Fig. 4.4a, b). Overall, our findings suggest that litter mixing affects stream microbial communities and that mixing has a stronger influence than litter quality on the diversity and communities of colonizing bacteria and fungi. These results represent a unique contribution to the literature, because most studies of litter breakdown in headwater streams are done with single-species litter that have emphasized the importance of individual litter species characteristics on breakdown dynamics. However, our results suggest that litter resource heteogeneity can have bottom-up effects on microbial communities and their influence on ecosystem processes. Further, because mixed-species leaf packs are the normal state of stream litter accumulations *in-situ*, understanding the effects of litter heterogeneity is crucial for placing the results of litter breakdown experiments in the context of real-world ecological relevance.

Our study shows that litter heterogeneity can stimulate microbial respiration. It is unclear whether this is due to a change in total activity of similar microbial communities across

experimental combinations of leaf litter, or due to differences in microbial community structure. Although changes in bacterial and fungal biomass related with litter chemistry (Webster & Benfield 1986, Gulis & Suberkropp 2003, Kominoski *et al.* 2007) and litter diversity (Kominoski *et al.* 2007) have been reported in the literature, biomass is a static measurement and may not fully integrate microbial response to resource quality during breakdown. In contrast, respiration is a measure of overall heterotrophic microbial activity and is a functional metric of microbial communities. Respiration appeared to be linked with litter quality and leaf pack structure, as microbial respiration increased on higher-quality litter when *R. maximum* was present. Because respiration rates quantify the activity of a broad range of biofilm constituents (i.e., all aerobic organisms), future understanding of the ecological importance of resource heterogeneity may benefit by measuring ecosystem processes that display greater variability among biofilm organisms, such as extracellular enzyme activity, nutrient transformation rates, or microbial production estimates.

Similar to our results for respiration, microbial community measurements suggest that aspects of litter heterogeneity that are not related to litter chemistry represent potential overarching control on microbial colonization of litter. In single-species treatments, we observed a positive relationship between litter quality and mass loss, however, the relationships between litter quality and microbial communities are variable and influenced by litter species heterogeneity. Although we recorded differences in microbial community diversity and structure among individual litter species from single-species, this relationship was not conserved for individual litter species in litter mixtures. For example, while *R. maximum* C:N was lower when incubated in litter mixtures, there was no change in its mass loss (Fig. 4.1) or microbial activity (Fig. 4.3), but there where changes in microbial community diversity (Fig. 4.4a, b). We recorded

similar complexities in the results for the other litter species. Litter species heterogeneity appears to have nonadditive effects on microbial community diversity and respiration.

Potential mechanisms for differential litter-mixing effects on microbial community diversity and processing of individual litter species include niche partitioning, resource competition (Tilman 1982), and competitive interactions between bacteria and fungi (Mille-Lindblom *et al.* 2006, Romani *et al.* 2006). Close proximity of bacteria and fungi on substrates can result in synergistic and antagonistic interactions. For example, bacterial growth on decomposing litter is enhanced by the presence of fungi, but bacteria can also inhibit fungal growth (Romani *et al.* 2006). Antagonistic interactions between bacteria and fungi have been linked to litter substrate competition (Mille-Lindblom *et al.* 2006). In our study, diversity of fungi was higher than bacteria on all litter, except *L. tulipifera* mixed with *R. maximum*. Therefore, antagonistic effects of bacteria on fungi do not appear to translate into community-level effects on diversity. We observed synergistic effects of litter mixing on microbial diversity associated with *R. maximum* and only slight antagonistic effects on high-quality litter mixed with *R. maximum*. Therefore, litter mixing generally enhanced microbial community diversity on low-quality *R. maximum*, which suggests that in mixtures both bacteria and fungi on *R. maximum* were competing for resources with bacteria and fungi on high-quality litter.

Our findings expand on previous studies that used molecular techniques to estimate stream microbial communities colonizing litter during breakdown (Nikolcheva & Bärlocher 2005, Nikolcheva *et al.* 2005, Das *et al.* 2007). Das *et al.* (2007) did not observe differences in bacterial and fungal communities colonizing individual litter species with different chemical qualities. The microbial communities in their study system were dominated by generalist taxa, and they concluded that interspecific differences in litter breakdown were explained by leaf

toughness and microbial activity (Das *et al.* 2007). We observed lower mass loss and microbial respiration on *R. maximum* than higher-quality litter species. However, mass loss and microbial activity associated with *R. maximum* were not different when incubated in litter mixtures with high-quality litter, despite significant increases in C:N. We observed differences in microbial community diversity (Figs. 4.4, 4.5) among individual litter species from single-species and mixtures. Although microbial communities on individual litter species were likely influenced by litter quality and, as we have shown, were altered by litter mixing, there were no significant functional effects (e.g., litter mass loss or microbial activity) of changes in microbial community diversity.

Our results represent DNA fingerprints of the bacterial and fungal communities associated with single- and mixed-species litter, and it should be noted that finer resolution techniques, such as cloning and DNA sequencing could have allowed us to further identify taxa associated with DNA ribotypes (Appendix C). In addition, we recognize the methodological limitations of PCR and DGGE, such as lack of detectability of low abundance taxa and lack of replication within treatments. These are realistic limitations to the current methodology that will likely be improved upon with future technological advances. Despite these limitations, our results show specific effects of resource heterogeneity on stream microbial community diversity and activity that altered organic matter processing of some litter species.

Environmental changes within riparian ecosystems are altering species diversity on a global scale, the ecosystem structural and functional implications of which need to be further tested. Species losses and composition shifts are likely to be nonrandom (Huston *et al.* 2000, Tilman & Lehman 2001). In eastern U.S. forests, loss of eastern hemlock (*Tsuga canadensis*) will alter riparian tree community composition (Orwig *et al.* 2002), and it is probable that *R.*

maximum, where present, will increase (Ellison *et al.* 2005). Our results suggest that changes in riparian tree species composition may alter stream microbial community structure and function through changes in litter resource heterogeneity.

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Table 4.1. Carbon to nitrogen ratio (C:N) per litter ash-free dry mass for individual litter species at day 0 and after 50 days of incubation. Values are means (± 1 SE). Differences in lower case letters denote significant ($P < 0.05$) differences among species on the same day species using ANOVA. Ratios calculated as mass.

	C:N	
Species	Day 0	Day 50
Acer rubrum	69.0 (2.9)[a]	43.2 (1.6)[a]
Liriodendron tulipifera	45.8 (2.9)[a]	35.4 (1.0)[a]
Quercus prinus	47.0 (8.3)[a]	40.7 (3.5)[a]
Rhododendron maximum	110.1 (3.1)[b]	80.3 (3.3)[b]

Figure legends

Figure 4.1 Percent litter ash-free dry mass (AFDM) lost from individual (A) high-quality litter species (A = *Acer rubrum*; L = *Liriodendron tulipifera*; Q = *Quercus prinus*) and (B) low-quality *Rhododendron maximum* (R) after 50 days incubation as single species and mixtures. For mixtures, the subscript letter corresponds to the litter species that was mixed with the individual litter species of interest. Values are means (± 1 SE). * denotes significant differences with t-test, and different lower case letters denote significant differences with Tukey's HSD.

Figure 4.2 Litter C:N (based on mass) of individual (A) high-quality litter species (A = *Acer rubrum*; L = *Liriodendron tulipifera*; Q = *Quercus prinus*) and (B) low-quality *Rhododendron maximum* (R) after 50 days incubation as single species and mixtures For mixtures, the subscript letter corresponds to the litter species that was mixed with the individual litter species of interest. Values are means (± 1 SE). * denotes significant differences with t-test, and different lower case letters denote significant differences with Tukey's HSD.

Figure 4.3 Respiration rates of individual (A) high-quality litter species (A = *Acer rubrum*; L = *Liriodendron tulipifera*; Q = *Quercus prinus*) and (B) low-quality *Rhododendron maximum* (R) after 50 days incubation as single species and mixtures For mixtures, the subscript letter corresponds to the litter species that was mixed with the individual litter species of interest. Values are means (± 1 SE). * denotes significant differences with t-test, and different lower case letters denote significant differences with Tukey's HSD.

Figure 4.4 Bacterial (A) and fungal (B) DNA ribotype richness (*n*) from denaturing gradient gel electrophoresis (DGGE) analyses of individual species litter (A = *Acer rubrum*; L = *Liriodendron tulipifera*; Q = *Quercus prinus*; R = *Rhododendron maximum*) from single-species and mixtures. For mixtures, the subscript letter corresponds to the litter species that was mixed with the individual litter species of interest.

Figure 4.5 Mean bacterial and fungal community diversity colonizing individual litter incubated in single-species and mixed-species for 50 d in Ball Creek, Coweeta Hydrologic Laboratory, Macon Co., North Carolina, USA.

Figure 4.1.

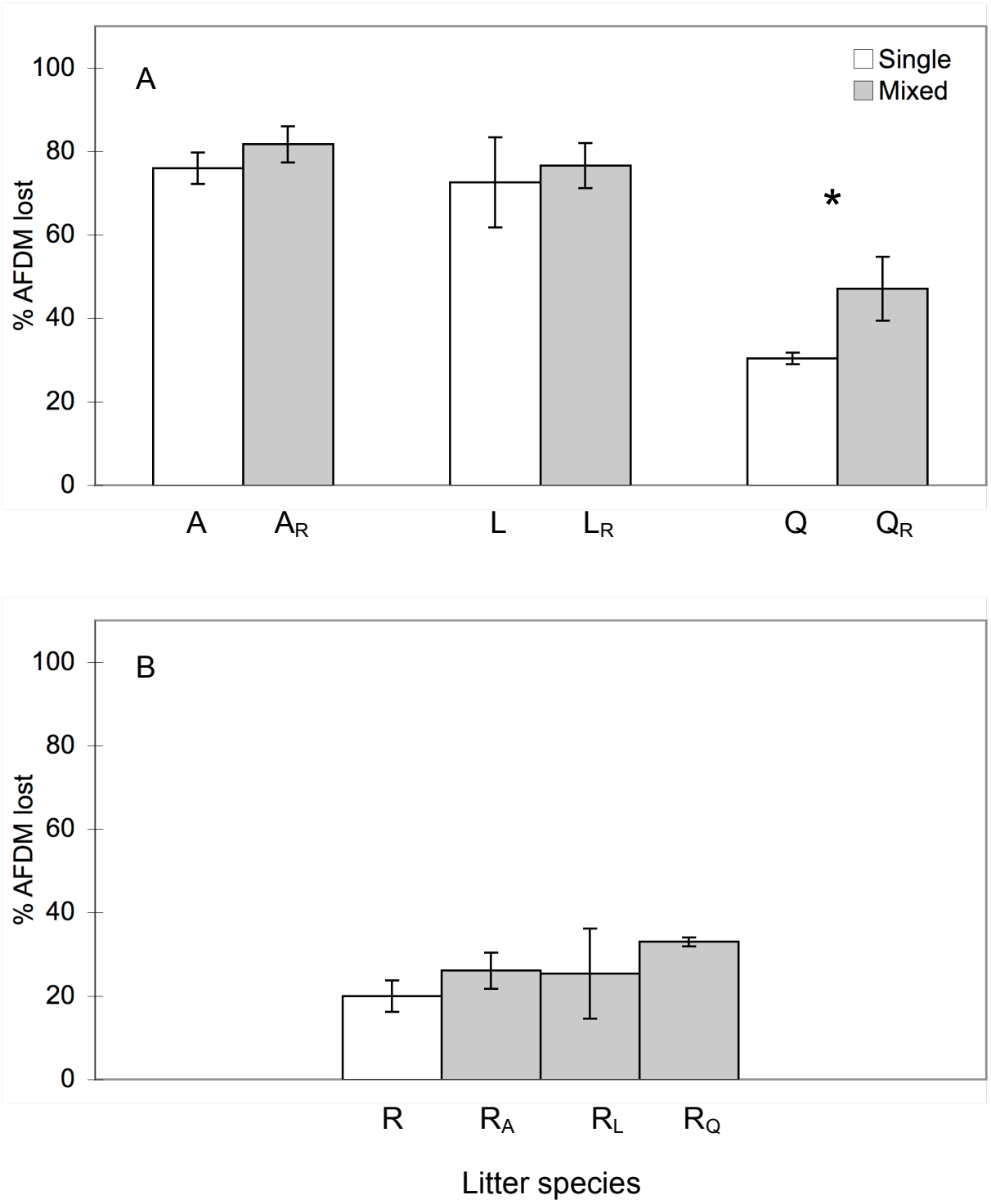
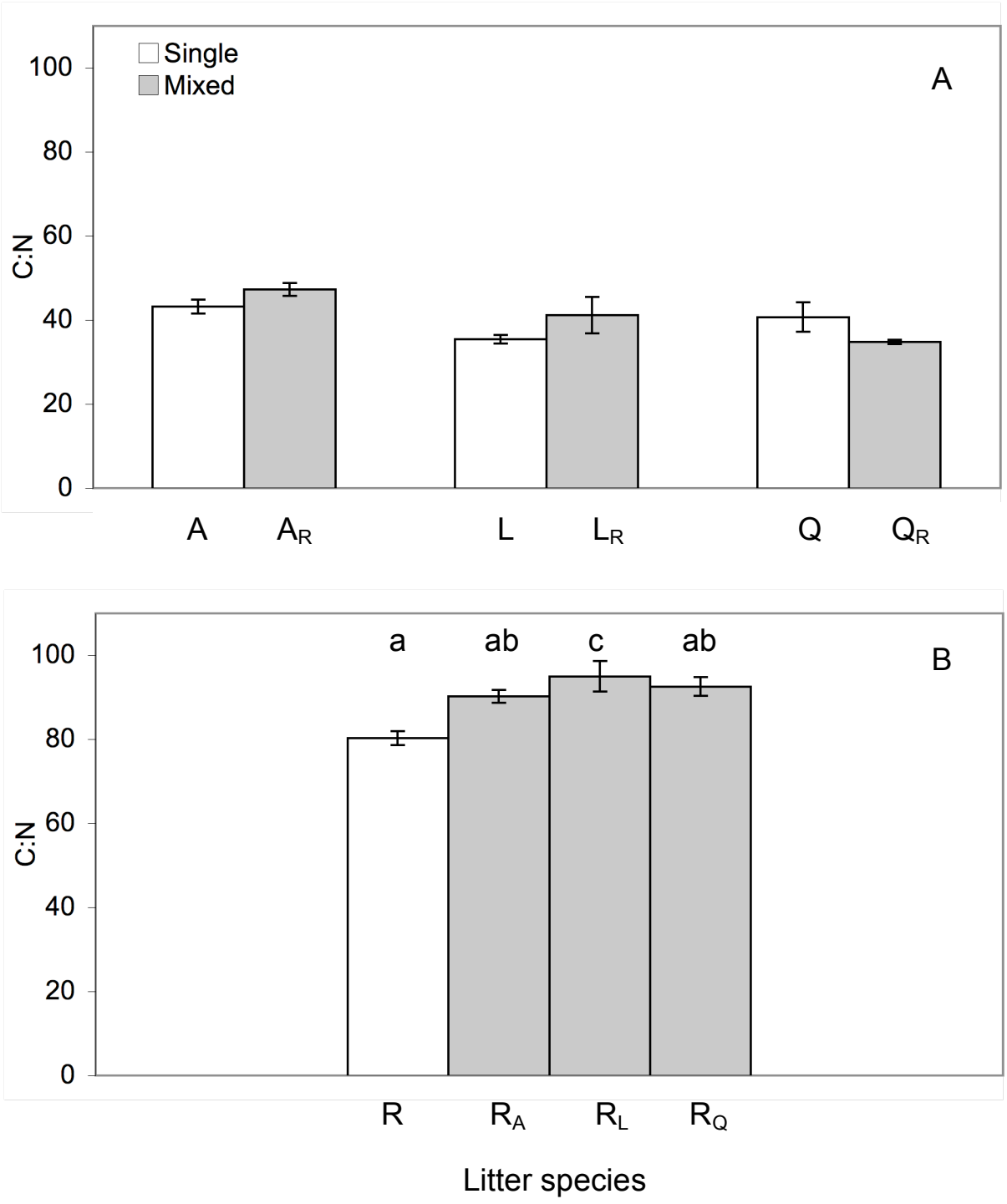

A
Single
Mixed
% AFDM lost
100
80
60
40
20
0
*
A
A_R
L
L_R
Q
Q_R
B
% AFDM lost
100
80
60
40
20
0
R
R_A
R_L
R_Q
Litter species

Figure 4.2.


Single
Mixed
A
C:N
100
80
60
40
20
0
A
A_R
L
L_R
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Q_R
a
ab
c
ab
B
R
R_A
R_L
R_Q
Litter species

Figure 4.3.

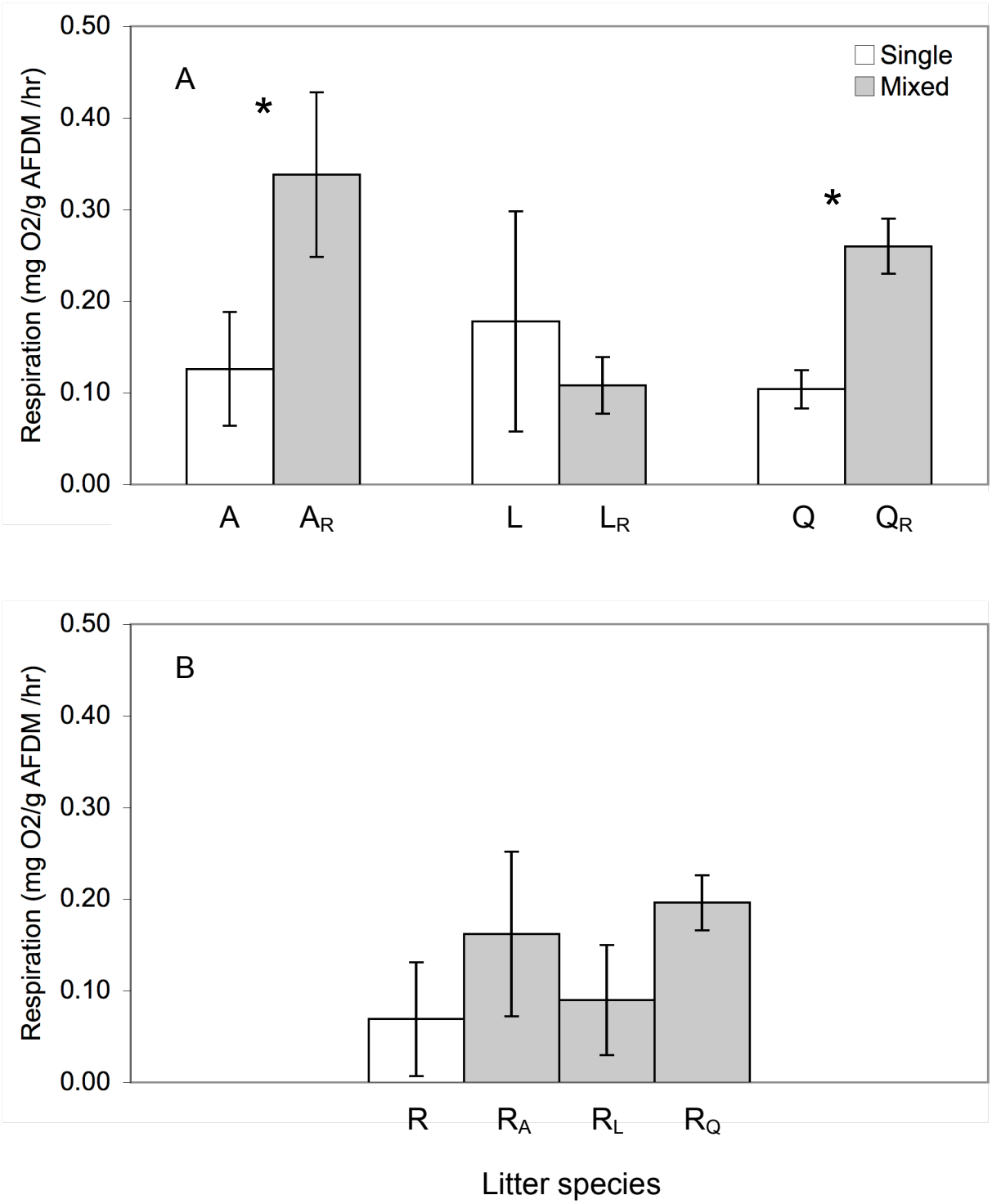

A
Single
Mixed
Respiration (mg O2/g AFDM /hr)
0.50
0.40
0.30
0.20
0.10
0.00
*
*
A
A_R
L
L_R
Q
Q_R
B
Respiration (mg O2/g AFDM /hr)
0.50
0.40
0.30
0.20
0.10
0.00
R
R_A
R_L
R_Q
Litter species

Figure 4.4.

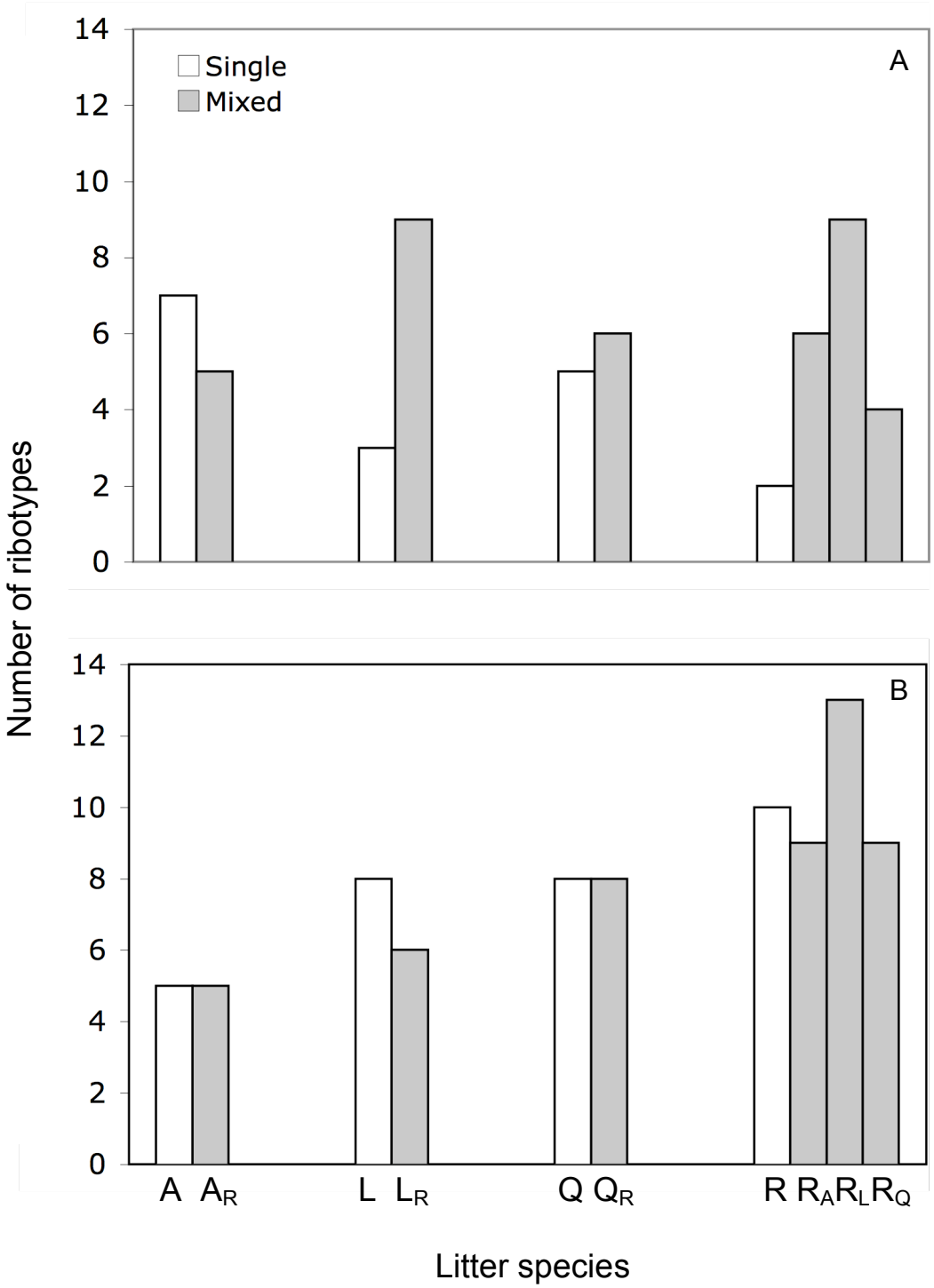
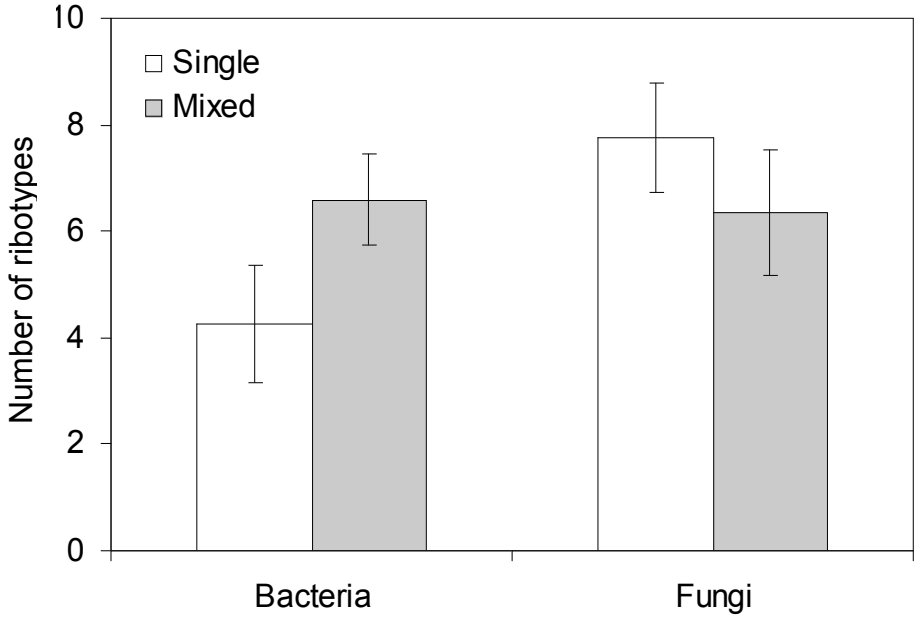

Single
Mixed
A
B
Number of ribotypes
0
2
4
6
8
10
12
14
A
A_R
L
L_R
Q
Q_R
R
R_A
R_L
R_Q
Litter species

Figure 4.5.



CHAPTER 5

LITTER PROCESSING IN TERRESTRIAL AND AQUATIC ECOSYSTEMS: IMPORTANCE OF SPECIES COMPOSITION AND TRAIT PERSISTENCE[4]

[4]Kominoski, J.S., C.M. Pringle, B.A. Ball, D.C. Coleman, M.D. Hunter, B.J. Mattsson. To be submitted to *Oikos*

Abstract

Differing environmental conditions in terrestrial and aquatic ecosystems likely influence effects of plant litter species traits and species composition on ecosystem processes, yet cross-ecosystem comparisons of litter processing have been constrained by differences in temporal scale and analytical methods. Here, we compare published data on processing dynamics of single- and mixed-species leaf litter in riparian and stream habitats of a forested, southern Appalachian watershed that were collected at similar successional stages throughout breakdown. Using an information-theoretic approach, we determined that the most parsimonious models for both riparian and stream datasets contained chemical and biological parameters, as well as litter species composition. Species composition effects were explained by species interactions in riparian litter and species presence/absence in stream litter. Litter C:N and fiber had positive effects and invertebrate abundance had negative effects on litter mass remaining in riparian habitats; whereas secondary compounds had positive effects and fungi had negative effects on litter mass remaining in stream habitats. Our data suggest that litter nutrient content, structural compounds, and invertebrate decomposers are the strongest traits associated with litter processing in terrestrial systems; whereas traits associated with secondary compounds and fungi most determine litter processing in aquatic ecosystems. Although litter species traits persisted during processing in both ecosystems, the relative importance of specific traits and species composition on litter processing varied between terrestrial and aquatic ecosystems. Identifying which species traits persist and interact to affect ecosystem function under varying environmental conditions may allow ecologists to make stronger predictions about functional consequences of species composition shifts across ecosystems.

Environmental differences between terrestrial and aquatic ecosystems make it difficult to generalize about the functional importance of species diversity in both systems (Cardinale et al. 2000, Giller et al. 2004). The relationship between species diversity and ecosystem function is likely dependent on ambient conditions, suggesting that species contributions to ecological processes may change over heterogeneous spatial and temporal environments (Cardinale et al. 2000, Swan and Palmer 2004). Early biodiversity-ecosystem function research focused on vascular plant diversity and grassland primary productivity (Tilman et al. 1996, Hector et al. 1999, Loreau et al. 2002), and recent studies have examined the importance of plant litter (hereafter litter) diversity on decomposition in terrestrial (Gartner and Cardon 2004, Hättenschwiler et al. 2005, Ball et al. 2008) and aquatic ecosystems (Swan and Palmer 2004, LeRoy and Marks 2006, Kominoski et al. 2007, Lecerf et al. 2007). As both terrestrial and aquatic food webs rely on detritus as a source of energy, nutrients, and habitat (Wallace et al. 1997, Moore et al. 2004), understanding how litter species diversity affects organic matter processing in different ecosystems is essential for predicting functional consequences of species loss at multiple temporal and spatial scales.

Although many studies have examined various aspects of breakdown dynamics (e.g., litter mass loss, litter chemistry, and biotic responses) for single- and mixed-species litter in either terrestrial or aquatic ecosystems, none have synthesized results across ecosystem types. The lack of an integrated terrestrial-aquatic perspective of litter species diversity effects on litter processing dynamics is in part due to variation in temporal scale of organic matter processing across ecosystem types. Litter processing in terrestrial and aquatic ecosystems is thought to follow similar patterns (Wagener et al. 1998), yet breakdown in both systems occurs over different temporal scales and under different physical, chemical, and biological conditions that

interactively influence breakdown (Couteaux et al. 1995, Aerts 1997). The lack of an integrated perspective of litter species diversity on breakdown dynamics for various types of detritus-based ecosystems limits our ability to predict functional implications of plant species declines across landscapes in which connections between terrestrial and aquatic habitats are ecologically important (sensu Grimm et al. 2003).

One approach to examining differential responses of terrestrial and aquatic ecosystems to litter species diversity is to test for relative persistence of litter species traits (sensu Haddad et al. 2008) in both systems. Species traits (functional characteristics) are known to influence ecosystem processes (Chapin et al. 2000), an idea that has advanced understanding of species diversity-ecosystem function relationships (Loreau et al. 2001, Hooper et al. 2005). As certain species have overlapping traits, composition of plant species *traits* (e.g., nitrogen-fixing, phenology), rather than species diversity per se, likely influences ecosystem function (Diaz and Cabido 2001, Lavorel and Garnier 2002). Similarly, traits of plant species litter (dead organic matter), such as litter chemical composition, associated decomposer biota, and resistance to decomposition, could be used to assess the effects of litter species diversity and persistence and composition of species traits on litter processing.

Hypotheses, predictions, objectives

Persistence of species traits (Fig. 5.1) is likely linked to biotic and abiotic conditions within ecosystems (Table 5.1). As detritus becomes more homogeneous during decomposition, labile compounds are broken down and recalcitrant compounds remain (Moore et al. 2004). This process occurs more rapidly in aquatic than terrestrial ecosystems due to rapid flow and physical abrasion (Couteaux et al. 1995, Wagener et al. 1998). Traits of fast-decomposing litter species

likely change more rapidly than slow-decomposing species, and this process will be further accelerated in lotic (i.e. flowing) systems.

Our previous studies independently analyzed effects of single- and mixed-species litter (hereafter species composition) on processing dynamics in riparian (Ball et al. 2008) and stream habitats (Kominoski et al. 2007). Although both studies were conducted in the same watershed, we ran separate analyses to test for significant effects on litter mass loss and associated chemical and biological traits. Here, we consider effects of all traits and combinations of traits (Fig. 5.1) within each ecosystem type to assess which selection of species traits best explain litter mass remaining in riparian and stream ecosystems. We categorize litter species traits as chemical (labile versus recalcitrant) or biological (high versus low decomposer abundance/biomass), which ultimately determine decomposability; Fig. 5.1). If individual litter species have distinct chemical and biological traits, the composition of litter species within single- and mixed-species litterbags results in different composition of litter species traits (Fig. 5.1).

We hypothesized that effects of litter species composition on litter mass remaining would differ between terrestrial and aquatic ecosystems based on the relative persistence and composition of distinct litter species traits. From this general hypothesis, we made the following specific hypotheses and predictions: (1) Due to persistence of autecological (individual species) traits among labile and recalcitrant species, litter species presence/absence (additive) will explain litter processing (e.g., litter mass remaining) in riparian habitats; whereas rapid changes in species traits of labile (readily changing) versus recalcitrant (resistant to change) litter within the connective matrix of water will generate species interactive effects on litter processing in stream habitats (Fig. 5.1); (2) Processing of riparian litter will be strongly influenced by various aspects of litter chemistry (e.g., nutrient content, structural and secondary compounds), and processing

of in-stream litter will be most influenced by structural chemical compounds. In general, chemical compounds in litter persist longer in terrestrial than aquatic environments, for both labile and recalcitrant species, based on differential abiotic and biotic factors, such as flow, climate, and decomposer organisms (Couteaux et al. 1995, Hunter et al. 2003). In addition, secondary compounds have been shown to rapidly leach from litter during in-stream processing (Rier et al. 2005, Ardón et al. 2008), suggesting that structural compounds are more important than secondary compounds in determining litter mass loss in streams (Ardón et al. 2008); (3) Although microbial (bacteria and fungi) and invertebrate decomposers are important biological contributors to litter processing in both riparian (Swift et al. 1979, Seastedt 1984, Chapin et al. 2002) and stream habitats (Gessner and Chauvet 1994, Wallace and Webster 1996, Hieber and Gessner 2002), biotic processes likely better explain litter processing in riparian than stream habitats due to greater physical stability in terrestrial litter that supports biota.

Our primary objectives were to: (1) explain the differential importance of litter species traits and species composition on litter mass remaining in terrestrial and aquatic ecosystems; (2) determine which, if any, species traits best explain variation in litter processing in terrestrial and aquatic systems. We conformed litterbag mesh and grams of initial litter to standard methods used by previous studies within each sub-discipline in order that our data would be comparable to previous terrestrial and aquatic studies. This prevents a direct comparison of riparian and stream data. However, we evaluate our hypotheses using separate, predictive models of time-specific litter mass remaining in riparian and stream habitats and offer suggested mechanisms for how litter species traits and species composition may differentially affect terrestrial and aquatic ecosystems.

Methods

Experimental design

We conducted research in a detritus-based, headwater stream (Ball Creek) and adjacent riparian habitats at Coweeta Hydrologic Laboratory (Coweeta), Macon County, NC, USA (35º00'N, 83º30' W). Physical and chemical data collected during the study were available through Coweeta and National Climatic Data Center (Table 5.1).

We selected four riparian tree species that are dominant and abundant at Coweeta [red maple, *Acer rubrum* (A); tulip poplar, *Liriodendron tulipifera* (L); chestnut oak, *Quercus prinus* (Q); and rhododendron, *Rhododendron maximum* (R)]. These species represent a range in initial litter chemistries and breakdown rates (Webster and Benfield 1986; Kominoski et al. 2007, Ball et al. 2008). We used a full-factorial design of all 15 possible single- (richness level = 1) and mixed-species (richness level = 2 - 4) litter combinations (Kominoski et al. 2007, Ball et al. 2008) to separate the confounding effects of litter species richness and composition (Huston 1997, Drake 2003) and to be able to test for species identity and interaction effects.

Measuring litter mass remaining

Freshly abscised leaves were collected and air-dried in the laboratory for two months during autumn 2003. For stream litterbags, approximately 15 g of single- and mixed-species litter in equal mass proportions were placed in plastic mesh bags (19.1 × 38.1 cm, 5 × 5 mm mesh) after initial dry mass determinations (Benfield 2006). Terrestrial litterbags (15 × 15 cm, 1 × 1 mm mesh) consisted of approximately 5 g of single- and mixed-species litter in equal mass proportions (Crossley and Hoglund 1962).

Litterbags were deployed in four replicate locations (blocks) in riparian plots on 17 November 2003 and in four replicate locations along a 75 m reach of Ball Creek on 10 January 2004. Additional litterbags were used to estimate handling loss and initial litter chemistry. Litterbags within each experimental block were grouped in arrays of 15 treatments and retrieved at similar successional stages throughout decomposition (riparian: 0.22, 0.33, 0.55, 0.77; stream: 0.33, 0.55, 0.66). Stream litterbags were randomly retrieved on harvest days 14, 70, and 118, and riparian litterbags were randomly retrieved on 92, 181, 365, and 730 d after incubation. Retrieved litterbags were transported to the laboratory on ice and processed within 12 h.

Litter from stream blocks was rinsed over nested sieves (1 mm and 250 μm) to collect macroinvertebrates and remove sediments and debris. Litter from riparian plots was place on Tullgren funnels to heat-extract invertebrates. Leaf disks (17 mm diameter) were sampled from a representative composite of litter species in each litterbag for both fungal and bacterial analyses. Litter was oven-dried at 60ºC for 24 h, and weighed. Ash-free dry mass (AFDM) was determined as the difference between pre- and post-combustion (at 550°C for 1 h). Remaining litter in each litterbag was milled with a Spex CertiPrep 8000-D Mixer Mill (Spex, Metuchen, NJ, USA) prior to chemical analyses.

Chemical and biological parameters

Chemical and biological data used for riparian and stream models were analyzed using standardized methods reported in detail in Kominoski et al. (2007) and Ball et al. (2008). Briefly, we measured litter C:N, secondary and structural compounds, as well as microbial (fungi, bacteria) biomass and invertebrate abundance during similar successional stages of

decomposition both riparian and stream systems. Data from all analyses were standardized per gram AFDM litter.

Statistical analyses

We constructed separate riparian and stream models that tested for parsimony of model parameters (chemical, biological, species composition), from a subset of data where parameters were measured concomitantly, which best explain patterns in litter mass remaining in each system. From our hypotheses and predictions, we identified a set of *a priori* candidate predictors that apply to both ecosystems (i.e., riparian and stream; Table 5.2). We combined continuous predictors into categories, comprising biological and chemical predictors to reflect the species trait hypothesis. Categorical variables for individual species occupancy and species combinations (i.e., species composition) reflected the additive and species-interaction hypotheses, respectively. In addition to a null model without predictors, the candidate set of models included a species composition variable (additive or interactive), biological predictors, chemical predictors, and any combination of these. As individual litterbags were sampled repeatedly throughout the study and were located in riparian and stream blocks, we constructed a repeated-measures linear model with all predictor variables and a random effect for block (henceforth, global model; Littell et al. 1998). We used a square-root transformation on proportion of AFDM remaining in the riparian dataset to meet the assumption of normally-distributed residuals. These data were back-transformed for plotting the raw data and predictions. We also scaled predictors whose means were large (i.e., >10) for both ecosystems (Table 5.2). This facilitated convergence and optimized the number of significant digits in regression coefficients.

Of five candidate temporal covariance structures for this global model, we selected the lowest AIC_c value, and hence was the most parsimonious (Burnham and Anderson 2002). An unstructured covariance structure was most parsimonious for both ecosystems, and thus we applied this covariance structure to all candidate models.

Our goal was to estimate the level of parsimony (i.e., ability to explain variation while accounting for the number of predictor variables) for each candidate model. To do so, we used maximized log-likelihood of each candidate model to calculate Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). We then ranked each model by its AIC_c weight (i.e., strength of evidence that a model is the most parsimonious of the candidates), so that models with the highest Akaike weight are the most parsimonious (Burnham and Anderson 2002). Models herein with an AIC_c within 4.0 of the model with the lowest AIC_c were defined as the confidence set of models (Burnham and Anderson 2002). We used the slopes and respective 95% confidence intervals (CIs) to assess the effect strength of each predictor on proportion of litter AFDM remaining.

Results

We observed much variation in biological and chemical composition of litter during processing in stream and riparian habitats (Table 5.2). Proportion AFDM remaining in riparian habitats was less variable than that of stream habitats. Estimates of C:N, secondary compounds, and fungal biomass in riparian habitats were less than those in stream habitats, and estimates of bacterial biomass were more than four orders of magnitude greater in riparian than in stream habitats. Remaining variables had similar estimates between ecosystems. In general, variance of predictor variables increased with their magnitude when comparing across habitat types.

Riparian habitat

The confidence set for proportion AFDM remaining in riparian habitats was comprised of models that included biological and chemical parameters in addition to species composition (Table 5.3). In particular, a model with all species interactions carried 56% of the weight of evidence, while a model with additive species effects carried 36% of the weight of evidence. Models without a combination of species composition and biological and chemical parameters had <10% of the cumulative weight of evidence (Table 5.3). Based on the top model, 95% CIs surrounding the least-square-mean litter AFDM for L, A, LA, LAQ, and LAQR were less than that for QR (Fig. 5.2A). C:N and fiber had clear, positive effects on litter mass remaining, and invertebrate abundance had negative effects on litter mass remaining (Table 5.4, Fig. 5.3). Confidence intervals (95%) for secondary compounds and bacterial biomass overlapped zero asymmetrically, suggesting positive effects of both traits on litter mass remaining. Likewise, negative effects were suggested for fungal biomass. There was also evidence that litter mass from different samples collected on the same day were positively correlated (Table 5.4). Litter mass measurements on days 92 and 181 were also positively correlated, but measurements on days 92 and 730, 181 and 730 were negatively correlated (Table 5.4).

Stream habitat

A model that included additive species effects, in addition to chemical and biological parameters dominated the candidate set, with 99% of the weight of evidence (Table 5.3). Remaining models individually had almost no weight of evidence. According to the top model, the least-square-mean litter AFDM for A had a 95% CI that was less than that of Q, while the others overlapped (Fig. 5.2B). Secondary compounds had clear positive effects, and fungi had clear negative effects

on litter AFDM remaining (Table 5.4, Fig. 5.3). Confidence intervals (95%) for fiber, C:N, bacterial biomass, and invertebrate abundance overlapped zero asymmetrically, suggesting negative effects of these traits on litter mass remaining (Table 5.4). Measurements on the same day were positively correlated, except for those on day 70 (Table 5.4). Measurements between days 14 and 70, 70 and 118 were also positively correlated.

Discussion

Before we discuss cross-ecosystem patterns of species traits and composition on litter mass remaining, it is important to note that we did not use identical litterbag methods for both systems, which may have contributed to some of the differences we observed in riparian and stream litter processing. We chose to use standard litterbag methods specific to terrestrial and aquatic sub-disciplines so that our data would comparable to previous studies that examine litter processing within each ecosystem type. If we had chosen to standardize litterbag methods for both ecosystems, our results may not have been comparable to previous research. The reader should note that we did not standardize litterbag mesh and initial litter mass when considering the cross-ecosystem patterns we report. Future cross-ecosystem studies should seek to minimize the confounding effects of mesh size and initial litter mass, while at the same time enabling data to be comparable to studies within each sub-discipline. Despite these limitations, we found that litter processing in both riparian and stream habitats was differentially influenced by species traits and species composition.

Different chemical and biological traits and species composition effects were important predictors of litter mass remaining in each system. Structural compounds and nutrient content were more important in riparian habitats, whereas secondary compounds had a stronger impact in

stream habitats. Although secondary compounds are rapidly lost from in-stream litter, their presence is positively associated with litter mass remaining. As for biological traits, our hypotheses were only partially supported. We anticipated that microbial decomposers would explain litter mass remaining in both ecosystems and that invertebrates would explain more variation in mass loss among single- and mixed-species litter in riparian than stream habitats. However, although invertebrates played a more dominant role in riparian litter processing, fungi only appeared to be important in explaining stream litter processing.

Species composition and trait persistence

Contrary to our hypothesis that additive species composition effects would explain riparian litter processing due to rapid turnover of species traits in streams (Fig. 5.1), we found additive and interactive effects of species composition on stream and riparian litter processing, respectively. Although these results appear to contradict results from our previous tests of additive and nonadditive effects of litter species diversity on breakdown dynamics (Ball et al. 2008, Kominoski et al. 2007), here we tested for parsimony of model parameters (chemical, biological, species composition), from a subset of the data where parameters where measured concomitantly, which best explain patterns in litter mass remaining in each system. Our results not only indicate that litter processing occurs at different magnitudes in terrestrial and aquatic ecosystems (Wagener et al. 1998; Table 5.2) but that distinct litter species traits (chemical and biological) and species compositions, rather than species richness per se, explain this ecosystem process (Tables 5.3, 5.4).

Our hypothesis that autecological differences among litter species traits would persist in riparian litter relative to stream litter was not supported. We predicted that rapid in-stream

processing would generate species interactions between labile and recalcitrant species. However, we observed additive effects of species composition on in-stream litter mass remaining attributed to the presence/absence of traits from high- (*A. rubrum*) and lower-quality litter species (*Q. prinus*). A possible mechanistic explanation for this may be that as litter processing occurs more rapidly in aquatic than terrestrial ecosystems, traits of labile and recalcitrant species may become more distinctly different compared to their initial conditions. Specifically, secondary compounds and fungi associated with *A. rubrum* and *Q. prinus* appear to have had consistent and independent effects on processing dynamics of single- and mixed-species litter (Table 5.4). These results for litter chemistry contradict our hypothesis; whereas biological results support our hypothesis. Changes in *A. rubrum* traits and persistence of *Q. prinus* traits likely also correspond with the additive species compositional effects on time-specific mass remaining for both species (Fig. 5.2B).

In contrast to autecological traits, interactions of species traits best explain species compositional effects on litter processing in riparian habitats. In particular, interactions between *A. rubrum* and *L. tulipifera* and both with *Q. prinus* and *R. maximum* indicated synergistic effects among species traits. Our data suggest that slower processing of litter in riparian compared to stream ecosystems likely enable persistence of litter traits, such as nutrient content, structural compounds, and invertebrate decomposers that interact with traits of other species when in mixtures. When litter mixtures are comprised of species with distinct traits, the persistence of these traits during terrestrial decomposition support chemical and biological interactions between labile and recalcitrant litter species that affect litter mass remaining.

Environmental conditions affect litter processing

In addition to intrinsic conditions (i.e., litter chemistry), litter processing is influenced by extrinsic abiotic and biotic factors, such as regional climate (Meentemeyer 1978, Couteaux et al. 1995, Aerts 1997), microclimate (Hector et al. 2000), microbes (Gessner and Chauvet 1994, Chapin et al. 2002, Hieber and Gessner 2002), and invertebrate decomposers (Seastedt 1984, Wallace and Webster 1996, Hieber and Gessner 2002, Hunter et al. 2003). Followed by climate, litter chemistry is believed to be the single-most important factor of plant traits that affects processing dynamics (Melillo et al. 1982, Webster and Benfield 1986). We have shown here that one chemical constituent of litter is important for litter processing in a terrestrial ecosystem (i.e., fiber), whereas another chemical constituent is important for litter processing in an aquatic ecosystem (i.e., secondary compounds). In contrast to other studies (Rier et al. 2005, Ardón and Pringle 2008) and our predictions, we found that secondary compounds were important in retarding litter processing in stream habitats (Table 5.4; Fig. 5.3A). On the other hand, invertebrates, which we predicted to be dominant contributors to litter processing in stream habitats, had negative effects on litter mass remaining only in riparian habitats (Table 5.4; Fig. 5.3B). These trends suggest that both fixed (controlled; e.g., time, species composition) and random effects (uncontrolled; e.g., physical, chemical, and biological environmental conditions) explain differential responses to species composition and species traits in terrestrial and aquatic ecosystems.

Water availability is a distinct difference between terrestrial and aquatic systems that likely determines the drivers of litter processing in the respective ecosystems. Water and dissolved organic nutrients control microbial metabolism, buffer changes in soil temperature (Coleman et al. 2004), drive organic matter processing and nutrient cycling (Chapin et al. 2002,

Hutchens and Wallace 2002), and support distinct invertebrate communities that drive litter breakdown dynamics (Hutchens and Wallace 2002). Although decomposer fauna are generally adapted to local environmental conditions, terrestrial invertebrates are moisture-limited with some taxa being more tolerant to desiccation than others (Coleman et al. 2004), and aquatic invertebrates are influenced by flow variability (Grimm and Fisher 1989). As litter breakdown rates are determined by climate, litter chemistry, and decomposer biota (Meentemeyer 1978, Webster and Benfield 1986, Couteaux et al. 1995, Aerts 1997, Hunter et al. 2003), differential effects of litter species traits and composition on processing in riparian and stream ecosystems are likely explained by physical, chemical, and biological properties that are unique to each system. Our study is the first to examine the relative importance of litter species traits across ecosystems as influenced by environmental conditions.

Physical, chemical, and biological ecosystem properties

One physical distinction between riparian and stream environments is water flow. Water flow promotes rapid chemical leaching (Petersen and Cummins 1974) and fragmentation of litter in streams, which enhances subsequent physical and biological breakdown. For example, litter breakdown at the land-water interface is enhanced by streamflow and moisture-limited biological processes, such as microbial and invertebrate activity (Hutchens and Wallace 2002). It is also important to note that leaf litter entrained along the margins of streams, often unsubmerged and exposed to ambient air, persists longer than litter that is submerged in the thalweg of the stream (Gregory et al. 1991, Hutchens and Wallace 2002). This is likely a combination of reduced abrasion by flow, litter dessication and subsequent decreases in microbial and invertebrate mineralization, as well as exposure to greater variation in ambient temperatures.

Multiple chemical attributes in riparian and stream ecosystems affect litter processing. Acidity appears to affect litter during the later stages of breakdown in drier versus moister environments (Neuvonen and Suomela 1990). In general, Coweeta soils have lower pH than Coweeta streams (Swank and Crossley 1988, Table 5.1). Changes in litter chemistry proceed differently during riparian versus stream processing, which may lead to greater accumulation of litter-derived, organic acids in terrestrial than aquatic environments. During in-stream breakdown, secondary chemical compounds (e.g., tannins and phenolics) are rapidly leached from litter (Rier et al. 2005, Ardón and Pringle 2008), resulting in decreased chemical heterogeneity of detritus throughout its ontogeny (Moore et al. 2004). This suggests that the effects of secondary compounds on litter processing dynamics are likely to be less persistent in streams than in riparian environments, where rapid leaching does not occur. However, we found that secondary compounds had negative effects on mass remaining during in-stream processing of single- and mixed-species litter. Discrepancies between our results and previous studies suggest that litter chemistry dynamics are specific to the species being tested and highly variable within ecosystem types, making generalizations difficult without further testing. However, by testing the same set of single- and mixed-species litter in riparian and stream ecosystems, our data suggest that differential persistence of secondary and structural compounds and subsequent litter processing dynamics are regulated by environmental conditions. Differential effects of litter species diversity on processing dynamics in riparian and stream ecosystems likely depend on both initial chemical differences among species as well as persistence and composition of these chemical traits during breakdown, which are influenced by physical fragmentation, moisture, as well as microbial and invertebrate detritivores that utilize litter as a food and habitat resource.

Bacteria and fungi are dominant microbial detritivores in terrestrial and aquatic ecosystems. Fungi have extracellular enzymes and hyphae, which enable them to penetrate and mineralize nutrients from within litter. Fungi also compete with bacteria colonizing litter in both terrestrial and aquatic ecosystems, whereby fungi are more dominant than bacteria in surface litter of undisturbed soils (e.g., no tillage; Coleman et al. 2004) and on submerged litter in streams (Gulis and Suberkropp 2003). In general, terrestrial decomposers are believed to be more nutrient-limited than aquatic decomposers (Swift et al. 1979). One area that has not been empirically tested is how differences in nutrient limitation between terrestrial and aquatic microbes might be driven by moisture. For example, exposure of terrestrial fungi to an air barrier may limit the extension of hyphae and subsequent nutrients that are readily available to aquatic fungi in the water column. Since aquatic hyphomycetes production and biomass are influenced by water chemistry (Suberkropp and Chauvet 1995), the availability of dissolved nutrients in streams serves as an additional resource that is readily available to stream fungi that may be particularly important in maintaining heterotrophic metabolism, especially when colonizing poor quality litter. This may explain our observation of stronger effects of fungi on stream than riparian litter processing (Table 5.4; Fig. 5.3B). Fungal presence on litter has also been shown to attract terrestrial (e.g., nematodes and collembolans; Coleman et al. 2004) and aquatic (e.g., shredders; Arsuffi and Suberkropp 1985) invertebrates.

Invertebrates are dominant decomposers of litter in soils (Seastedt 1984) and streams (Wallace and Webster 1996). Invertebrate communities colonizing litter in riparian and stream habitats vary in composition, abundance, and biomass (Hutchens and Wallace 2002). Terrestrial detritivores are generally more abundant and diverse than their aquatic counterparts (Shurin et al. 2006), yet despite their higher abundance, terrestrial invertebrates are reported to be less efficient

at processing detritus than aquatic invertebrates (Cebrian and Lartigue 2004, Shurin et al. 2006). We observed stronger invertebrate effects on litter processing in riparian than stream environments, suggesting that the persistence of litter in terrestrial ecosystems enables stronger influences on mass remaining by invertebrates compared to aquatic ecosystems.

Conclusions

The importance of biodiversity to ecosystem function is influenced by environmental conditions. Therefore, ecosystem responses to species diversity will likely differ at heterogeneous spatial and temporal scales, such as within and among ecosystem types and from season to season within the same system (Swan and Palmer 2004). We suggest that differential effects of litter species diversity on litter processing in terrestrial and aquatic ecosystems are explained by differences in environmental conditions, which affect persistence of species traits. To better understand the functional consequences of biodiversity at larger spatial and temporal scales, future studies should consider how environmental context could alter species composition effects through the persistence of species traits.

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Table 5.1. Chemical and physical characteristics in riparian (February 2004 – July 2006) and stream habitats (January - May 2004) along Ball Creek, Coweeta Hydrologic Laboratory, Macon County, NC, USA. NA = data not available.

		Riparian habitat			Stream habitat		
Variable	Units	Mean	Range	SD	Mean	Range	SD
Physical							
Discharge	$m^3 \bullet s^{-1}$	NA	NA - NA	NA	0.28	0.16 - 1.11	0.12
Precipitation*	$cm \bullet d^{-1}$	0.22	0.00 - 7.06	0.59	NA	NA - NA	NA
Relative Humidity*	%	72.28	59.00 - 81.00	6.64	NA	NA - NA	NA
Temperature*	$^{o}C \bullet d^{-1}$	13.96	-7.22 - 26.66	9.90	5.88	1.50 - 12.40	2.91
Chemical							
pH**		4.60	-		6.70	-	

* Air temperature, relative humidity, and precipitation data from National Climatic Data Center (www.ncdc.noaa.gov)

** Mean values reported in Swank and Crossley (1988).

Table 5.2. Descriptions of variables in time-specific models of ash-free dry mass (AFDM) for leaf litter in riparian (February 2004 – July 2006) and stream habitats (January - May 2004) along Ball Creek, Coweeta Hydrologic Laboratory, Macon County, NC, USA.

			Riparian habitat			Stream habitat		
Variable	Units	Description	Mean	Range	SD	Mean	Range	SD
AFDM	Proportion	Proportion of ash-free dry mass remaining; response variable	0.60	0.23 - 0.95	0.16	0.58	0.07 - 0.99	0.21
Chemical								
CN**	Ratio	Carbon-to-nitrogen ratio	45.41	23.64 - 127.26	16.92	65.44	34.93 - 149.30	20.52
Fiber**	Percent of litter AFDM	Sum of cellulose, hemicellulose, and lignin concentrations	49.86	21.73 - 83.83	7.40	52.43	25.75 - 68.38	6.63
Secmpnds**	Relative index[1]	Sum of condensed tannin, hydrolysable tannin, and total phenolics concentrations	182.58	15.74 - 673.20	131.99	252.40	26.10 - 795.10	208.47
Biological								
Fungi	mg C•g litter AFDM^{-1}	Fungal biomass	1.23	0.01 - 7.47	1.13	5.03	0.06 - 37.5	7.61
Bacteria*	mg C•g litter AFDM^{-1}	Bacterial biomass	17.00	6.54 - 57.13	12.44	5.7E-05	4.0E-06 - 2.9E-04	4.8E-05
Iabund**	individuals per litter bag	Invertebrate abundance	129	3 - 862	121	145	1 - 778	168
Species composition								
CompAdditive	NA[2]	Presence/absence of four individual litter species (Fig. 1)	NA	NA	NA	NA	NA	NA
CompInteract	NA	All possible combinations of the four litter species (Fig. 1)	NA	NA	NA	NA	NA	NA

[1] Values for condensed tannins, hydrolysable tannins, and total phenolics were generated against standards from pooled litter and represent indices of concentration relative to the bulk standard.

[2] Units and parameter values are not applicable to species composition, which is a categorical variable.

* Raw values presented here were multiplied by 0.1 for analysis

** Raw values presented here were multiplied by 0.01 for analysis

Table 5.3. Model selection results for time-specific measurements of litter mass remaining in riparian (February 2004 - July 2006) and stream habitats (January - May 2004) along Ball Creek, Coweeta Hydrologic Laboratory, Macon County, NC, USA. Models in bold are in the confidence set. Number of parameters includes the intercept, fixed effects, random effect of block, and repeated measures. Model parameters are described in Table 5.2.

Model	K[a]	AIC_c[b]	log (L)[c]	Δ[d]	w_i[e]
Riparian habitat					
Chem, CompInteract, Biol	**33**	**-577.9**	**328.3**	**0.0**	**0.56**
Chem, CompAdditive, Biol	21	-577.0	312.0	0.9	0.36
CompInteract, Biol	30	-573.7	322.1	4.2	0.07
Chem, Biol	18	-568.9	304.2	9.0	0.01
CompAdditive, Biol	18	-558.7	299.2	19.2	0.00
Biol	15	-549.8	291.1	28.2	0.00
Chem, CompInteract	30	-548.2	309.3	29.7	0.00
Chem, CompAdditive	18	-537.9	288.8	40.0	0.00
CompInteract	27	-533.1	297.7	44.8	0.00
Chem	15	-522.7	277.6	55.2	0.00
CompAdditive	15	-509.1	270.8	68.8	0.00
Null	12	-490.4	258.0	87.6	0.00

Table 5.3. Continued.

Model	K[a]	AIC_c[b]	log (L)[c]	Δ[d]	w_i[e]
Stream habitat					
Chem, CompAdditive, Biol	**17**	**-196.0**	**117.4**	**0.0**	**0.99**
Chem, CompInteract, Biol	29	-184.7	128.8	11.2	0.00
Chem, CompAdditive	14	-184.1	107.6	11.9	0.00
Chem, CompInteract	26	-178.1	120.9	17.8	0.00
CompAdditive, Biol	14	-174.0	102.6	22.0	0.00
Chem, Biol	14	-171.8	101.5	24.1	0.00
CompInteract, Biol	26	-167.0	115.3	29.0	0.00
Biol	11	-158.4	91.2	37.5	0.00
Chem	11	-157.8	90.9	38.2	0.00
CompInteract	23	-135.9	95.4	60.1	0.00
CompAdditive	11	-134.9	79.4	61.1	0.00
Null	8	-117.0	67.0	78.9	0.00

[a] Number of parameters, including intercept.

[b] Akaike's Information Criterion, corrected for small sample size

[c] Log-likelihood.

[d] Difference in AIC_c between current model and top model.

[e] AIC_c weight of evidence.

Table 5.4. Parameter estimates from top model of litter decomposition in riparian and stream habitats along Ball Creek, Coweeta Hydrologic Laboratory, Macon County, NC, USA, from February 2004 - July 2006. Parameters in bold type have confidence intervals that do not include zero. Model parameters are described in Table 5.2.

Riparian			95% CI	
Parameter	Estimate	SE	Lower	Upper
Intercept	0.6973	0.0481	0.6031	0.7915
Chemical				
Fiber	**0.1896**	**0.0681**	**0.0562**	**0.3231**
Secmpnds	0.0029	0.0030	-0.0031	0.0088
CN	**0.0909**	**0.0356**	**0.0210**	**0.1607**
Biological				
Bacteria	0.0240	0.0220	-0.0190	0.0660
Fungi	-0.0039	0.0020	-0.0078	-0.00001
Iabund	**-0.0302**	**0.0044**	**-0.0387**	**-0.0216**
Species composition				
A	**-0.0717**	**0.0171**	**-0.1051**	**-0.0383**
AQ	-0.0280	0.0176	-0.0626	0.0065
AQR	-0.0120	0.0181	-0.0475	0.0234
AR	-0.0091	0.0147	-0.0379	0.0196
L	**-0.0537**	**0.0187**	**-0.0903**	**-0.0170**
LA	**-0.0558**	**0.0174**	**-0.0899**	**-0.0218**
LAQ	**-0.0514**	**0.0187**	**-0.0880**	**-0.0148**
LAQR	**-0.0420**	**0.0166**	**-0.0746**	**-0.0094**
LAR	-0.0255	0.0168	-0.0585	0.0075
LQ	-0.0050	0.0194	-0.0430	0.0331
LQR	-0.0032	0.0173	-0.0372	0.0307
LR	-0.0307	0.0176	-0.0651	0.0037
Q	-0.0167	0.0184	-0.0528	0.0193
QR	0.0210	0.0167	-0.0118	0.0538
R	0.0000		0.0000	0.0000
Temporal covariance				
(1,1)	**0.0023**	**0.0009**	**0.0006**	**0.0040**
(1,2)	**0.0023**	**0.0009**	**0.0005**	**0.0041**
(2,2)	**0.0033**	**0.0010**	**0.0013**	**0.0054**
(3,1)	-0.0007	0.0005	-0.0017	0.0002
(3,2)	-0.0011	0.0006	-0.0022	0.0001
(3,3)	**0.0041**	**0.0009**	**0.0022**	**0.0060**
(4,1)	**-0.0037**	**0.0014**	**-0.0063**	**-0.0010**
(4,2)	**-0.0050**	**0.0014**	**-0.0078**	**-0.0022**
(4,3)	-0.0001	0.0013	-0.0026	0.0025
(4,4)	**0.0115**	**0.0031**	**0.0054**	**0.0177**

Table 5.4. Continued.

Stream				95% CI	
Parameter		Estimate	SE	Lower	Upper
Intercept		0.7565	0.1296	0.5025	1.0105
Chemical					
	Fiber	-0.2370	0.2046	-0.6380	0.1640
	Secmpnds	**0.0244**	**0.0060**	**0.0127**	**0.0361**
	CN	0.0342	0.0456	-0.0550	0.1235
Biological					
	Bacteria	-52829.0	32587.0	-116699.0	11041.0
	Fungi	**-0.0050**	**0.0021**	**-0.0090**	**-0.0010**
	Iabund	-0.0151	0.0079	-0.0305	0.0004
Species additive					
	A	**-0.0956**	**0.0161**	**-0.1272**	**-0.0639**
	L	-0.0221	0.0172	-0.0558	0.0117
	Q	**0.0388**	**0.0175**	**0.0044**	**0.0731**
	R	0.0000		0.0000	0.0000
Temporal covariance					
	(1,1)	**0.0048**	**0.0010**	**0.0029**	**0.0067**
	(1,2)	**0.0030**	**0.0014**	**0.0003**	**0.0057**
	(2,1)	**0.0152**	**0.0033**	**0.0087**	**0.0218**
	(2,2)	-0.0055	0.0031	-0.0116	0.0007
	(3,1)	0.0011	0.0062	-0.0111	0.0133
	(3,2)	**0.0473**	**0.0133**	**0.0212**	**0.0733**
	(3,3)	**0.0048**	**0.0010**	**0.0029**	**0.0067**

Figure Legends

Figure 5.1. Conceptual diagram of litter species traits and species composition used in full-factorial litter breakdown studies in riparian and stream habitats at Coweeta Hydrologic Laboratory, Macon County, NC, USA. Litter species [*Acer rubrum* (A), *Liriodendron tulipifera* (L), *Quercus prinus* (Q), *Rhododendron maximum* (R)] have distinct traits. "Labile" refers to litter chemistry that readily changes, and "recalcitrant" refers to litter chemistry that is resistant to change. Composition represents all possible combinations of single- and mixed-species litter and their subsequent traits. Symbols represent distinct litter species traits.

Figure 5.2. Variation in time-specific measurements of proportion ash-free dry mass remaining among single- and mixed-species litter during an experiment in A) riparian (February 2004 – July 2006) and B) stream habitats (January – May 2004) along Ball Creek, Coweeta Hydrologic Laboratory, Macon County, NC, USA. Values are predicted least-squared means (± 95% CI), generated using the LSMEANS statement in PROC MIXED. Riparian and stream data represent species composition and presence/absence effects, respectively.

Figure 5.3. Variation in time-specific measurements of proportion ash-free dry mass remaining in relation to A) chemical and B) biological composition of leaf litter during an experiment in riparian (February 2004 – July 2006) and stream habitats (January – May 2004) along Ball Creek, Coweeta Hydrologic Laboratory, Macon County, NC, USA. Open and closed circles represent raw sample data points for riparian and stream litter, respectively. Solid and dashed lines represent predicted values and 95% confidence limits, respectively, based on a repeated-measures model that included chemical and biological predictor variables (i.e., species

composition was ignored). Only those variables with slopes that had 95% confidence intervals above or below zero (Tables 5.3, 5.4) are shown.

Figure 5.1.

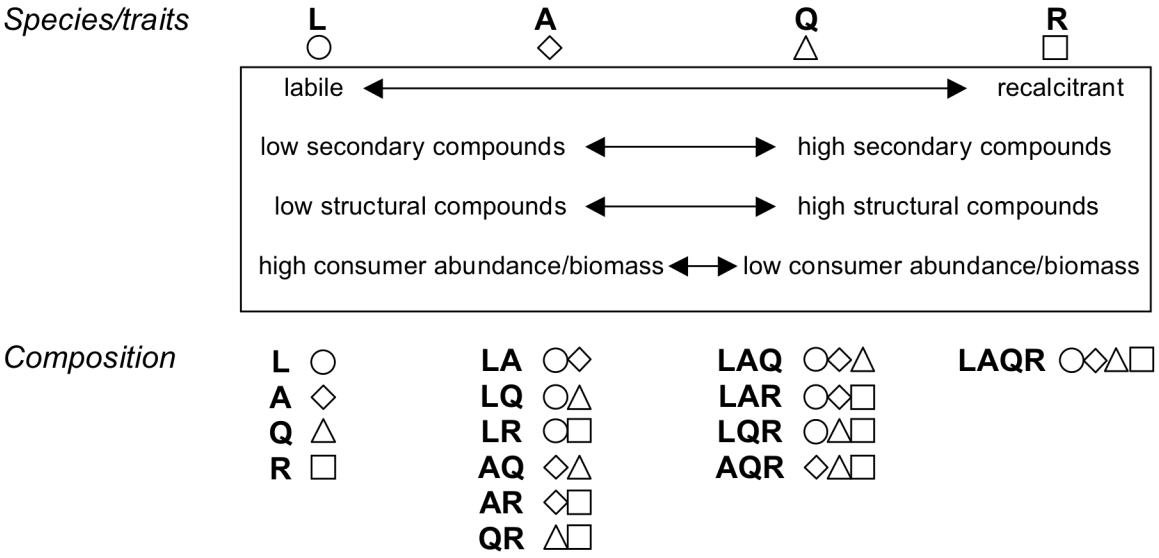
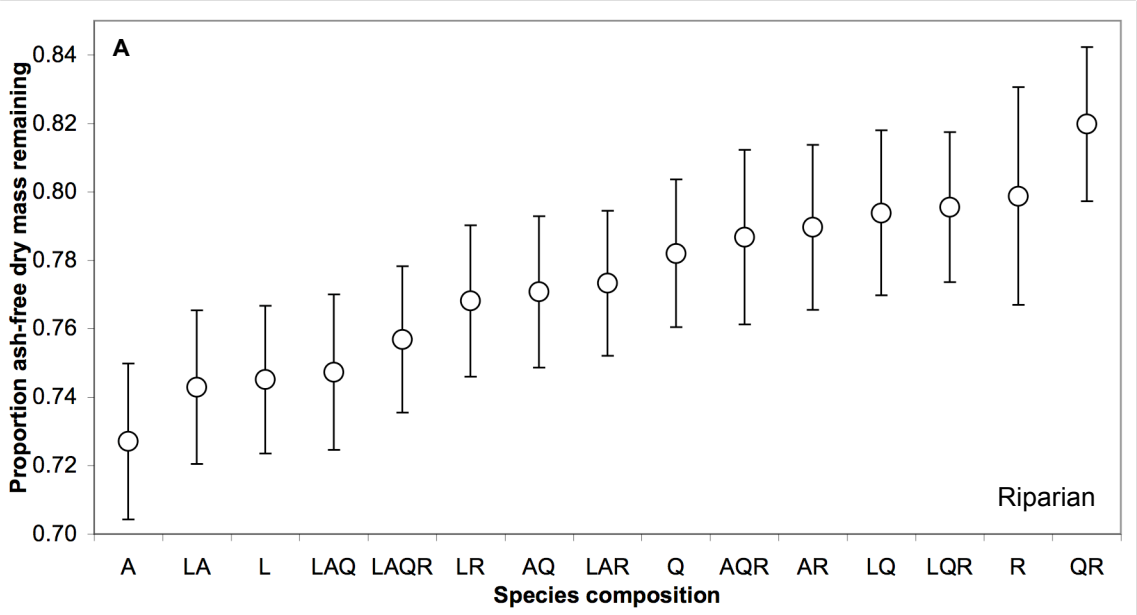

Species/traits
L
A
Q
R
labile
recalcitrant
low secondary compounds
high secondary compounds
low structural compounds
high structural compounds
high consumer abundance/biomass
low consumer abundance/biomass
Composition
L
A
Q
R
LA
LQ
LR
AQ
AR
QR
LAQ
LAR
LQR
AQR
LAQR

Figure 5.2.


A
Proportion ash-free dry mass remaining
0.84
0.82
0.80
0.78
0.76
0.74
0.72
0.70
Riparian
A
LA
L
LAQ
LAQR
LR
AQ
LAR
Q
AQR
AR
LQ
LQR
R
QR
Species composition

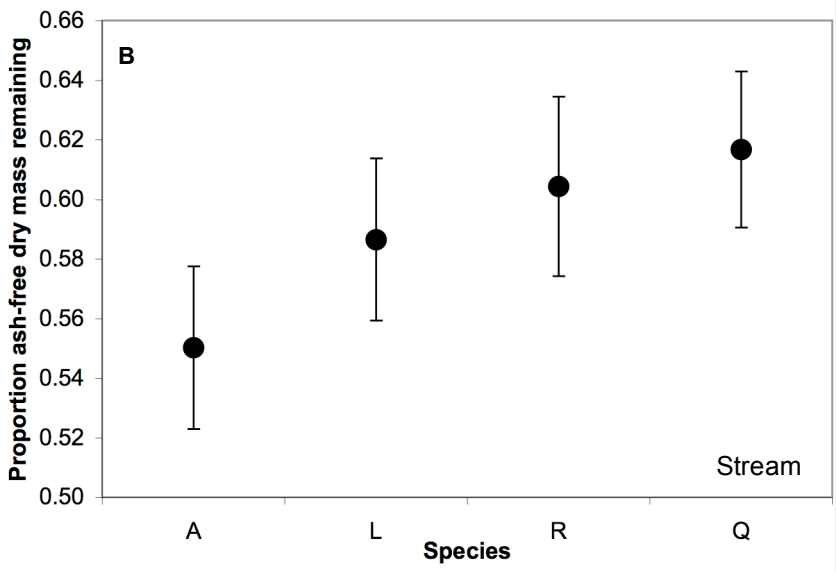

B
Proportion ash-free dry mass remaining
0.66
0.64
0.62
0.60
0.58
0.56
0.54
0.52
0.50
Stream
A
L
R
Q
Species

Figure 5.3

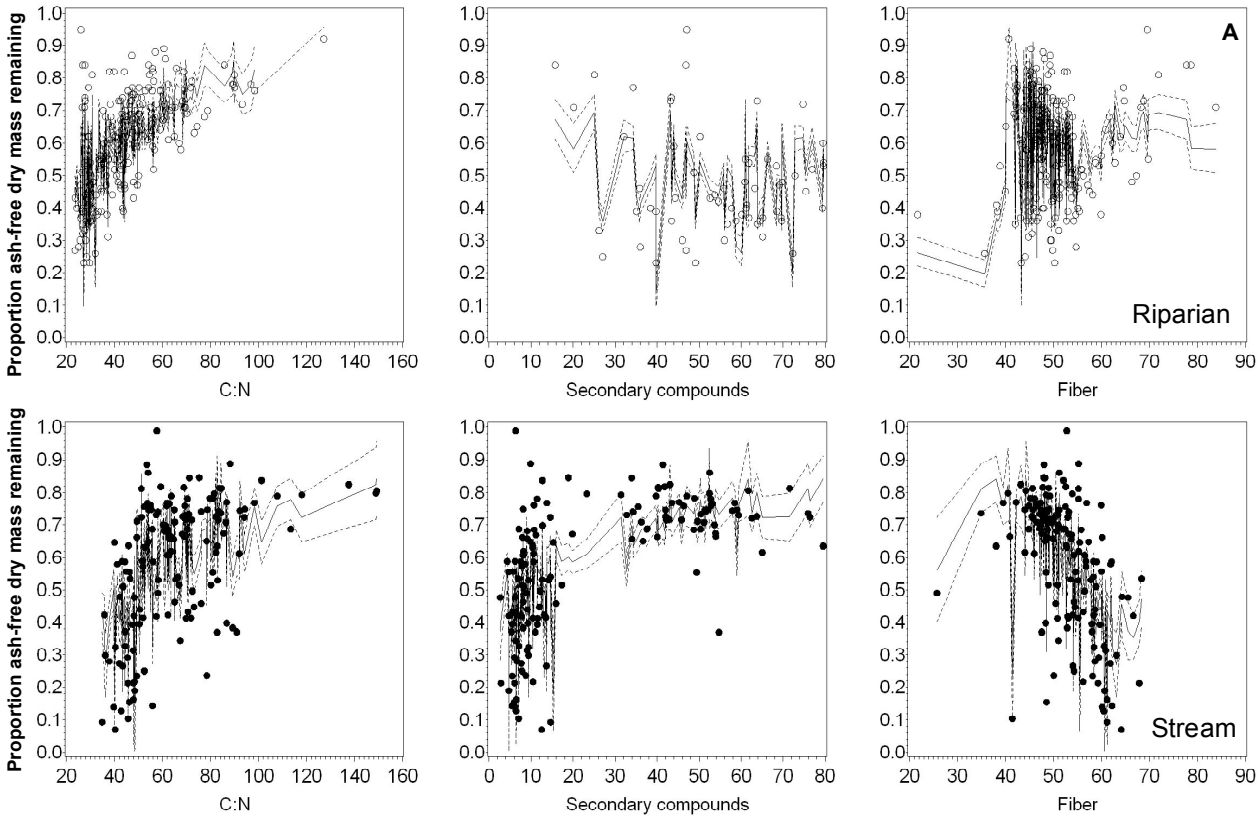
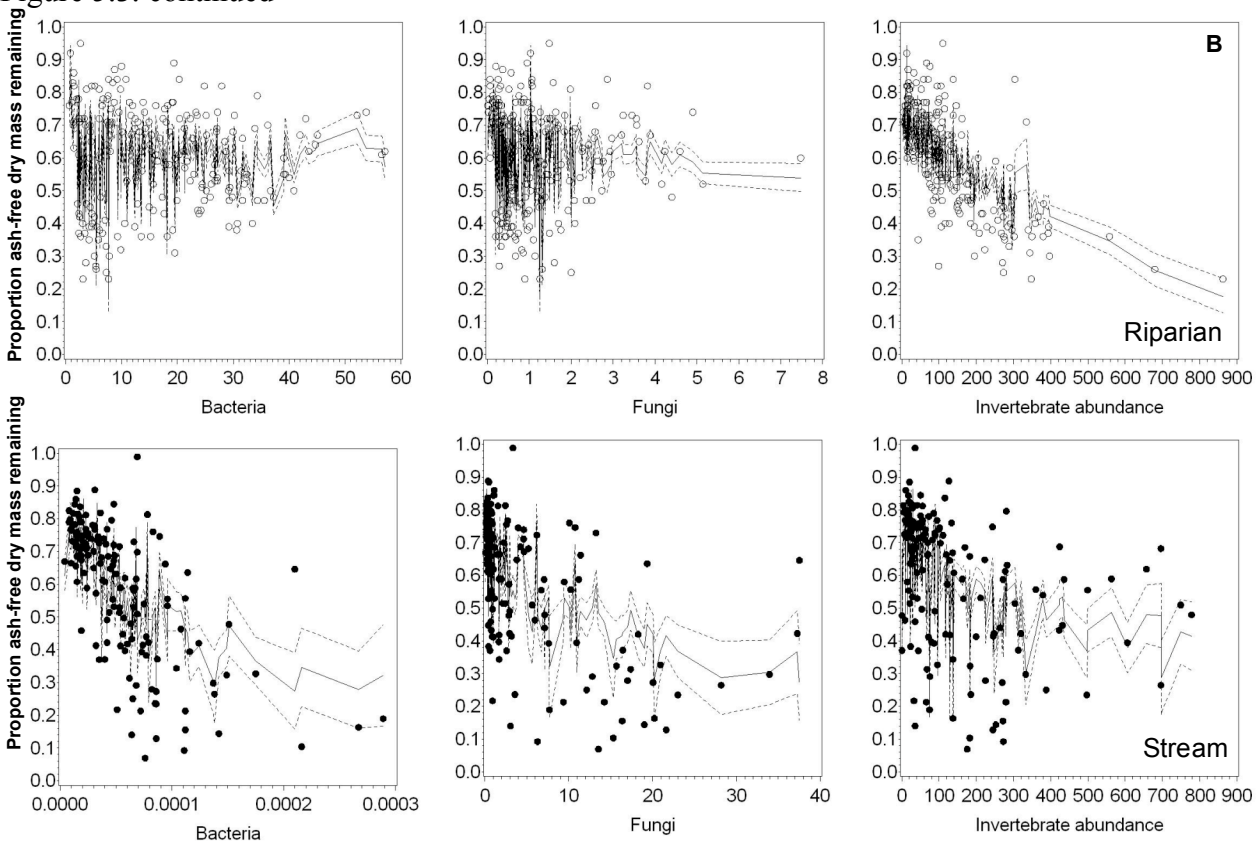

Proportion ash-free dry mass remaining
C:N
Secondary compounds
Fiber
A
Riparian
Stream

Figure 5.3. continued



CHAPTER 6

INVASIVE WOOLLY ADELGID APPEARS TO DRIVE SEASONAL HEMLOCK AND CARCASS INPUTS TO A DETRITUS-BASED STREAM[5]

[5]Kominoski, J.S., B.A. Ball, C.M. Pringle. 2008. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* 30:00-00. Reprinted here with permission of publisher.

Introduction

Ecosystems are experiencing rapid ecological changes due to human-driven alterations in climate, land-use, nutrient availability, and introduction of pests and pathogens. Many of these environmental changes are predicted to result in non-random loss of species that will alter community composition (VITOUSEK et al. 1997, LOREAU et al. 2001, ELLISON et al. 2005). For example, in eastern U.S. forests, current declines in eastern hemlock (*Tsuga canadensis*) resulting from infestation of the woolly adelgid (*Adelges tsugae*) are altering riparian tree community composition (ORWIG et al. 2002). Declines in eastern hemlock in southern Appalachian forests are projected to result in long-term increases in tulip poplar (*Liriodendron tulipifera*) or rhododendron (*Rhododendron maximum*) (ELLISON et al. 2005), but short-term, seasonal effects of woolly adelgid infestation on allochthonous inputs to streams have not been studied. The life cycle of the woolly adelgid contains two generations. Overwintering adult woolly adelgids deposit eggs in ovisacs from February to late March, and larvae emerge in early April (MCCLURE 1989, 1991, MCCLURE & CHEAH 1999). These larvae develop into the adult stage, and deposit a second generation of eggs in June. Emergent larvae remain inactive until October, when feeding resumes (MCCLURE 1989, 1991, MCCLURE & CHEAH 1999). Larvae feed on sap from the base of hemlock needles (MCCLURE 1987), which causes the needles to fall off. Needle inputs from infested riparian hemlock trees may serve as an important resource to stream ecosystems.

Terrestrial litter subsidies are important organic matter and energy resources for recipient stream ecosystems (FISHER & LIKENS 1973, VANNOTE et al. 1980, HALL et al. 2001), and the chemical quality of litter can be altered by terrestrial herbivores (HUTCHENS & BENFIELD 2000, CHAPMAN et al. 2003, 2006). Herbivory on evergreens results in higher litter quality and

accelerated decomposition and nutrient cycling in terrestrial environments compared to herbivory on deciduous trees (CHAPMAN et al. 2003, 2006), and eastern hemlock litter from infested trees has been reported to contain higher nitrogen concentrations than litter from uninfested trees (STRADLER et al. 2006).

Here we present data from a two-year litter trap study, conducted during the early stages of woolly adelgid infestation and hemlock decline, to assess the contribution of eastern hemlock to direct litterfall and lateral inputs to streams as well as entrainment of woolly adelgid carcasses by leaf packs in a second-order reach of Ball Creek, a headwater stream located at Coweeta Hydrologic Laboratory (Coweeta), Macon Co., North Carolina, USA (35º00'N; 83º30'W).

Key words: eastern hemlock (*Tsuga canadensis*), eastern U.S. forests, invasive species, life cycle, litterfall, streams, woolly adelgid (*Adelges tsugae*)

Materials and methods

We estimated litter inputs from August 2004 – August 2006 using directfall (0.1 m^2, n = 10) and lateral (0.5 × 0.2 × 0.3 m, n = 10) traps. Six directfall traps were randomly placed along the circumference of a 10-m diameter circle that incorporated both the riparian zone on either side of Ball Creek, and four directfall traps were randomly placed along 30-m reaches on either side of Ball Creek. Lateral traps were randomly placed in 5-m segments along both margins of the 75-m stream reach. Contents within traps were collected approximately monthly, except during peak litterfall (October – November) when traps were emptied every two weeks. Hemlock needles were separated from total litterfall, and both hemlock and the remaining litter material were oven-dried (at 60 °C for 48 h) and weighed to determine dry mass (DM).

A random composite of hemlock needles was collected from multiple directfall litter traps over several dates and ground using a Spex Mill. The ratio of carbon to nitrogen concentrations of hemlock needles (C:N) was measured using a Carlo Erba 1500N CHN analyzer (Carlo Erba, Milan, Italy).

To measure woolly adelgid carcass entrainment by submerged leaf packs, we used 15-g leaf packs (n = 480) containing litter from four dominant riparian species along the 75-m reach of Ball Creek (KOMINOSKI et al. 2007). Leaf packs were randomly retrieved on days 7, 14, 28, 70, 118, 169, 183, and 190. Retrieved packs were placed on ice and transported to the laboratory for processing within 12 h. Litter was rinsed over nested sieves (1 mm and 250 μm) to collect macroinvertebrates. Abundance of woolly adelgid carcasses was determined for all leaf packs retrieved on harvest days 14, 70, and 118, and woolly adelgid biomass was estimated using mean length and width calculations for 10 individuals within each size class and length-mass regressions (BENKE et al. 1999).

Analyses were conducted with SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA) using an alpha of 0.10. Data were log-transformed when necessary to meet assumptions of homoscedasticity. One-way analysis of variance (ANOVA) was used to determine monthly variation in proportion and dry mass of hemlock litter inputs (directfall and lateral). T-tests were used to compare annual proportion and dry mass of hemlock litter in directfall and lateral traps. One-way ANOVA was also used to test differences in abundance and biomass of woolly adelgid carcasses entrained by leaf packs over time.

Results and discussion

Mean annual proportion of hemlock litter was higher in directfall (0.16 ± 0.04) than lateral traps (0.08 ± 0.04; $p < 0.10$), and mean annual dry mass of hemlock was higher in directfall (4.32 g DM/m^2 ± 1.09) than lateral traps (0.32 ± 0.13; $p < 0.10$). The proportion of hemlock dry mass to directfall and lateral inputs varied among months ($F_{11,209} = 14.8$, $p < 0.0001$; $F_{11,209} = 2.64$, $p = 0.008$, respectively) and was higher in April than in March, September, or October ($p < 0.05$) (Fig. 6.1). Absolute hemlock litter dry mass, as directfall and lateral inputs, varied among months ($F_{11,209} = 9.07$, $p < 0.0001$; $F_{11,209} = 3.31$, $p = 0.001$, respectively). For directfall, dry mass was greater in October than any other month ($p < 0.05$; Fig. 6.2), and dry mass in lateral traps was higher in October than May, June, August, or September ($p < 0.05$).

Abundance and biomass of woolly adelgid carcasses entrained in submerged leaf packs increased through time ($F_{2,93} = 2.79$, $p = 0.07$ and $F_{2,101} = 53.0$, $p < 0.0001$, respectively; Fig. 6.3). Leaf packs in spring and summer had higher woolly adelgid biomass than leaf packs in winter ($p < 0.05$), and leaf packs in summer had higher woolly adelgid biomass than those in spring ($p < 0.05$; Fig. 6.3). Predator abundance and biomass also increased from winter and summer in stream leaf packs (J.S. Kominoski, unpubl.).

Hemlock litter inputs and carcass entrainment were directly linked to woolly adelgid emergence and feeding patterns. We observed highest proportions of directfall and lateral inputs of hemlock litter in mid-April (during larval emergence and feeding) and woolly adelgid carcass entrainment increased steadily following this period. Increases in abundance and biomass of woolly adelgid carcasses in leaf packs from winter to summer are in accordance with the woolly adelgid life cycle, and subsequent increases in abundance and biomass of stream predators

during this time suggest that carcasses may provide a high quality resource for stream consumers.

Both hemlock litter and woolly adelgid carcasses provide substantial allochthonous subsidies to streams. Hemlock litter C:N levels were lower than other labile, high quality litter species reported from Coweeta. For example, KOMINOSKI et al. (2007) measured higher C:N for tulip poplar, a fast-decomposing species, from the same watershed. Hemlock litter from infested trees likely has low C:N because the litter has not senesced, and therefore, the nitrogen has not been reabsorbed, resulting in litter with high nutrient concentrations. Woolly adelgid carcasses contribute terrestrially (specifically hemlock) derived energy and nutrients to stream ecosystems, which are retained in part, through leaf pack entrainment. This resource increased during spring and summer to high densities (> 60 individuals per leaf pack), and concomitant increases in stream predators (J.S. Kominoski, unpubl.) suggest that infested hemlock trees may support higher abundances of stream consumers during a time when most resources are typically low in abundance and quality.

Biological invaders alter ecosystem-level properties and therefore serve to integrate population and ecosystem ecology (VITOUSEK 1990). Understanding the biology of invasive pests and their effects on host species and subsequent ecosystem processes are vital to predict spatial and temporal ecological patterns associated with species invasions. Our dataset represents a quantitative record of hemlock litter and carcass inputs to a detritus-based stream during a period of early hemlock senescence due to woolly adelgid infestation. Even in the absence of pre-infestation baseline data on hemlock inputs, our findings suggest that the life cycle of woolly adelgids affects seasonal trends of hemlock needle and adelgid carcass inputs to streams draining adelgid-infested, forested catchments. Further research quantifying hemlock

needle inputs to streams in uninfested hemlock forests is needed to understand and compare the relative contribution of hemlock organic matter and energy to stream ecosystems prior to eastern hemlock decline.

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Figure legends

Figure 6.1. Proportion of hemlock biomass in directfall and lateral traps from August 2004 – August 2006 at Ball Creek, Coweeta Hydrologic Laboratory, N. C., U.S. Values are means ± 1 SE. Note gap in monthly sampling.

Figure 6.2. Hemlock litter biomass in directfall and lateral traps from August 2004 – August 2006 at Ball Creek, Coweeta Hydrologic Laboratory, N. C., U.S. Values are means ± 1 SE. Note gap in monthly sampling.

Figure 6.3. Mean abundance (individuals per leaf pack) and biomass (mg per leaf pack) of hemlock woolly adelgid (*Adelges tsugae*) carcasses in leaf packs incubated in Ball Creek (Coweeta Hydrologic Laboratory, N. C., U.S.) during January – May 2004. Different letters denote significant differences using ANOVA. Values are means ± 1 SE.

Figure 6.1.

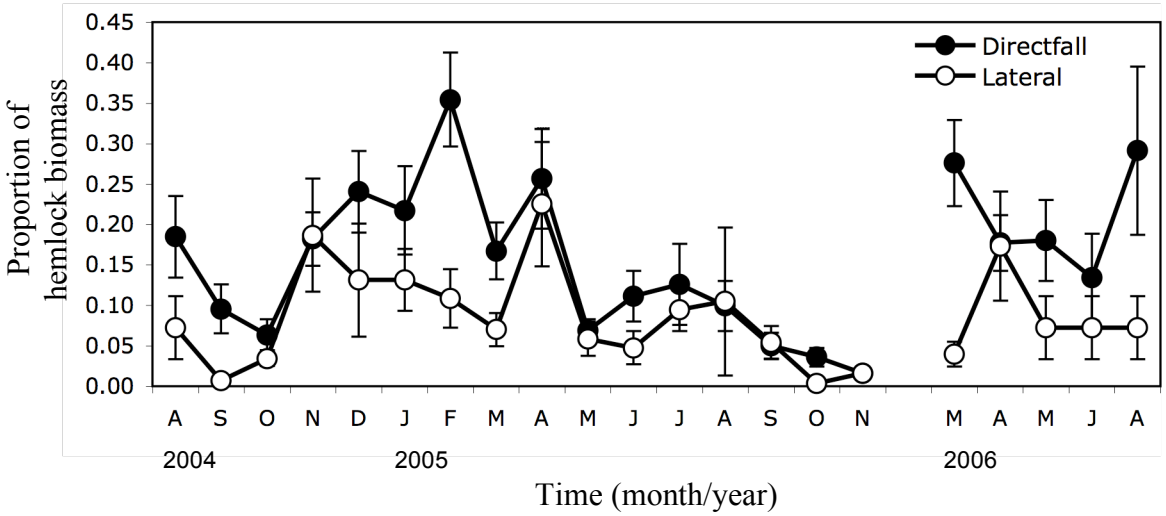

Proportion of hemlock biomass
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Directfall
Lateral
A S O N D J F M A M J J A S O N M A M J A
2004
2005
2006
Time (month/year)

Figure 6.2.

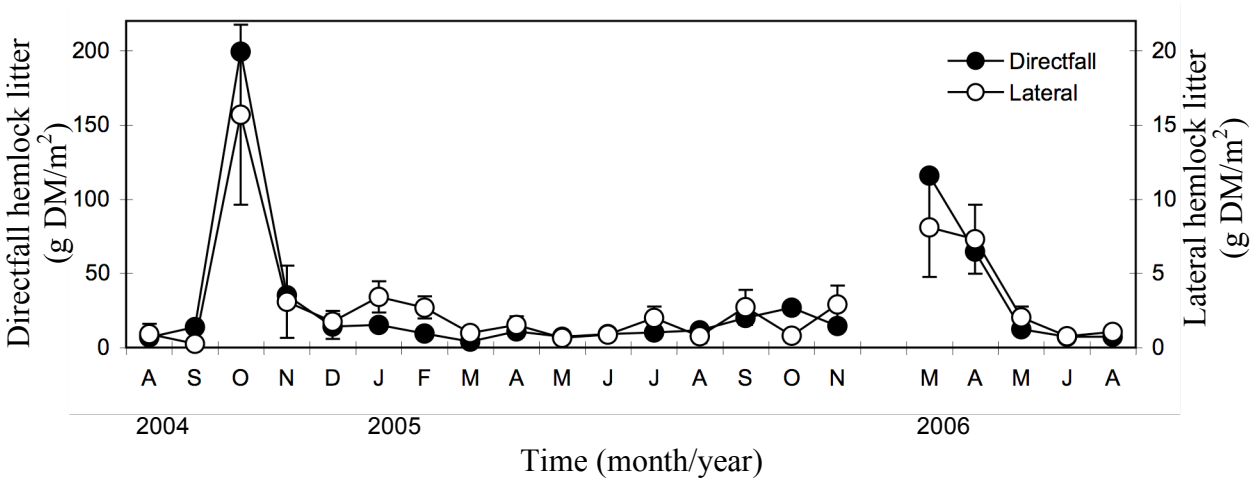
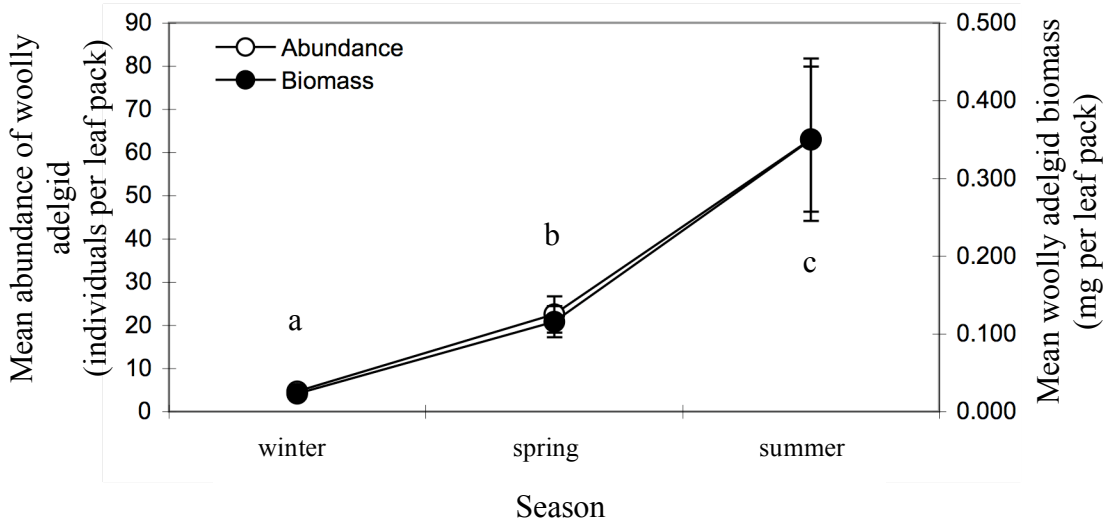

Directfall hemlock litter (g DM/m2)
Lateral hemlock litter (g DM/m2)
Directfall
Lateral
200
150
100
50
0
20
15
10
5
0
A S O N D J F M A M J J A S O N M A M J A
2004
2005
2006
Time (month/year)

Figure 6.3.


Mean abundance of woolly adelgid (individuals per leaf pack)
Mean woolly adelgid biomass (mg per leaf pack)
Abundance
Biomass
90
80
70
60
50
40
30
20
10
0
0.500
0.400
0.300
0.200
0.100
0.000
a
b
c
winter
spring
summer
Season

CHAPTER 7

CONCLUSIONS

Riparian ecosystems help maintain regional biodiversity (Naiman et al. 1993) and support ecosystem function and stability in adjacent streams through leaf litter inputs (Wallace et al. 1997,1999). Of current concern in North American forests is the loss of eastern hemlock (*Tsuga canadensis*) due to introduction of the hemlock woolly adelgid (*Adelges tsugae*), a rapidly infesting insect from which the hemlock is undefended (Orwig et al. 2002). We were interested in the effects of litter resource heterogeneity on consumer dynamics and feedbacks onto litter processing in detritus-based ecosystems (terrestrial and aquatic). Our results suggest that shifts in riparian tree species composition will affect stream ecosystem functioning by changing dynamic interactions that naturally occur during breakdown of mixed-species litter. However, nonrandom changes in riparian forest composition may affect terrestrial and aquatic ecosystems differently.

Although previous studies have primarily found nonadditive effects of litter species diversity on mass loss (Gartner and Cardon 2004, Swan and Palmer 2004, Hättenschwiler and Gasser 2005, LeRoy and Marks 2006, Lecerf et al. 2007), we found both nonadditive effects on in-stream breakdown rates, explained by litter species richness and composition (Kominoski et al. 2007), and additive effects of litter species presence/absence on mass loss in riparian habitats (Ball et al. 2008). Using an information-theoretic approach to compare stream and riparian datasets, we found that although litter species traits persisted during processing in both ecosystems, the relative importance of specific traits and species composition on litter processing varied between terrestrial and aquatic ecosystems. Structural compounds and nutrient content were more important in riparian habitats, and secondary compounds had a stronger impact in

stream habitats. As for biological traits, invertebrates played dominant roles in riparian litter processing, and fungi best explained stream litter processing. Contrary to our hypothesis that additive species composition effects would explain riparian litter processing due to rapid turnover of species' traits in streams, we found additive and interactive effects of species composition on stream and riparian litter processing, respectively. Although these results appear to contradict results from our previous tests of additive and nonadditive effects of litter species diversity on breakdown dynamics (Ball et al. 2008, Kominoski et al. 2007), here we tested for parsimony of model parameters (chemical, biological, species composition), from a subset of the data where parameters where measured concomitantly, which best explain patterns in litter mass remaining in each system. It is important here to note that litter species composition had both antagonistic and synergistic effects on mass remaining in stream habitats and only synergistic effects in riparian habitats. Our results not only suggest that litter processing occurs at different magnitudes in terrestrial and aquatic ecosystems (Wagener et al. 1998) but that distinct litter species' traits (chemical and biological) and species compositions, rather than species richness *per se*, explain this ecosystem process. We have shown that both fixed (controlled; e.g., time, species composition) and random effects (e.g., physical, chemical, and biological environmental conditions) explain differential responses to species composition and species' traits in terrestrial and aquatic ecosystems.

Stream microbial and invertebrate consumers appear to respond differently to litter species diversity. We found both nonadditive effects of litter species diversity and additive effects of species identity on macroinvertebrates that varied with time and litter chemistry; however, microbial community diversity appeared to respond more to litter resource heterogeneity than litter quality. Although mixing high-quality litter with low-quality litter

resulted in shifts in microbial community diversity and altered processing dynamics of individual litter species, bacterial and fungal diversity varied among individual litter species.

Changes in plant litter chemistry, due to herbivory or pest infestation, may alter the dynamics of organic matter processing in terrestrial and aquatic ecosystems. For example, herbivory differentially induces chemical changes in evergreen and deciduous trees (Chapman et al. 2006). Similarly, we found that eastern hemlock trees infested by the woolly adelgid shed higher quality litter than most reported litter chemistry values for deciduous trees (Kominoski et al. 2008). The hemlock woolly adelgid also appeared to drive seasonal hemlock and carcass inputs to our study stream (Kominoski et al. 2008). These results suggest that predicted changes in tree species composition in riparian forests may affect detrital quality, quantity, and processing dynamics in coupled terrestrial-aquatic ecosystems.

Suggestions for future research

A logical, and often suggested, next step to assessing the functional consequences of nonrandom species loss or shifts in species composition would be to conduct more studies that concomitantly test for the effects of species diversity across various ecosystem types on a global scale. However, I suggest that first we should identify and categorize threatened ecosystem functions and services (Daily 1997), as well as the species that perform them. This task could begin by identifying the most spatially and temporally widespread stressors that independently and interactively influence ecosystem function. Of course, this would require a better understanding of how drivers, such as global climate change and land use change, will influence not only biotic communities but also the abiotic environment in which they exist. This brings us back to influence of environmental context on the biodiversity-ecosystem function relationship

(Cardinale et al. 2000). To better understand the functional consequences of biodiversity at larger spatial and temporal scales, future studies should consider how environmental context might alter species composition effects through the persistence of species' traits.

Future biodiversity-ecosystem function research involving plant communities and litter breakdown dynamics should establish common gardens of the species of interest. Since there is known intraspecific variation in litter processing attributed to phenotypic (Madritch and Hunter 2002, 2003) and genetic variation (Schweitzer et al. 2005, Madritch et al. 2006, LeRoy et al. 2006), common gardens would enable for the control or explicit testing of geographic variation in plant genes. Species of interest should represent a wide range of plant litter species' traits, so as to better understand the distinction between functional diversity and species diversity effects (Diaz and Cabido 2001) on organic matter processing dynamics. Future studies should also try to mimic natural proportions of species, so that species evenness is a realistic representation of communities within actual ecosystems (Swan, unpublished manuscript).

One final suggestion for future research deals with ecological versus statistical significance of biodiversity and ecosystem function. We observed statistically significant effects of litter species presence/absence on riparian mass loss (Ball et al. 2008) and species richness and interaction effects on in-stream breakdown rates (Kominoski et al. 2007). In both studies, time explained the most variation in litter breakdown among litter species treatments, which is not unexpected given that litter breakdown is a process that is driven by time. Although we found statistical significance of litter species diversity in both systems, it is important to note that our treatments explained less variation on litter mass loss than did time. Results from our studies suggest: 1) despite the overwhelming influence of time on litter breakdown, we were able to detect statistical significance of treatment effects on litter breakdown, which indicates that our

treatment effects had ecological significance, as well; 2) as we tested our treatment effects in systems that have heterogeneous litter resources, the magnitude of our treatment effects are likely conservative compared to what we would expect for a system that has undergone a loss or shift in litter species composition. Future studies that test for biodiversity effects on ecosystem process-based function should consider the importance of time and ambient conditions on the ecological significance of treatment effects.

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Appendix A. Litter chemistry from single- and mixed-species litter during breakdown in Ball Creek, Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA. Red maple, *Acer rubrum* (*A*); tulip poplar, *Liriodendron tulipifera* (*L*); chestnut oak, *Quercus prinus* (*Q*); rhododendron, *Rhododendron maximum* (*R*). Treatment (Trt), Carbon (C), Nitrogen (N), Phosphorus (P), proportion of litter ash-free dry mass remaining (propAFDM). Values for cellulose, hemicellulose, lignin are percentages. Values for condensed tannins, hydrolysable tannins, and total phenolics are generated against standards from pooled litter and represent indices of concentration relative to the bulk standards. Missing values are indicated with "."

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
I	0	1	1	L	57.15	2855.22	21.02	7.95	10.51	.	.	.	1
I	0	2	1	A	92.16	7447.57	14.95	7.56	9.75	14.77	19.70	22.68	1
I	0	3	1	Q	61.73	5224.41	21.03	12.90	15.53	1.50	8.05	11.89	1
I	0	4	1	R	151.48	21350.86	18.38	11.23	13.40	.	.	.	1
I	0	5	2	LA	69.31	4298.42	17.73	10.45	11.17	24.95	42.73	25.66	1
I	0	6	2	LQ	65.61	3909.25	20.72	12.97	14.98	8.27	18.33	7.29	1
I	0	7	2	LR	78.28	5604.82	19.87	9.69	11.61	14.57	23.83	20.35	1
I	0	8	2	AQ	70.75	4914.70	18.89	11.03	12.62	14.50	17.32	11.51	1
I	0	9	2	AR	119.98	10443.96	18.15	8.57	10.95	17.32	21.10	19.95	1
I	0	10	2	QR	93.67	9001.30	21.76	11.15	13.23	15.26	18.16	14.70	1
I	0	11	3	LAQ	61.23	3696.95	19.28	11.79	13.59	8.13	9.38	10.97	1
I	0	12	3	LAR	88.65	6199.34	18.88	8.82	11.65	15.32	25.09	16.46	1
I	0	13	3	LQR	74.58	6117.86	20.71	11.31	12.70	11.15	25.25	20.96	1
I	0	14	3	AQR	103.18	8611.92	19.92	10.40	12.41	15.01	13.69	20.23	1
I	0	15	4	LAQR	80.64	5833.83	20.53	10.11	13.47	10.98	15.91	13.75	1
II	0	1	1	L	56.17	2723.55	19.99	11.42	11.91	17.13	18.27	25.07	1
II	0	2	1	A	96.15	6684.46	16.71	8.62	10.41	7.81	2.81	0.69	1
II	0	3	1	Q	63.63	4949.70	21.10	12.64	14.47	3.22	9.65	14.64	1
II	0	4	1	R	173.92	26904.07	19.28	7.88	10.87	17.03	25.47	27.58	1
II	0	5	2	LA	76.75	4450.74	18.14	11.72	11.25	8.21	15.47	8.81	1
II	0	6	2	LQ	60.82	3570.03	19.73	14.03	13.16	11.27	21.79	10.41	1
II	0	7	2	LR	80.06	5346.55	20.17	9.78	12.79	11.27	20.43	12.07	1
II	0	8	2	AQ	70.54	5479.01	17.63	11.25	13.02	12.59	14.34	11.11	1
II	0	9	2	AR	126.94	14715.83	18.06	8.79	10.21	20.10	23.97	24.88	1
II	0	10	2	QR	94.65	8966.60	19.98	10.74	13.00	18.73	22.58	19.67	1
II	0	11	3	LAQ	69.07	4229.42	19.11	11.51	13.18	9.40	13.00	16.96	1
II	0	12	3	LAR	84.24	5714.97	17.73	9.68	12.20	18.51	24.35	17.86	1
II	0	13	3	LQR	66.40	3799.78	19.03	11.53	12.03	14.99	21.33	19.36	1
II	0	14	3	AQR	82.70	6496.21	19.13	10.61	12.67	19.31	21.85	19.93	1
II	0	15	4	LAQR	86.03	6315.82	19.65	10.83	11.70	14.44	17.49	15.09	1
III	0	1	1	L	56.59	2845.31	18.75	12.04	11.88	7.58	19.26	21.01	1
III	0	2	1	A	96.48	9667.99	15.95	10.31	9.79	14.38	18.61	22.33	1
III	0	3	1	Q	57.79	3982.38	19.28	15.91	13.32	6.19	13.06	25.37	1
III	0	4	1	R	158.88	22539.08	20.01	9.57	10.73	12.34	19.19	20.37	1
III	0	5	2	LA	85.21	5663.04	19.11	13.99	12.18	7.82	15.05	9.69	1
III	0	6	2	LQ	55.31	3203.94	20.96	13.31	13.73	10.01	19.77	11.19	1
III	0	7	2	LR	74.74	5238.87	20.07	12.86	11.36	11.58	19.21	12.95	1
III	0	8	2	AQ	74.39	5700.54	17.32	13.45	12.12	15.52	19.60	12.93	1
III	0	9	2	AR	114.21	11468.91	17.36	9.29	9.77	17.55	20.39	20.51	1
III	0	10	2	QR	95.41	9018.68	19.31	12.90	12.30	20.88	24.43	21.98	1
III	0	11	3	LAQ	63.14	5168.63	17.78	14.84	12.16	12.05	15.54	17.56	1
III	0	12	3	LAR	85.08	6673.05	18.84	8.87	12.95	11.75	18.20	12.47	1
III	0	13	3	LQR	78.89	7526.51	18.94	13.13	11.60	13.68	21.54	19.67	1
III	0	14	3	AQR	96.55	10073.30	17.66	11.75	10.71	19.82	21.79	18.78	1
III	0	15	4	LAQR	83.39	7726.28	17.88	12.67	11.01	14.58	19.84	17.10	1

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
IV	0	1	1	L	55.44	2538.98	19.04	12.37	12.70	10.99	19.46	23.52	1
IV	0	2	1	A	89.05	8100.67	14.39	9.68	9.33	13.46	19.17	19.39	1
IV	0	3	1	Q	63.10	4992.70	19.97	15.53	14.23	7.80	14.15	23.80	1
IV	0	4	1	R	166.59	33235.06	20.10	9.83	10.39	12.37	19.51	22.90	1
IV	0	5	2	LA	71.93	4390.55	16.42	13.30	10.70	9.74	20.91	12.10	1
IV	0	6	2	LQ	54.76	3316.27	19.33	13.01	13.31	12.07	20.31	11.25	1
IV	0	7	2	LR	78.68	5623.12	18.16	12.13	10.77	16.63	25.25	17.98	1
IV	0	8	2	AQ	70.16	5189.26	17.11	12.23	12.41	15.11	18.11	14.25	1
IV	0	9	2	AR	126.19	13357.53	18.61	9.23	10.41	24.25	23.45	23.67	1
IV	0	10	2	QR	77.55	6779.81	19.74	10.27	12.34	16.32	19.27	17.82	1
IV	0	11	3	LAQ	69.10	4402.08	18.92	11.71	12.54	12.96	15.23	18.46	1
IV	0	12	3	LAR	79.14	6345.43	18.90	9.43	11.09	21.02	26.80	19.20	1
IV	0	13	3	LQR	87.65	6191.70	20.74	11.34	12.06	19.97	25.39	27.69	1
IV	0	14	3	AQR	90.38	8557.97	19.86	10.26	13.11	16.26	19.33	25.07	1
IV	0	15	4	LAQR	73.00	4990.67	19.37	10.71	12.90	14.81	20.09	18.38	1
I	7	1	1	L	51.44	2754.74	19.57	17.02	10.77	13.51	15.34	23.62	0.69
I	7	2	1	A	80.48	7648.89	14.86	9.98	11.10	20.64	28.37	23.18	0.64
I	7	3	1	Q	50.21	2945.57	19.73	18.04	14.98	6.32	7.75	10.91	0.81
I	7	4	1	R	161.39	28919.51	21.89	10.88	12.73	12.06	15.64	16.63	0.85
I	7	5	2	LA	65.07	4850.83	16.73	13.74	10.37	10.35	32.12	16.42	0.67
I	7	6	2	LQ	50.46	3558.82	18.92	17.53	12.33	12.86	28.97	12.99	0.77
I	7	7	2	LR	71.76	6692.40	19.08	14.33	10.71	13.79	22.80	17.61	0.75
I	7	8	2	AQ	59.57	4472.86	17.83	13.57	13.57	15.52	22.65	16.72	0.75
I	7	9	2	AR	93.05	12197.14	18.02	10.41	12.49	13.41	17.77	19.30	0.78
I	7	10	2	QR	64.06	6045.39	20.53	13.99	12.97	11.89	12.19	11.64	0.85
I	7	11	3	LAQ	61.82	3757.39	17.01	13.45	11.22	14.99	24.57	36.55	0.79
I	7	12	3	LAR	73.27	5678.28	11.95	9.95	15.21	18.28	34.39	26.67	0.79
I	7	13	3	LQR	75.90	5210.37	20.04	14.82	11.54	13.36	18.03	15.68	0.81
I	7	14	3	AQR	74.74	7762.96	18.01	12.73	12.55	14.38	21.48	15.56	0.81
I	7	15	4	LAQR	66.53	5546.77	18.29	13.84	12.42	14.69	18.68	14.24	0.75
II	7	1	1	L	61.54	3575.42	17.41	19.07	11.62	10.87	14.39	23.34	0.67
II	7	2	1	A	74.10	6683.31	17.02	10.59	11.55	18.34	20.32	22.74	0.67
II	7	3	1	Q	54.17	3600.56	20.94	18.43	15.28	4.66	6.19	10.33	0.86
II	7	4	1	R	137.66	27227.62	20.35	8.90	11.97	13.02	18.35	16.72	0.85
II	7	5	2	LA	65.90	5769.49	16.68	15.00	10.36	7.84	22.95	14.69	0.70
II	7	6	2	LQ	52.11	2911.93	17.81	16.55	11.28	12.34	33.36	12.86	0.79
II	7	7	2	LR	87.27	9263.58	19.57	13.63	9.86	15.37	24.82	18.91	0.77
II	7	8	2	AQ	62.15	4631.37	17.85	13.37	13.53	12.08	21.86	17.39	0.78
II	7	9	2	AR	98.47	11733.59	18.01	9.91	11.55	17.08	20.98	23.66	0.74
II	7	10	2	QR	73.81	6730.44	18.43	13.05	13.19	13.52	15.20	15.07	0.90
II	7	11	3	LAQ	55.28	3778.91	17.82	14.82	11.51	8.76	14.62	26.16	0.81
II	7	12	3	LAR	84.81	8489.25	17.17	11.74	11.05	14.92	23.96	19.26	0.77
II	7	13	3	LQR	64.42	5141.08	20.70	15.39	12.45	7.51	12.65	9.74	0.78
II	7	14	3	AQR	82.14	8203.82	17.46	13.01	13.57	13.83	19.52	10.49	0.79
II	7	15	4	LAQR	76.90	6552.18	18.40	14.12	12.14	11.03	15.46	13.03	0.77

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
III	7	1	1	L	51.74	697.85	19.19	19.29	10.47	12.79	18.26	27.28	0.86
III	7	2	1	A	90.37	8194.26	16.37	10.52	11.11	20.75	30.17	27.80	0.72
III	7	3	1	Q	53.59	3354.38	19.04	16.87	15.57	6.36	7.75	12.34	0.87
III	7	4	1	R	157.18	26521.12	20.18	10.68	10.96	11.00	16.41	19.84	0.85
III	7	5	2	LA	64.40	4826.78	18.00	14.96	11.82	9.39	24.52	11.63	0.61
III	7	6	2	LQ	53.20	3244.46	20.18	16.40	12.13	13.25	39.14	15.03	0.77
III	7	7	2	LR	77.40	6986.37	18.56	13.77	11.66	16.51	27.04	15.16	0.76
III	7	8	2	AQ	58.86	4089.00	17.65	14.38	13.61	15.43	22.95	14.51	0.75
III	7	9	2	AR	125.97	20715.32	18.15	9.64	10.61	17.50	23.84	23.83	0.74
III	7	10	2	QR	88.87	7899.49	19.16	12.85	11.65	16.28	21.01	18.53	0.85
III	7	11	3	LAQ	72.96	4996.68	16.22	14.23	10.58	15.56	26.71	39.36	0.83
III	7	12	3	LAR	91.17	8223.62	17.46	10.67	11.17	21.99	38.92	27.94	0.79
III	7	13	3	LQR	60.98	4089.60	19.52	13.86	12.21	11.82	17.62	14.12	0.82
III	7	14	3	AQR	94.39	8039.26	18.14	12.44	11.25	17.57	22.48	14.32	0.85
III	7	15	4	LAQR	80.67	5868.57	17.98	13.68	11.87	14.57	20.58	18.33	0.77
IV	7	1	1	L	55.80	3144.27	21.09	16.82	13.96	3.27	8.14	12.51	0.88
IV	7	2	1	A	99.80	9731.10	16.13	10.86	11.95	10.70	11.54	11.72	0.77
IV	7	3	1	Q	61.84	5199.96	19.62	15.96	17.58	3.12	4.35	5.35	0.86
IV	7	4	1	R	172.07	37463.77	20.39	9.82	12.07	10.45	14.32	14.60	0.82
IV	7	5	2	LA	63.44	4855.53	17.44	13.87	13.30	3.74	11.82	6.84	0.77
IV	7	6	2	LQ	52.21	4208.37	18.74	16.37	15.66	6.55	12.68	4.02	0.86
IV	7	7	2	LR	70.82	6572.77	19.22	12.32	12.94	8.19	14.03	8.50	0.81
IV	7	8	2	AQ	72.97	6603.43	17.13	12.28	13.82	9.15	15.19	11.05	0.80
IV	7	9	2	AR	112.77	13655.84	17.29	9.64	11.82	16.29	20.38	21.85	0.81
IV	7	10	2	QR	83.83	7783.42	19.00	12.35	13.69	14.53	15.83	14.94	0.85
IV	7	11	3	LAQ	59.94	4542.91	17.98	14.26	14.65	4.08	6.89	7.15	0.78
IV	7	12	3	LAR	79.69	7630.48	19.47	12.56	12.05	11.24	14.05	9.89	0.78
IV	7	13	3	LQR	65.07	6129.94	19.51	14.55	16.21	9.61	12.32	9.38	0.81
IV	7	14	3	AQR	88.37	8485.79	19.42	12.50	14.77	10.39	13.67	9.77	0.77
IV	7	15	4	LAQR	69.83	7310.16	19.30	12.87	15.08	6.58	11.35	6.70	0.77
I	14	1	1	L	55.40	3672.52	18.06	17.00	9.03	11.86	19.34	27.79	0.75
I	14	2	1	A	84.42	6464.54	14.79	10.22	9.96	21.90	26.89	27.13	0.73
I	14	3	1	Q	54.00	4873.87	20.62	15.60	15.02	14.72	15.54	22.23	0.86
I	14	4	1	R	137.61	18936.45	21.25	10.05	11.92	13.95	10.23	18.85	0.82
I	14	5	2	LA	63.49	4405.97	17.05	13.02	10.86	9.78	29.24	14.92	0.66
I	14	6	2	LQ	49.41	2781.82	20.70	16.23	12.98	8.76	33.00	7.83	0.71
I	14	7	2	LR	71.05	8053.34	21.19	11.05	14.98	12.06	27.32	11.03	0.73
I	14	8	2	AQ	62.98	5849.53	17.56	14.96	13.93	19.91	14.23	19.00	0.76
I	14	9	2	AR	98.34	9700.14	18.14	9.86	11.55	19.87	13.03	25.57	0.77
I	14	10	2	QR	71.27	6853.60	21.53	13.20	13.58	12.40	8.93	12.61	0.84
I	14	11	3	LAQ	65.58	5004.36	17.88	15.57	11.33	15.62	8.10	30.67	0.67
I	14	12	3	LAR	86.79	8903.05	17.22	12.17	12.87	16.90	9.85	18.48	0.77
I	14	13	3	LQR	61.78	4367.30	20.12	13.06	13.30	13.67	17.30	15.34	0.76
I	14	14	3	AQR	78.72	7319.25	19.54	12.34	13.88	14.74	21.39	16.01	0.75
I	14	15	4	LAQR	65.15	4982.45	20.06	13.57	12.97	14.55	6.71	14.97	0.71

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
II	14	1	1	L	51.30	3043.43	19.42	17.07	11.65	18.78	22.28	35.28	0.72
II	14	2	1	A	82.86	7649.00	15.57	10.91	11.59	26.55	26.59	26.37	0.63
II	14	3	1	Q	53.54	3213.56	19.51	14.88	13.69	8.15	22.21	11.02	0.88
II	14	4	1	R	148.95	24885.66	20.37	9.37	10.84	14.99	18.04	19.39	0.80
II	14	5	2	LA	61.97	4371.61	19.65	13.79	13.89	7.81	24.38	11.32	0.77
II	14	6	2	LQ	55.85	3655.13	21.39	17.43	13.65	9.39	19.68	8.47	0.69
II	14	7	2	LR	83.27	7887.33	21.14	12.87	13.99	10.68	20.11	11.35	0.71
II	14	8	2	AQ	61.36	5504.76	18.52	14.63	13.96	8.70	20.83	8.14	0.69
II	14	9	2	AR	92.32	14532.96	21.19	12.30	14.76	19.74	18.56	19.60	0.74
II	14	10	2	QR	68.96	7720.62	20.49	13.69	13.63	10.65	20.28	9.30	0.82
II	14	11	3	LAQ	61.86	3683.15	19.83	15.26	13.72	10.02	21.13	17.57	0.69
II	14	12	3	LAR	85.42	8350.71	18.94	13.60	15.04	13.84	28.24	11.82	0.67
II	14	13	3	LQR	64.93	4985.18	22.49	14.89	13.86	13.64	14.85	13.50	0.75
II	14	14	3	AQR	69.41	5587.03	19.11	12.51	13.28	16.67	23.77	12.41	0.76
II	14	15	4	LAQR	69.96	5888.34	20.57	14.70	14.22	13.91	14.02	14.88	0.72
III	14	1	1	L	54.27	3532.42	17.60	18.04	11.79	12.65	15.48	23.22	0.75
III	14	2	1	A	82.28	5865.22	18.32	12.22	13.54	24.11	18.60	22.29	0.62
III	14	3	1	Q	51.23	4846.15	22.61	15.80	16.81	8.37	21.60	10.38	0.81
III	14	4	1	R	118.10	17046.68	24.14	8.54	15.84	4.75	21.99	4.65	0.79
III	14	5	2	LA	78.44	6454.87	21.46	12.98	13.88	7.97	19.71	8.95	0.65
III	14	6	2	LQ	52.39	3414.01	21.15	15.67	15.69	9.72	19.34	6.40	0.76
III	14	7	2	LR	83.51	9038.17	22.65	10.29	15.68	18.21	14.45	19.02	0.74
III	14	8	2	AQ	64.64	5408.29	21.57	14.94	17.26	12.54	13.51	7.94	0.66
III	14	9	2	AR	113.44	14985.19	21.92	8.99	13.98	17.76	16.16	16.40	0.69
III	14	10	2	QR	83.68	12227.49	21.98	13.02	14.04	13.98	12.52	13.68	0.81
III	14	11	3	LAQ	60.38	5325.79	20.79	15.07	15.19	11.82	25.72	16.10	0.70
III	14	12	3	LAR	86.45	7960.39	22.03	13.42	14.24	17.32	19.23	14.58	0.71
III	14	13	3	LQR	63.75	5137.07	21.58	13.35	14.36	11.05	16.64	12.03	0.79
III	14	14	3	AQR	82.27	8994.58	21.30	12.64	16.55	23.78	27.65	12.27	0.73
III	14	15	4	LAQR	69.34	6215.95	21.95	14.47	14.15	15.49	31.14	12.79	0.73
IV	14	1	1	L	57.43	4571.50	20.44	16.31	14.20	3.05	21.75	7.95	0.73
IV	14	2	1	A	81.00	7327.11	20.96	12.36	15.17	14.74	23.76	10.86	0.55
IV	14	3	1	Q	59.33	4605.85	18.38	16.08	18.12	10.11	19.42	12.23	0.82
IV	14	4	1	R	149.30	28842.22	22.21	10.18	11.89	16.80	21.22	23.66	0.81
IV	14	5	2	LA	69.13	5076.56	20.62	14.79	13.35	7.46	21.33	11.24	0.66
IV	14	6	2	LQ	58.13	4416.74	21.19	17.65	14.39	9.19	17.79	7.33	0.74
IV	14	7	2	LR	76.19	6007.63	21.96	13.39	13.21	7.88	19.19	7.14	0.74
IV	14	8	2	AQ	72.24	6420.20	20.26	14.25	14.63	13.59	19.12	13.07	0.72
IV	14	9	2	AR	69.25	7856.05	20.91	11.24	13.66	18.78	24.23	19.59	0.72
IV	14	10	2	QR	107.85	10644.19	21.00	14.31	13.76	12.77	23.85	10.46	0.79
IV	14	11	3	LAQ	84.64	5673.47	17.53	15.64	12.51	17.67	21.50	32.36	0.81
IV	14	12	3	LAR	68.49	5034.48	19.93	11.35	14.22	11.49	20.60	9.94	0.73
IV	14	13	3	LQR	70.36	5941.01	20.19	13.09	12.83	15.41	22.10	15.22	0.78
IV	14	14	3	AQR	79.75	7377.10	18.60	12.01	14.63	16.13	17.97	14.79	0.78
IV	14	15	4	LAQR	82.82	7237.03	20.88	13.22	13.50	15.38	21.80	17.55	0.37

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
I	28	1	1	L	48.45	2834.19	20.37	17.45	13.36	5.29	4.53	6.96	0.68
I	28	2	1	A	71.53	7233.40	18.73	10.57	16.09	12.65	5.32	4.99	0.59
I	28	3	1	Q	51.93	3501.09	20.35	17.52	15.66	4.54	4.08	4.63	0.78
I	28	4	1	R	126.27	18521.45	23.07	9.38	13.45	11.85	5.43	4.42	0.75
I	28	5	2	LA	54.02	6141.27	18.20	11.79	18.04	4.62	6.29	2.29	0.54
I	28	6	2	LQ	49.40	3892.41	20.87	14.50	16.53	4.91	5.45	3.58	0.69
I	28	7	2	LR	68.20	5005.30	22.18	10.89	16.05	7.37	10.93	7.47	0.70
I	28	8	2	AQ	59.52	5297.04	19.11	13.94	15.31	7.63	6.40	10.31	0.70
I	28	9	2	AR	108.36	15193.79	21.14	10.23	14.18	10.91	8.40	20.73	0.68
I	28	10	2	QR	74.68	7177.51	21.95	11.25	16.09	6.08	7.53	3.10	0.80
I	28	11	3	LAQ	56.71	4148.27	20.18	13.84	15.97	5.53	8.45	5.85	0.67
I	28	12	3	LAR	69.25	9542.49	20.59	12.60	15.98	4.88	2.74	0.00	0.97
I	28	13	3	LQR	59.56	4413.05	21.84	12.58	16.14	3.84	5.18	2.69	0.47
I	28	14	3	AQR	68.20	5975.12	20.05	11.63	13.30	11.93	10.53	10.93	0.76
I	28	15	4	LAQR	51.52	3498.66	19.64	12.50	21.56	4.65	3.38	2.52	0.67
II	28	1	1	L	40.79	2660.28	18.78	14.05	19.90	5.17	5.25	7.84	0.63
II	28	2	1	A	65.24	7589.11	18.13	10.68	14.08	10.33	4.71	4.31	0.52
II	28	3	1	Q	52.52	3248.29	21.41	16.93	15.00	3.34	3.49	3.57	0.77
II	28	4	1	R	149.54	30857.88	21.76	9.97	13.32	7.77	6.16	3.72	0.87
II	28	5	2	LA	49.14	3421.62	16.56	14.36	19.14	4.98	6.86	3.43	0.50
II	28	6	2	LQ	47.35	2925.56	19.69	14.90	17.26	7.16	7.14	3.94	0.56
II	28	7	2	LR	73.35	4334.97	22.54	10.66	13.63	7.37	9.64	8.37	0.64
II	28	8	2	AQ	53.77	3549.54	19.44	13.39	15.91	9.80	7.02	10.28	0.71
II	28	9	2	AR	107.69	13194.32	21.31	10.05	13.10	10.26	8.04	11.59	0.62
II	28	10	2	QR	73.14	6001.95	21.68	12.89	13.30	5.86	9.23	3.70	0.94
II	28	11	3	LAQ	56.14	3865.27	16.84	14.56	20.10	5.87	11.10	6.58	0.71
II	28	12	3	LAR	71.59	8291.36	21.55	11.63	16.86	8.24	7.70	2.44	0.67
II	28	13	3	LQR	66.36	6393.77	21.14	12.80	15.15	6.02	6.67	3.75	0.87
II	28	14	3	AQR	83.62	8959.12	21.35	10.96	15.21	9.66	10.16	5.71	1.09
II	28	15	4	LAQR	59.03	4771.65	19.02	12.17	16.26	6.87	4.52	6.20	0.94
III	28	1	1	L	56.61	3354.83	21.20	15.30	12.80	16.32	9.85	17.41	1.11
III	28	2	1	A	80.40	6911.62	20.86	13.40	14.67	20.76	9.61	10.17	0.92
III	28	3	1	Q	61.44	5132.19	21.14	14.99	18.39	12.72	8.64	11.50	0.95
III	28	4	1	R	131.49	22243.63	22.29	9.94	14.67	21.52	10.99	10.89	0.90
III	28	5	2	LA	61.73	7139.94	20.53	15.97	15.12	10.31	9.44	7.13	0.80
III	28	6	2	LQ	47.21	4767.53	18.83	15.94	19.93	5.61	5.60	4.51	0.71
III	28	7	2	LR	68.47	8741.55	19.17	11.74	20.20	7.41	9.63	7.15	0.78
III	28	8	2	AQ	54.87	5294.28	20.39	15.40	18.98	10.11	6.86	10.93	0.66
III	28	9	2	AR	91.80	10176.90	21.31	11.71	19.43	14.23	7.99	12.58	0.76
III	28	10	2	QR	63.89	7118.72	20.78	14.10	18.01	6.10	8.18	3.69	1.05
III	28	11	3	LAQ	52.75	3681.30	22.52	15.34	19.10	5.08	5.41	2.92	0.65
III	28	12	3	LAR	63.24	5378.26	21.15	15.32	16.43	8.72	7.33	1.27	0.76
III	28	13	3	LQR	66.33	5733.60	21.12	14.60	15.63	9.41	10.24	7.17	0.71
III	28	14	3	AQR	79.53	8802.73	22.05	14.23	15.66	9.11	9.62	4.93	0.75
III	28	15	4	LAQR	60.72	4480.87	21.16	13.79	16.65	10.29	7.47	6.09	0.86

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
IV	28	1	1	L	46.70	2665.46	20.13	17.49	16.97	5.63	5.25	6.62	0.87
IV	28	2	1	A	66.41	4491.70	17.43	10.75	17.29	7.51	4.06	3.40	0.66
IV	28	3	1	Q	57.14	4754.90	22.80	17.34	17.58	8.88	6.49	8.75	0.86
IV	28	4	1	R	122.09	21749.51	21.26	10.07	14.53	13.12	9.08	4.86	0.86
IV	28	5	2	LA	56.14	3797.98	21.28	17.16	19.06	3.09	4.23	0.77	0.80
IV	28	6	2	LQ	45.92	3011.20	21.39	16.87	17.47	5.11	6.52	4.54	0.88
IV	28	7	2	LR	66.69	5942.26	21.83	14.14	17.27	9.00	11.47	9.41	0.77
IV	28	8	2	AQ	66.36	6052.79	18.99	15.07	15.17	9.96	6.36	9.33	0.86
IV	28	9	2	AR	103.77	16018.01	19.98	11.81	14.01	10.15	7.72	10.63	0.80
IV	28	10	2	QR	69.38	6478.18	21.13	13.75	15.95	9.24	11.70	7.03	0.80
IV	28	11	3	LAQ	60.67	6601.97	20.59	15.67	15.45	7.48	8.83	6.12	0.76
IV	28	12	3	LAR	72.22	6333.46	23.08	13.51	15.28	6.48	5.58	0.00	0.76
IV	28	13	3	LQR	63.13	5497.57	21.23	14.78	17.85	6.17	6.91	4.99	0.89
IV	28	14	3	AQR	73.22	7414.36	21.60	13.09	15.51	9.30	8.35	4.59	0.78
IV	28	15	4	LAQR	63.41	5637.00	21.62	14.55	17.21	9.58	6.38	5.77	0.81
I	70	1	1	L	35.87	2108.86	18.04	14.96	25.43	3.56	4.86	4.71	0.42
I	70	2	1	A	51.95	3907.03	19.69	12.49	22.97	8.16	3.21	2.16	0.41
I	70	3	1	Q	43.23	3239.12	21.72	16.14	20.51	1.30	2.22	0.77	0.59
I	70	4	1	R	101.30	14654.18	23.43	9.27	19.41	6.22	5.50	0.95	0.84
I	70	5	2	LA	40.43	2165.15	20.63	15.34	22.52	3.48	5.13	0.80	0.32
I	70	6	2	LQ	41.20	2293.29	17.89	14.91	29.14	2.26	4.80	1.52	0.58
I	70	7	2	LR	71.28	9213.34	23.91	10.78	21.41	3.40	8.14	3.94	0.45
I	70	8	2	AQ	47.83	3114.71	22.37	14.55	24.00	3.27	2.61	3.16	0.31
I	70	9	2	AR	76.18	9285.94	22.26	8.77	19.48	5.67	5.45	4.81	0.46
I	70	10	2	QR	62.75	6367.96	22.61	10.93	20.75	2.47	5.07	0.52	0.61
I	70	11	3	LAQ	43.61	2555.34	19.65	14.64	24.58	2.77	4.19	1.32	0.51
I	70	12	3	LAR	64.32	6515.65	20.17	10.51	23.31	5.42	3.74	0.00	0.56
I	70	13	3	LQR	52.78	4523.38	20.80	12.54	19.48	3.61	4.88	1.84	0.63
I	70	14	3	AQR	62.70	5019.71	22.06	12.14	19.62	3.73	5.96	1.44	0.67
I	70	15	4	LAQR	54.08	4475.30	22.76	13.03	21.58	4.22	3.94	1.68	0.65
II	70	1	1	L	36.22	1755.02	18.10	16.93	28.14	2.06	2.45	4.89	0.30
II	70	2	1	A	45.60	2974.52	20.55	13.57	33.79	2.61	0.04	0.17	0.21
II	70	3	1	Q	44.95	2894.50	24.16	15.38	20.50	1.37	2.10	2.40	0.56
II	70	4	1	R	94.12	13553.27	22.25	9.38	21.40	6.29	6.08	2.21	0.72
II	70	5	2	LA	42.07	2116.21	20.58	12.61	28.70	2.88	3.93	0.86	0.27
II	70	6	2	LQ	42.22	3819.92	21.77	14.71	27.83	1.72	3.36	1.15	0.48
II	70	7	2	LR	66.46	7407.68	20.56	11.66	26.13	2.82	7.01	4.81	0.54
II	70	8	2	AQ	50.65	3477.17	21.68	13.95	23.11	3.57	2.09	3.43	0.44
II	70	9	2	AR	73.16	6983.72	24.15	9.72	20.65	3.89	4.82	3.25	0.45
II	70	10	2	QR	65.55	6228.00	22.49	9.96	21.16	3.75	6.64	2.23	0.53
II	70	11	3	LAQ	44.40	2696.63	24.63	13.80	22.17	2.96	3.60	0.54	0.33
II	70	12	3	LAR	62.79	5834.07	21.42	11.48	23.45	4.78	3.64	0.00	0.35
II	70	13	3	LQR	61.92	4930.11	23.50	10.71	22.34	2.11	4.41	1.59	0.61
II	70	14	3	AQR	72.48	7317.16	24.08	10.80	21.64	4.35	6.33	1.49	0.50
II	70	15	4	LAQR	58.39	5164.62	22.84	11.56	23.42	3.63	3.95	1.80	0.53

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
III	70	1	1	L	40.10	2104.71	18.42	14.40	22.68	4.08	4.11	7.10	0.65
III	70	2	1	A	48.16	3814.16	12.74	10.98	42.93	3.56	0.88	0.26	0.42
III	70	3	1	Q	49.37	3998.74	20.16	13.33	26.69	2.77	2.84	2.29	0.66
III	70	4	1	R	88.22	21026.26	22.11	8.26	24.88	4.81	4.93	0.12	0.89
III	70	5	2	LA	37.91	1681.90	17.61	11.90	29.16	2.46	3.64	0.51	0.28
III	70	6	2	LQ	55.09	4419.97	16.29	12.75	30.94	3.04	4.63	3.01	0.76
III	70	7	2	LR	81.52	7334.37	21.20	10.70	22.06	5.60	10.56	7.09	0.80
III	70	8	2	AQ	56.05	4044.57	20.10	11.26	30.77	4.69	2.45	3.43	0.59
III	70	9	2	AR	90.48	6814.01	10.02	8.31	59.37	2.09	3.67	1.21	0.37
III	70	10	2	QR	63.89	6983.17	11.36	8.38	58.50	2.09	4.00	0.00	0.58
III	70	11	3	LAQ	55.49	3954.06	19.41	13.91	25.93	4.47	5.00	2.25	0.64
III	70	12	3	LAR	74.66	5848.53	19.82	12.54	23.95	4.10	3.77	0.00	0.64
III	70	13	3	LQR	64.28	4578.40	21.33	12.96	21.96	4.50	5.52	3.16	0.80
III	70	14	3	AQR	78.07	11421.96	21.98	11.81	21.39	4.64	6.29	1.72	0.71
III	70	15	4	LAQR	72.47	7047.00	21.63	12.96	19.41	8.29	5.78	4.36	0.71
IV	70	1	1	L	45.92	3226.59	18.54	14.74	19.36	3.21	2.92	4.22	0.64
IV	70	2	1	A	65.09	6978.81	19.97	11.47	22.88	4.55	2.23	1.30	0.46
IV	70	3	1	Q	53.76	4159.73	21.82	14.17	20.94	4.94	4.38	4.42	0.77
IV	70	4	1	R	80.90	8689.98	25.04	7.90	22.30	4.84	5.40	1.18	0.78
IV	70	5	2	LA	38.72	2441.79	14.66	11.69	41.45	1.34	2.52	0.00	0.42
IV	70	6	2	LQ	44.35	2683.40	18.95	13.19	26.89	2.12	3.74	1.70	0.59
IV	70	7	2	LR	68.31	6322.86	21.82	10.03	21.35	4.35	7.95	7.52	0.67
IV	70	8	2	AQ	47.69	3007.45	21.79	11.14	26.77	4.63	2.65	4.19	0.39
IV	70	9	2	AR	83.06	11991.91	22.48	8.45	24.22	5.06	5.28	3.80	0.53
IV	70	10	2	QR	58.19	4679.48	10.40	4.84	10.51	2.86	5.20	0.79	0.49
IV	70	11	3	LAQ	45.54	3741.43	23.45	12.82	23.21	2.22	3.28	0.54	0.29
IV	70	12	3	LAR	68.75	7952.25	21.19	9.27	22.64	4.27	3.37	0.00	0.64
IV	70	13	3	LQR	51.83	4614.80	18.29	8.92	29.59	2.27	3.97	1.53	0.57
IV	70	14	3	AQR	62.50	4926.23	20.55	8.72	26.53	3.49	6.07	1.17	0.69
IV	70	15	4	LAQR	48.37	2963.24	20.88	10.61	24.70	4.12	4.10	2.24	0.22
I	118	1	1	L	46.53	4627.12	7.81	9.19	51.38	1.36	2.14	3.43	0.53
I	118	2	1	A	49.38	4698.68	2.86	8.53	68.52	0.60	0.00	0.00	0.34
I	118	3	1	Q	49.38	2623.88	22.12	12.86	23.22	1.88	2.45	1.19	0.24
I	118	4	1	R	94.31	14541.09	21.32	8.06	19.74	3.35	4.68	0.05	0.75
I	118	5	2	LA	39.72	1669.78	22.36	12.43	25.38	2.52	3.61	0.08	0.14
I	118	6	2	LQ	46.25	2406.74	18.72	11.59	18.26	2.03	2.57	1.38	0.16
I	118	7	2	LR	86.76	12272.48	21.91	7.91	18.57	1.54	5.83	1.91	0.40
I	118	8	2	AQ	47.93	2959.92	22.53	13.08	25.59	3.29	1.24	1.92	0.16
I	118	9	2	AR	89.26	12369.76	22.48	7.66	22.76	2.47	4.35	1.27	0.38
I	118	10	2	QR	66.88	8629.27	22.18	8.36	20.39	2.47	5.06	0.23	0.51
I	118	11	3	LAQ	43.82	3317.83	22.15	13.09	27.85	1.44	2.28	0.00	0.23
I	118	12	3	LAR	71.24	7097.17	20.03	9.51	26.54	2.09	1.73	0.00	0.47
I	118	13	3	LQR	62.94	5386.29	18.66	10.44	20.81	2.47	4.55	2.04	0.66
I	118	14	3	AQR	70.34	6990.31	20.68	10.59	20.64	1.78	5.09	0.22	0.69
I	118	15	4	LAQR	62.77	6899.72	18.71	18.18	26.38	2.51	3.64	1.61	0.55

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
II	118	1	1	L	34.93	2868.05	21.42	17.36	22.43	4.35	3.49	6.79	0.09
II	118	2	1	A	58.48	2523.60	26.84	13.10	26.60	12.15	0.65	0.51	0.11
II	118	3	1	Q	48.50	4346.73	25.85	14.68	20.17	1.86	1.99	0.84	0.19
II	118	4	1	R	92.00	15039.39	20.47	7.57	17.99	4.54	5.41	0.62	0.61
II	118	5	2	LA	44.80	2606.39	21.86	13.33	33.45	1.74	2.69	0.00	0.13
II	118	6	2	LQ	42.32	3173.72	.	.	.	1.27	1.65	3.16	0.47
II	118	7	2	LR	61.29	8413.48	19.08	9.44	18.68	2.91	6.69	3.09	0.70
II	118	8	2	AQ	50.48	4295.60	21.92	11.14	24.94	2.43	1.51	1.56	0.39
II	118	9	2	AR	70.67	10741.85	19.65	8.29	28.31	1.50	3.84	0.33	0.43
II	118	10	2	QR	60.11	5885.89	19.47	9.38	22.73	2.12	4.18	0.00	0.53
II	118	11	3	LAQ	52.58	3049.10	.	.	.	1.17	1.66	0.00	0.02
II	118	12	3	LAR	80.82	9799.38	22.98	8.21	19.13	3.32	3.19	0.00	0.28
II	118	13	3	LQR	67.45	6412.23	23.05	8.38	19.65	1.98	3.79	0.51	0.34
II	118	14	3	AQR	57.47	5934.22	23.63	10.01	19.37	2.08	5.12	0.53	0.42
II	118	15	4	LAQR	78.53	8813.52	23.79	9.31	17.01	3.12	4.60	1.02	0.24
III	118	1	1	L	40.35	2756.92	26.36	14.95	22.84	4.17	2.51	5.84	0.07
III	118	2	1	A	48.21	2426.97	29.35	12.29	25.69	3.90	0.13	0.00	0.11
III	118	3	1	Q	47.91	2762.75	24.53	12.69	22.08	2.13	2.31	1.62	0.21
III	118	4	1	R	77.48	11123.19	20.53	7.07	21.92	3.37	4.73	0.00	0.42
III	118	5	2	LA	47.37	2507.09	27.93	14.12	21.65	1.50	2.33	0.00	0.14
III	118	6	2	LQ	46.02	3132.87	22.58	13.73	18.80	2.53	3.65	1.72	0.30
III	118	7	2	LR	70.46	9691.06	21.12	9.18	20.80	2.28	5.70	3.24	0.59
III	118	8	2	AQ	48.38	7204.24	14.63	11.15	39.78	1.56	0.29	0.76	0.48
III	118	9	2	AR	91.01	12473.36	19.98	7.16	20.44	3.56	4.78	2.64	0.37
III	118	10	2	QR	68.19	8857.38	20.80	8.71	26.61	2.37	4.51	0.00	0.37
III	118	11	3	LAQ	46.28	3307.08	17.75	12.19	24.68	1.49	3.17	0.02	0.56
III	118	12	3	LAR	67.61	6419.50	21.60	10.92	21.52	3.33	2.75	0.00	0.51
III	118	13	3	LQR	51.47	3965.64	18.55	10.21	28.02	1.77	3.51	0.90	0.59
III	118	14	3	AQR	63.51	5369.19	22.25	9.88	23.16	2.35	5.31	0.51	0.62
III	118	15	4	LAQR	71.90	6339.43	21.62	10.85	20.67	4.31	4.43	1.71	0.41
IV	118	1	1	L	43.44	2518.35	19.29	15.18	19.61	3.90	4.52	5.24	0.26
IV	118	2	1	A	52.67	2697.81	26.67	14.83	22.54	4.72	0.38	0.00	0.08
IV	118	3	1	Q	44.50	3241.39	15.24	12.48	30.34	1.98	2.56	0.80	0.37
IV	118	4	1	R	78.95	9992.44	20.74	8.68	19.45	3.41	4.41	0.00	0.63
IV	118	5	2	LA	42.84	2900.92	22.38	13.82	24.29	3.03	3.31	0.08	0.13
IV	118	6	2	LQ	52.49	3437.36	20.62	13.66	20.04	2.73	3.06	2.01	0.25
IV	118	7	2	LR	62.33	6585.58	20.74	9.31	24.01	0.87	4.57	1.15	0.42
IV	118	8	2	AQ	55.93	3179.24	25.36	14.78	22.08	2.79	0.87	1.76	0.14
IV	118	9	2	AR	80.20	9189.07	21.04	9.60	18.35	3.80	4.90	8.60	0.51
IV	118	10	2	QR	69.89	6884.21	20.86	10.03	20.01	4.39	6.34	0.84	0.41
IV	118	11	3	LAQ	45.76	2265.03	14.17	9.16	18.13	2.74	4.06	0.21	0.10
IV	118	12	3	LAR	62.68	4283.78	20.33	10.05	21.82	2.29	1.94	0.00	0.56
IV	118	13	3	LQR	57.69	2107.65	20.65	10.34	21.83	1.85	3.69	0.78	0.99
IV	118	14	3	AQR	75.34	9204.09	19.72	11.21	17.05	7.49	8.23	3.14	0.84
IV	118	15	4	LAQR	60.76	4420.23	19.83	10.94	19.93	3.37	3.95	1.78	0.68

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
I	169	1	1	L	38.73	2871.45	11.85	8.79	38.60	1.55	1.76	5.54	0.08
I	169	2	1	A	43.60	2259.37	10.95	8.36	36.68	3.60	0.63	1.52	0.22
I	169	3	1	Q	46.47	1958.85	16.37	11.09	31.17	1.48	2.84	2.89	0.35
I	169	4	1	R	73.33	5676.53	21.14	5.08	43.73	1.04	3.92	0.02	0.39
I	169	5	2	LA	35.50	1307.65	14.12	9.59	28.37	1.05	3.26	1.07	0.20
I	169	6	2	LQ	43.69	2036.34	15.20	9.95	35.58	1.78	4.49	3.53	0.39
I	169	7	2	LR	73.33	7107.27	16.48	4.81	36.25	0.82	7.25	2.84	0.36
I	169	8	2	AQ	44.85	2797.12	13.80	11.02	57.36	1.51	0.93	1.26	0.05
I	169	9	2	AR	75.21	6293.78	12.32	7.02	40.11	0.64	4.21	1.48	0.05
I	169	10	2	QR	66.36	5294.64	19.24	7.74	36.59	2.28	6.42	1.11	0.71
I	169	11	3	LAQ	39.81	2154.79	12.91	10.19	47.21	0.65	2.65	0.14	0.45
I	169	12	3	LAR	56.85	4481.48	18.57	8.44	48.50	1.12	2.00	0.00	0.55
I	169	13	3	LQR	51.21	3289.74	12.93	7.22	44.43	0.10	3.52	0.94	0.68
I	169	14	3	AQR	55.07	4483.99	6.98	7.14	50.03	0.00	4.09	0.00	0.40
I	169	15	4	LAQR	57.90	2615.80	18.58	9.61	38.70	1.02	3.35	0.30	0.48
II	169	1	1	L	93.49	.	.	.	.	6.90	7.07	12.92	0.01
II	169	2	1	A	54.43	3311.83	26.64	16.58	41.50	2.01	0.41	1.13	0.15
II	169	3	1	Q	43.96	2663.44	10.65	8.08	37.73	0.59	1.58	0.18	0.13
II	169	4	1	R	85.65	9544.26	15.87	7.61	51.98	1.23	3.71	0.00	0.33
II	169	5	2	LA	51.76	3245.00	15.44	11.36	52.66	1.29	1.82	0.00	0.07
II	169	6	2	LQ	38.77	.	23.98	16.86	37.57	3.77	4.23	3.56	0.04
II	169	7	2	LR	70.41	4760.70	21.10	9.61	44.90	1.28	6.16	3.66	0.16
II	169	8	2	AQ	41.35	1797.84	22.28	13.96	34.62	2.19	1.47	1.60	0.20
II	169	9	2	AR	77.11	5429.67	26.24	11.59	44.50	1.81	4.00	1.71	0.07
II	169	10	2	QR	65.08	.	26.00	13.96	48.45	4.91	6.71	1.53	0.05
II	169	11	3	LAQ	44.88	2487.00	20.66	14.30	39.59	1.18	3.17	0.65	0.46
II	169	12	3	LAR	60.44	3909.94	19.90	10.12	43.72	1.85	2.92	0.00	0.13
II	169	13	3	LQR	59.69	4379.34	20.61	9.57	41.81	0.69	3.83	0.78	0.20
II	169	14	3	AQR	49.88	2575.50	.	.	.	1.57	5.04	0.98	0.04
II	169	15	4	LAQR	65.45	4785.64	17.24	8.17	39.98	1.08	3.61	0.64	0.19
III	169	1	1	L	36.83	1389.36	15.05	12.14	27.23	3.78	4.37	8.52	0.29
III	169	2	1	A	41.98	1554.14	19.43	13.30	31.00	3.52	0.71	0.43	0.48
III	169	3	1	Q	38.04	1750.15	16.42	11.01	35.20	0.78	2.48	2.11	0.00
III	169	4	1	R	117.41	14625.47	19.76	5.79	38.09	1.58	5.49	0.76	0.65
III	169	5	2	LA	42.26	2122.20	13.19	10.44	32.21	0.73	2.16	0.00	0.17
III	169	6	2	LQ	40.29	1715.57	16.04	9.99	27.22	1.35	2.99	2.81	0.14
III	169	7	2	LR	74.26	7537.96	20.50	7.56	43.09	0.94	6.36	3.36	0.41
III	169	8	2	AQ	41.02	2137.35	19.96	12.17	38.60	2.77	2.14	3.56	0.14
III	169	9	2	AR	72.15	4722.71	22.86	9.21	45.52	1.59	5.02	2.70	0.24
III	169	10	2	QR	61.76	3187.77	20.06	12.42	44.13	2.37	5.66	2.58	0.15
III	169	11	3	LAQ	42.76	1305.49	22.48	15.60	35.12	1.80	4.00	2.03	0.08
III	169	12	3	LAR	50.36	2061.85	20.14	9.98	42.44	1.68	3.70	0.00	0.14
III	169	13	3	LQR	47.70	2899.22	19.66	10.39	37.70	0.81	4.07	1.68	0.14
III	169	14	3	AQR	62.15	3541.95	29.14	13.99	39.03	0.50	5.06	0.36	0.12
III	169	15	4	LAQR	34.06	.	.	.	.	1.34	3.68	1.86	0.01

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
IV	169	1	1	L	49.18	.	20.04	14.46	37.79	2.68	3.03	7.16	0.05
IV	169	2	1	A	50.98	2533.59	16.40	11.07	24.98	1.65	0.56	0.28	0.11
IV	169	3	1	Q	47.13	2687.94	21.03	12.98	34.29	0.99	2.58	1.86	0.28
IV	169	4	1	R	85.53	8424.70	19.26	4.71	37.25	1.34	4.61	1.03	0.61
IV	169	5	2	LA	50.51	2846.61	.	.	.	1.10	3.47	0.87	0.03
IV	169	6	2	LQ	40.66	1951.97	16.04	11.93	37.77	1.27	2.57	2.12	0.12
IV	169	7	2	LR	82.11	5370.32	18.28	7.21	38.87	1.31	6.80	3.89	0.06
IV	169	8	2	AQ	37.75	1775.89	10.27	10.09	29.30	1.19	0.81	0.98	0.07
IV	169	9	2	AR	37.52	1600.58	9.20	6.98	39.05	0.61	3.67	1.27	0.06
IV	169	10	2	QR	54.46	3520.89	20.14	10.37	45.06	2.25	5.91	0.65	0.13
IV	169	11	3	LAQ	54.88	3104.84	23.11	14.67	42.81	2.21	4.93	1.14	0.08
IV	169	12	3	LAR	48.70	3757.76	.	.	.	2.18	4.14	0.00	0.02
IV	169	13	3	LQR	60.99	3840.12	21.10	9.56	39.66	0.63	4.84	1.61	0.33
IV	169	14	3	AQR	69.28	.	18.04	10.10	35.61	1.26	6.93	1.38	0.00
IV	169	15	4	LAQR	57.75	.	20.77	11.22	32.23	1.83	3.63	1.52	0.00
I	183	1	1	L	52.92	5100.78	6.33	9.34	55.09	1.21	2.33	6.65	0.05
I	183	2	1	A	47.21	2901.34	12.91	11.45	57.98	1.71	0.47	0.00	0.27
I	183	3	1	Q	43.40	2344.59	20.50	12.89	46.24	0.09	2.14	0.85	0.27
I	183	4	1	R	58.90	3715.42	20.45	8.89	45.36	1.15	6.46	0.45	0.44
I	183	5	2	LA	47.24	2892.71	13.00	10.97	62.33	1.90	1.78	0.00	0.14
I	183	6	2	LQ	14.84	1079.04	6.96	5.50	28.89	1.75	0.00	0.00	0.03
I	183	7	2	LR	46.45	1516.45	.	.	.	0.08	2.06	1.04	0.04
I	183	8	2	AQ	42.59	.	23.31	15.16	41.31	1.60	3.22	0.00	0.05
I	183	9	2	AR	88.66	7595.36	24.07	8.38	38.11	2.63	4.85	0.14	0.49
I	183	10	2	QR	48.65	2582.12	19.31	11.89	40.49	1.16	7.39	0.00	0.79
I	183	11	3	LAQ	44.32	2297.05	20.50	13.18	42.99	1.52	1.77	0.47	0.52
I	183	12	3	LAR	62.03	4078.68	22.59	10.57	41.28	3.39	4.33	1.46	0.49
I	183	13	3	LQR	72.16	5974.67	.	.	.	2.40	6.14	3.00	0.02
I	183	14	3	AQR	60.50	5670.27	24.61	9.99	43.80	2.14	5.80	0.23	0.26
I	183	15	4	LAQR	49.59	2308.50	27.91	13.70	42.89	0.40	5.18	0.26	0.11
II	183	1	1	L	42.88	2468.13	9.55	10.94	59.40	0.93	1.43	7.61	0.09
II	183	2	1	A	41.82	3498.03	4.83	8.29	68.82	0.56	0.00	0.00	0.21
II	183	3	1	Q	43.68	2406.25	11.69	9.60	48.86	0.00	1.79	0.08	0.24
II	183	4	1	R	63.80	5951.38	15.32	8.45	58.12	1.00	5.50	0.33	0.55
II	183	5	2	LA	39.10	2175.16	14.90	12.01	47.75	1.60	3.31	0.00	0.42
II	183	6	2	LQ	39.91	2152.62	20.07	13.50	41.83	1.45	1.89	0.00	0.40
II	183	7	2	LR	55.03	5335.51	18.86	11.08	50.19	0.64	4.32	0.00	0.55
II	183	8	2	AQ	48.01	3142.89	21.33	14.44	38.40	2.46	4.44	0.21	0.11
II	183	9	2	AR	110.12	13797.69	24.75	8.41	43.45	1.59	7.05	0.68	0.21
II	183	10	2	QR	60.83	4682.81	21.12	10.22	42.44	1.84	4.63	0.00	0.40
II	183	11	3	LAQ	46.09	2041.99	.	.	.	1.00	2.94	0.16	0.02
II	183	12	3	LAR	85.56	9968.10	19.33	10.20	47.45	2.97	2.62	1.30	0.09
II	183	13	3	LQR	55.99	3506.88	.	.	.	1.54	5.65	1.45	0.04
II	183	14	3	AQR	50.53	2942.71	23.09	12.77	45.73	1.96	4.68	0.56	0.10
II	183	15	4	LAQR	68.18	5768.35	19.45	6.89	41.08	0.50	6.31	0.54	0.11

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
III	183	1	1	L	63.39	3758.39	.	.	.	2.79	9.61	14.72	0.03
III	183	2	1	A	8.78	959.62	3.53	4.26	46.51	0.30	0.00	0.00	0.07
III	183	3	1	Q	51.56	2861.27	13.18	10.41	54.85	0.00	1.58	0.01	0.21
III	183	4	1	R	77.63	7748.47	17.11	7.09	58.37	0.87	4.53	0.01	0.21
III	183	5	2	LA	63.97	3573.26	.	.	.	1.82	1.35	0.00	0.03
III	183	6	2	LQ	48.43	2080.48	25.63	14.41	41.98	4.03	7.90	1.69	0.17
III	183	7	2	LR	32.40	3438.13	6.36	8.03	55.16	0.06	1.62	0.00	0.06
III	183	8	2	AQ	50.83	2363.77	23.40	14.34	44.20	2.36	4.49	0.00	0.12
III	183	9	2	AR	61.66	4683.71	10.77	8.66	69.21	0.40	4.63	0.00	0.29
III	183	10	2	QR	58.10	3945.70	10.27	11.40	59.88	1.42	3.35	0.00	0.69
III	183	11	3	LAQ	42.64	2164.29	.	.	.	0.96	0.81	0.00	0.03
III	183	12	3	LAR	78.05	4184.69	20.32	12.16	48.90	2.59	3.17	0.48	0.05
III	183	13	3	LQR	79.67	.	22.75	12.44	46.17	2.21	6.77	2.19	0.06
III	183	14	3	AQR	60.91	5053.66	23.35	13.13	43.81	1.47	3.95	0.00	0.07
III	183	15	4	LAQR	56.99	3943.06	24.00	10.43	46.00	1.41	8.21	0.73	0.09
IV	183	1	1	L	39.36	1520.41	10.82	8.44	22.99	3.70	16.99	19.11	0.23
IV	183	2	1	A	50.92	3013.62	.	.	34.92	2.06	1.11	0.00	0.54
IV	183	3	1	Q	48.08	2630.36	16.49	14.13	40.65	0.97	3.13	1.72	0.57
IV	183	4	1	R	121.12	15061.86	22.44	8.70	36.34	2.37	7.69	2.65	0.73
IV	183	5	2	LA	72.24	3702.15	22.68	10.39	35.58	4.04	9.19	3.30	0.13
IV	183	6	2	LQ	16.41	1211.28	4.65	5.70	32.01	0.66	0.00	0.00	0.02
IV	183	7	2	LR	64.51	4205.22	19.49	9.56	38.63	1.46	5.81	0.37	0.67
IV	183	8	2	AQ	32.87	2153.27	5.71	8.44	75.73	0.00	2.07	0.00	0.30
IV	183	9	2	AR	93.01	10011.01	23.14	7.96	40.79	3.24	8.03	2.33	0.69
IV	183	10	2	QR	74.49	9250.51	20.75	9.37	36.88	3.64	6.12	1.27	0.84
IV	183	11	3	LAQ	46.34	1939.05	19.02	12.29	41.86	2.81	3.78	2.27	0.10
IV	183	12	3	LAR	54.59	3244.25	23.04	9.79	40.88	1.59	1.79	0.30	0.20
IV	183	13	3	LQR	63.26	4261.58	23.36	9.04	47.71	1.21	6.54	1.53	0.22
IV	183	14	3	AQR	47.13	2719.29	23.32	9.17	46.75	0.56	4.22	1.56	0.14
IV	183	15	4	LAQR	51.01	3419.84	22.68	10.39	41.35	0.43	1.93	0.00	0.22
I	190	1	1	L	39.76	1775.52	21.51	15.66	39.59	4.60	8.76	5.77	0.14
I	190	2	1	A	39.07	1428.88	20.40	11.53	40.95	1.64	0.00	2.36	0.10
I	190	3	1	Q	42.46	2217.12	22.24	12.11	37.10	0.20	1.28	0.00	0.33
I	190	4	1	R	66.04	6635.13	21.37	5.62	44.43	0.56	4.65	0.00	0.43
I	190	5	2	LA	39.51	.	.	.	.	1.27	4.88	1.46	0.00
I	190	6	2	LQ	76.46	6808.17	.	.	.	2.00	1.01	0.00	0.03
I	190	7	2	LR	75.32	8530.55	13.43	7.66	54.02	0.53	4.00	2.99	0.27
I	190	8	2	AQ	63.87	6226.77	9.51	10.16	38.62	0.00	0.73	0.00	0.12
I	190	9	2	AR	82.47	8667.40	8.80	6.16	40.11	0.52	4.30	0.00	0.24
I	190	10	2	QR	83.32	7141.30	13.52	6.95	51.30	0.16	4.71	0.00	0.49
I	190	11	3	LAQ	51.41	3913.81	13.89	11.31	51.73	0.62	1.11	0.00	0.29
I	190	12	3	LAR	75.46	7705.91	15.04	11.14	48.37	2.04	1.50	0.08	0.10
I	190	13	3	LQR	63.53	3746.02	.	.	.	0.49	3.26	0.60	0.02
I	190	14	3	AQR	72.21	5119.19	.	.	.	0.88	3.26	0.00	0.03
I	190	15	4	LAQR	88.24	9542.72	15.72	10.55	45.00	0.46	4.77	0.34	0.05

Appendix A. (cont.)

Block	Time	Trt	Richness	Composition	C:N	C:P	Cellulose	Hemicellulose	Lignin	Condensed Tannins	Hydrolysable Tannins	Total Phenolics	propAFDM
II	190	1	1	L	35.55	1506.29	15.13	11.85	34.77	7.45	22.75	8.76	0.47
II	190	2	1	A	41.85	2190.94	18.12	12.84	32.44	2.02	0.00	5.29	0.19
II	190	3	1	Q	49.03	3244.07	16.60	10.81	32.79	0.43	2.17	0.00	0.35
II	190	4	1	R	77.83	6602.55	14.89	8.60	33.90	0.39	3.79	0.00	0.44
II	190	5	2	LA	90.61	7777.29	2.74	2.76	15.51	0.00	0.58	0.00	0.04
II	190	6	2	LQ	44.17	.	.	.	.	.	.	.	0.00
II	190	7	2	LR	96.65	.	.	.	.	.	.	.	0.00
II	190	8	2	AQ	41.44	2438.01	13.43	10.52	40.78	.	4.86	0.00	0.27
II	190	9	2	AR	60.64	3934.16	18.03	10.51	33.35	.	7.23	0.00	0.17
II	190	10	2	QR	.	.	.	.	.	.	0.00	.	0.00
II	190	11	3	LAQ	42.74	3849.53	17.31	13.52	32.67	0.80	0.86	0.00	0.33
II	190	12	3	LAR	.	.	.	.	.	0.00	0.00	0.00	0.00
II	190	13	3	LQR	39.23	3206.49	10.72	11.66	39.06	0.00	0.00	0.00	0.46
II	190	14	3	AQR	45.65	2440.68	15.41	10.35	30.79	0.00	0.00	0.00	0.63
II	190	15	4	LAQR	47.22	3819.35	1.99	23.12	45.37	0.00	0.00	0.00	0.45
III	190	1	1	L	49.25	4613.71	7.98	9.49	55.65	4.50	4.70	0.00	0.22
III	190	2	1	A	55.59	3402.92	16.62	10.87	42.11	2.84	0.00	0.00	0.43
III	190	3	1	Q	44.59	3496.52	16.92	11.56	27.64	0.17	2.40	0.00	0.47
III	190	4	1	R	96.71	12679.86	15.98	8.20	28.03	1.15	5.43	0.00	0.42
III	190	5	2	LA	49.44	.	14.89	14.13	40.04	0.00	2.54	0.00	0.04
III	190	6	2	LQ	31.46	.	.	.	.	.	.	.	0.00
III	190	7	2	LR	53.20	3104.54	.	.	.	.	.	.	0.03
III	190	8	2	AQ	43.55	2088.25	19.80	14.17	36.69	1.83	4.12	0.00	0.05
III	190	9	2	AR	70.99	8140.26	17.14	10.43	28.94	.	.	.	0.10
III	190	10	2	QR	76.76	7575.33	16.18	9.44	23.17	2.94	5.12	0.99	0.80
III	190	11	3	LAQ	44.62	2591.81	13.10	11.58	31.46	1.59	2.59	0.91	0.62
III	190	12	3	LAR	53.46	4636.19	17.85	10.44	29.96	0.77	1.23	0.08	0.60
III	190	13	3	LQR	54.02	4422.07	16.52	9.85	25.60	0.66	6.11	1.43	0.65
III	190	14	3	AQR	62.36	4042.96	14.40	9.18	29.33	0.61	4.56	1.49	0.61
III	190	15	4	LAQR	47.06	3481.14	12.36	12.95	41.62	0.19	2.38	0.00	0.50
IV	190	1	1	L	44.35	1437.50	.	.	.	15.12	42.18	42.99	0.02
IV	190	2	1	A	43.82	1503.89	18.80	14.28	30.47	8.85	0.00	0.29	0.09
IV	190	3	1	Q	42.72	2001.32	21.41	15.10	27.74	1.33	2.60	0.08	0.14
IV	190	4	1	R	63.17	3925.88	15.89	9.46	28.32	0.61	3.83	0.00	0.33
IV	190	5	2	LA	45.24	1728.34	15.40	12.50	23.01	4.24	4.87	0.00	0.05
IV	190	6	2	LQ	44.91	2325.23	23.56	14.74	23.95	3.10	5.91	1.97	0.19
IV	190	7	2	LR	69.41	4159.90	21.69	10.96	29.01	1.38	6.14	0.97	0.17
IV	190	8	2	AQ	49.40	2895.56	21.05	13.10	29.15	1.10	3.40	0.00	0.23
IV	190	9	2	AR	78.25	6542.67	20.74	9.51	21.33	2.18	6.44	1.22	0.39
IV	190	10	2	QR	67.06	4671.62	17.76	11.67	29.13	4.34	7.71	0.00	0.12
IV	190	11	3	LAQ	45.86	.	.	.	.	2.02	1.47	2.27	0.01
IV	190	12	3	LAR	54.68	3438.35	.	.	.	2.86	1.52	2.20	0.02
IV	190	13	3	LQR	60.58	5341.13	6.19	8.51	56.24	0.00	2.28	0.00	0.18
IV	190	14	3	AQR	37.45	2984.44	5.54	7.17	55.56	0.00	2.06	0.00	0.12
IV	190	15	4	LAQR	81.09	5174.99	8.68	9.06	44.03	0.38	1.59	1.14	0.04

Appendix B. Average abundance (A; no./litterbag), biomass (B; mg/litterbag) of individual taxa and functional feeding groups in single- and mixed-species litterbags in Ball Creek, Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA on harvest days 14, 70, and 118 (January – May 2004). Red maple, *Acer rubrum* (*A*); tulip poplar, *Liriodendron tulipifera* (*L*); chestnut oak, *Quercus prinus* (*Q*); rhododendron, *Rhododendron maximum* (*R*). Coleoptera (C), Collembola (CO), Diptera (D), Ephemeroptera (E), Hemiptera (H), Megaloptera (M), Odonata (O), Plecoptera (P), Trichoptera (T), Non-insect (NI).

			Single- and Mixed-Species Leaf Litter																													
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
C-Filterers																																
Dixa sp.	D	14	2	0.04	1	0.05	0	0.00	1	0.02	2	0.07	0	0.00	0	0.00	0	0.00	1	0.004	1	0.01	1	0.03	1	0.03	0	0.00	1	0.004	1	0.06
		70	1	0.004	1	0.06	0	0.00	0	0.00	0	0.00	0	0.00	2	0.15	2	0.15	5	0.02	0	0.00	1	0.01	0	0.00	2	0.15	0	0.00	1	0.13
		118	4	0.06	0	0.00	0	0.00	1	0.09	0	0.00	0	0.00	0	0.00	0	0.12	0	0.00	1	0.38	0	0.00	4	0.01	3	0.20	2	0.08	3	0.06
Dixella sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.02	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Prosimulium sp.	D	14	1	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	3	0.13	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.02
		70	2	0.003	0	0.00	0	0.00	1	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Simulium sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Ceratopsyche sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0
		70	0	0.00	1	0.35	1	1.91	2	1.40	0	0.03	0	0.00	0	0.00	0	0.00	2	1.74	3	1.30	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	1	0.54	1	0.69	1	0.35	3	1.34	0	0.00	0	0.07	0	0.00	0	0.00	1	1.06	1	0.85	0	0.00	0	0.07	0	0.00	0	0.00
Hydropsyche sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.20	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	1	0.85	1	0.12	0	0.00	0	0.00	0	0.00	0	0.00	1	0.31	0	0.00	0	0.00	0	0.00	1	0.20	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Dolophilodes sp.	T	14	1	0.21	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Wormaladia sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	2	1.32	0	0.04	0	0.00	0	0.00	0	0.00	0	0.00	0	0.17	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Cyrnellus sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.02	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	1	0.47	0	0.09	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total C-Filterers		**14**	**4**	**0.27**	**1**	**0.05**	**0**	**0.00**	**1**	**0.04**	**2**	**0.07**	**0**	**0.00**	**4**	**0.14**	**1**	**0.00**	**2**	**0.01**	**3**	**0.21**	**1**	**0.03**	**1**	**0.03**	**0**	**0.00**	**2**	**0.02**	**2**	**0.08**
		70	**3**	**0.01**	**2**	**0.41**	**4**	**4.08**	**4**	**2.06**	**1**	**0.12**	**0**	**0.00**	**2**	**0.15**	**2**	**0.15**	**9**	**2.24**	**3**	**1.30**	**1**	**0.01**	**0**	**0.00**	**3**	**0.35**	**0**	**0.00**	**1**	**0.13**
		118	**4**	**0.06**	**1**	**0.54**	**1**	**0.69**	**1**	**0.43**	**3**	**1.34**	**0**	**0.00**	**1**	**0.07**	**0**	**0.12**	**0**	**0.00**	**2**	**1.44**	**1**	**0.85**	**4**	**0.01**	**3**	**0.26**	**2**	**0.08**	**3**	**0.06**

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
C-Gatherers																																
Collembola	CO	14	44	6.35	9	1.16	8	0.76	5	0.46	21	2.44	9	1.08	2	0.20	2	0.16	4	0.38	6	0.58	14	1.48	7	0.74	11	1.02	8	0.82	13	1.62
		70	9	1.70	0	0.00	27	4.22	4	0.62	2	0.36	16	2.94	16	3.45	30	5.10	22	3.95	2	0.28	36	5.90	10	1.96	20	3.02	21	3.96	21	4.88
		118	2	0.32	0	0.00	11	0.88	44	4.68	4	0.42	6	0.68	25	2.40	6	0.68	10	1.50	13	1.40	18	2.56	22	3.09	69	8.90	58	8.47	45	6.43
Non Tanypodinae	D	14	2	0.02	0	0.00	1	0.02	1	8.00	5	0.02	4	0.06	4	0.05	3	0.04	1	1.000	2	5.00	1	9.00	1	0.01	1	1.000	2	0.03	5	0.03
		70	72	1.61	28	0.25	30	0.51	22	0.24	56	0.96	156	1.83	58	0.73	32	0.54	73	0.86	16	0.45	97	1.20	10	0.22	45	0.71	44	0.33	18	0.33
		118	49	1.03	5	0.04	50	0.42	6	0.07	15	0.08	74	1.37	32	0.35	80	0.58	45	0.57	12	0.13	65	0.60	34	0.30	24	0.32	46	0.44	82	0.76
Nymphomyia sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	2	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Pericoma sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.03	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	2	0.21	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	5.00	0	0.00	0	0.00	0	0.00
Psychoda	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	4	0.01	0	0.00	0	0.00	0	0.00	0	0.00
Antocha sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	1	0.35	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Ameletus sp.	E	14	0	0.00	1	0.43	0	0.00	0	0.00	2	0.23	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.10	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.37	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Attenella sp.	E	14	3	0.13	0	0.00	1	0.07	1	0.02	4	0.19	2	0.12	4	0.24	0	0.00	2	0.03	4	0.16	1	0.04	1	0.22	1	0.07	2	0.07	3	0.16
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Ephemerella sp.	E	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.42
		70	0	0.00	1	0.09	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.35	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Serratella sp.	E	14	2	0.35	1	0.31	0	0.00	1	0.29	1	0.33	4	1.50	2	0.62	2	0.16	1	0.18	1	0.35	0	0.02	0	0.00	1	0.29	0	0.00	2	0.61
		70	4	0.45	1	0.16	4	0.42	1	0.14	15	3.08	2	0.15	9	1.23	3	0.74	9	0.84	7	1.49	3	0.62	3	0.25	3	0.24	1	0.12	5	1.08
		118	0	0.00	3	0.65	9	0.85	1	0.21	3	2.92	3	0.73	0	0.14	2	2.08	4	2.18	1	0.89	0	0.00	2	1.48	1	0.42	1	0.42	0	0.00
Paraleptophlebia sp	E	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.20	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																													
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Stenonema sp.	E	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.45	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.98	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Choroterpes sp.	E	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Leptophlebia sp.	E	14	0	0.03	0	0.00	0	0.00	0	0.00	0	0.00	2	0.29	1	0.10	0	0.00	1	0.06	0	0.00	0	0.00	0	0.00	1	0.26	0	0.00	0	0.00
		70	1	0.65	1	0.67	1	0.78	2	0.63	1	0.47	2	0.24	1	0.36	1	0.44	16	13.49	1	0.14	3	0.30	1	0.47	1	0.87	0	0.00	1	0.43
		118	9	2.33	6	1.29	10	3.47	1	0.30	2	0.76	8	0.81	1	0.20	9	2.48	4	1.84	1	0.29	0	0.00	2	0.31	1	0.29	0	0.00	5	2.06
Oligochaeta	NI	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	1.77	0	0.00	0	0.00	2	0.24	0	0.00	0	0.00	0	0.00	0	0.00
		118	4	0.02	0	0.00	0	0.00	2	0.13	0	0.00	6	0.11	0	0.00	6	0.41	2	0.05	0	0.00	6	0.15	4	0.29	0	0.00	6	0.15	2	0.02
Amphinemura sp.	P	14	3	0.10	1	0.03	1	0.04	0	0.00	2	0.07	2	0.13	2	0.04	2	0.14	2	0.16	2	0.18	1	0.03	0	0.00	1	0.05	1	0.04	1	0.04
		70	9	0.85	3	0.92	3	0.72	6	1.33	20	1.19	12	1.18	3	0.38	7	0.22	16	1.08	7	0.50	5	0.30	0	0.00	5	0.68	4	0.47	2	0.32
		118	6	0.31	3	0.37	21	1.79	5	0.40	4	0.62	8	0.90	4	0.67	15	2.53	10	1.81	2	0.81	4	0.11	5	0.27	4	0.18	6	0.23	10	2.23
Nemoura sp.	P	14	1	4.000	0	0.00	0	0.00	0	0.00	0	0.00	1	4.00	0	0.00	0	0.12	1	0.01	0	0.06	0	0.00	1	0.18	0	0.00	0	0.00	0	0.00
		70	2	0.09	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Soyedina sp.	P	14	1	3.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.12	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Zapoda sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	1	3.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	0	0.00	1	6.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Beraea sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.01	1	0.01	1	0.003	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total C-Gatherers		**14**	**55**	**14**	**12**	**2**	**13**	**1**	**7**	**9**	**35**	**3**	**24**	**7**	**15**	**1**	**11**	**1**	**10**	**2**	**15**	**6**	**18**	**11**	**11**	**1**	**16**	**3**	**12**	**1**	**25**	**3**
		70	**98**	**8**	**35**	**2**	**65**	**7**	**35**	**3**	**94**	**6**	**190**	**7**	**87**	**7**	**76**	**9**	**136**	**21**	**34**	**3**	**147**	**15**	**24**	**3**	**73**	**6**	**70**	**5**	**46**	**7**
		118	**72**	**4**	**16**	**2**	**101**	**7**	**58**	**6**	**29**	**5**	**105**	**5**	**63**	**4**	**118**	**9**	**76**	**9**	**28**	**4**	**97**	**3**	**71**	**11**	**99**	**10**	**117**	**10**	**145**	**11**

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Predators																																
Acari	NI	14	1	0.03	1	0.04	1	0.04	1	0.06	1	0.05	0	0.00	0	0.00	1	0.03	1	0.04	0	0.00	1	0.04	0	0.00	0	0.00	0	0.00	1	0.05
		70	0	0.00	12	0.59	1	0.04	1	0.05	2	0.10	2	0.10	5	0.25	10	0.51	10	0.51	5	0.25	6	0.29	1	0.06	3	0.14	4	0.20	6	0.28
		118	18	0.90	0	0.00	13	0.63	16	0.80	8	0.40	6	0.30	6	0.31	10	0.48	4	0.20	2	0.11	11	0.54	14	0.70	8	0.40	11	0.53	10	0.48
Helophorus sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.01	0	0.00	2	0.12	1	0.03	0	0.05	0	0.01	0	0.00	0	0.00	0	0.00	2	0.12	2	0.12	2	0.87
Helocombus sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.12	0	0.00	0	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.01	0	0.00
		118	0	0.00	0	0.00	2	0.12	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.03	0	0.00
Hydrobiomorpha sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	1	1.56	0	0.00	1	1.56	0	0.00	0	0.00	1	5.09	0	0.00	0	0.00	0	0.00	1	2.06	0	0.00
Hydrobius sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	1	3.35	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Bledius sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	1	0.07	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.11	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Stenus sp.	C	14	0	0.00	0	0.00	1	0.11	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	0	0.00	0	0.00	1	0.09	0	0.00
Atherix sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.05	0	0.00	0	0.00	0	0.00	0	0.00	2	76.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Atrichopogon sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.08	0	0.00	0	0.00	0	0.00
Palpomyia sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	1	0.17	0	0.00	1	0.17	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	2	0.69	2	1.27	0	0.00	0	0.00	0	0.16	4	1.26	2	0.69	1	0.17	0	0.12	0	0.00	2	0.09	0	0.16	2	0.09	7	0.94	2	0.69

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Tanypodinae	D	14	4	0.07	2	0.03	2	0.02	0	0.00	9	0.15	5	0.06	2	0.02	1	0.02	3	0.09	3	0.06	1	5.00	3	0.03	2	0.04	2	0.03	5	0.10
		70	22	0.47	17	0.37	15	0.26	16	0.37	20	0.31	18	0.34	18	0.29	12	0.30	20	0.39	39	0.68	42	1.12	4	0.07	19	0.33	7	0.15	19	0.46
		118	6	0.12	6	0.79	12	0.54	28	0.64	0	0.00	6	0.65	10	0.20	12	0.60	18	2.05	2	0.04	2	0.04	4	0.02	2	0.04	6	0.50	9	0.48
Chelifera sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.05	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Dicranota sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	3	0.16	1	0.32	0	0.00	0	0.00	0	0.00	4	0.95	0	0.00	2	0.03	0	0.00	0	0.00	2	0.21	0	0.00	0	0.00	3	0.63	0	0.00
		118	1	0.07	0	0.00	0	0.00	0	0.00	2	0.03	2	0.21	2	0.26	1	0.18	2	0.91	0	0.00	0	0.00	4	0.63	1	0.04	1	0.07	3	0.46
Hexatoma sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.04	0	0.07	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	4.17
Limonia sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05
Lipsothrix sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Saldula sp.	H	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	4	0.04	0	0.00	2	0.14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Corydalus sp.	M	14	0	0.00	0	0.00	0	0.00	1	0.10	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Gomphus sp.	O	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.08	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.48	0	0.00	0	4.19	0	0.00	0	0.00	1	3.62	0	0.00	0	0.00	0	0.00	0	0.30	0	0.00	0	0.00
Lanthus sp.	O	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	7.42	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Haploperla sp.	P	14	1	0.02	0	0.00	0	0.00	0	0.00	0	0.01	0	0.00	0	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.01	0	0.00	0	0.00	1	0.02
		70	0	0.03	1	0.48	3	0.19	3	0.08	4	0.17	0	0.00	7	0.67	2	0.09	2	0.09	1	0.03	1	0.10	2	0.02	0	0.00	1	0.03	1	0.20
		118	2	0.01	2	0.01	5	0.37	2	0.01	0	0.00	4	0.23	3	0.15	3	0.29	4	0.23	0	0.00	2	0.01	4	0.10	4	0.10	1	0.20	1	0.15

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Suwallia sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	2	0.05	1	5.00	2	0.02	2	0.03	1	8.00	2	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.26	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Sweltsa sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.07	4	1.54	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Acroneuria sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.41	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Beloneuria sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	1	0.29	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	9.65	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Diura sp.	P	14	1	0.84	1	1.24	0	0.00	1	1.17	2	2.87	3	1.67	1	1.42	1	0.60	2	0.60	1	0.47	1	1.74	0	0.00	0	0.67	1	0.20	2	1.39
		70	1	2.70	3	3.82	6	4.97	2	2.47	8	7.75	0	0.00	1	0.42	2	6.77	8	4.72	3	5.60	2	4.26	0	0.00	5	5.15	2	0.89	1	5.63
		118	0	0.00	0	0.00	2	0.80	1	1.69	0	0.00	0	0.00	0	0.00	1	4.18	2	1.85	0	0.00	0	0.00	1	2.92	0	0.00	0	0.00	0	0.00
Isoperla sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.47	1	0.24	0	0.00	0	0.00	0	0.00	0	0.00	0	0.10	1	0.28	0	0.00
		70	3	0.86	1	0.73	0	0.00	1	0.38	1	0.49	0	0.00	0	0.00	0	0.00	1	1.07	1	0.48	1	1.71	1	0.49	0	0.00	1	0.49	1	0.20
		118	1	0.15	0	0.10	8	5.66	1	0.77	4	5.10	0	0.00	0	0.00	1	0.68	1	1.16	1	0.95	3	2.68	4	1.73	2	1.34	0	0.00	0	0.00
Remenus sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	1	0.62	0	0.00	0	0.00	2	1.20	0	0.00	0	0.00	1	0.10	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Araneae	NI	14	1	0.12	0	0.00	1	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.10	1	0.17	0	0.00	1	0.27	0	0.00	0	0.00	0	0.00	2	0.10	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	3	0.60	0	0.00	0	0.00	0	0.00	1	0.17	1	0.17	1	0.35	1	0.17	2	0.30
Cernotina sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	2.61	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Polycentropus sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	1	0.34	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																													
			L		***A***		***Q***		***R***		***LA***		***LQ***		***LR***		***AQ***		***AR***		***QR***		***LAQ***		***LAR***		***LQR***		***AQR***		***LAQR***	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Rhyacophila sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	5	5.59	0	0.00	2	3.75	1	0.50	0	0.00	0	0.00	0	0.00	0	0.00	2	0.30	1	0.17	2	0.69	0	0.00	0	0.00	1	0.46	0	0.00
		118	2	4.01	0	0.00	0	0.00	0	0.00	0	0.43	1	1.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	4	1.69	0	0.00	0	0.00	0	0.00
Total Predators		**14**	**7**	**1**	**4**	**1**	**5**	**0**	**4**	**1**	**16**	**3**	**9**	**7**	**7**	**2**	**5**	**1**	**7**	**9**	**7**	**1**	**4**	**7**	**4**	**0**	**3**	**1**	**4**	**1**	**9**	**2**
		70	**34**	**10**	**36**	**7**	**27**	**9**	**25**	**4**	**39**	**10**	**32**	**2**	**32**	**2**	**32**	**8**	**44**	**7**	**50**	**7**	**59**	**16**	**8**	**1**	**33**	**84**	**20**	**3**	**28**	**7**
		118	**32**	**7**	**11**	**2**	**42**	**11**	**50**	**6**	**20**	**8**	**26**	**8**	**31**	**4**	**28**	**7**	**35**	**20**	**7**	**6**	**22**	**4**	**37**	**8**	**21**	**3**	**30**	**5**	**31**	**8**
Scrapers																																
Optioservus sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	2	0.20	0	0.00	0	0.00	0	0.00	0	0.00	2	0.06	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Ouliminis sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	1	10.3	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Stenelmis sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.10	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Ectopria sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	2	0.03	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Psephenus sp.	C	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.002	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.002	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Baetis sp.	E	14	0	0.00	0	0.00	0	0.00	0	0.00	1	0.09	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05
		70	1	0.02	1	0.01	0	0.00	2	0.06	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.04	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	4	0.20	4	0.39	0	0.00	0	0.00	2	0.02	2	0.33	2	0.46	0	0.00	0	0.00	0	0.00	0	0.00	2	0.10	0	0.00	2	0.10
Eurylophella sp.	E	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	1	0.16	0	0.00	0	0.00	1	0.16	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.08	1	0.15	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Heptageniidae	E	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.45	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Cinygmula sp.	E	14	1	0.27	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	1	3.34	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Epeorus sp.	E	14	0	0.00	0	0.00	0	0.00	1	0.02	1	0.03	1	0.01	1	0.08	1	0.02	0	0.03	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00	1	0.04
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	2	0.09	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Neophylax sp.	T	14	1	0.21	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	2	1.05	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total Scrapers		**14**	**1**	**0.21**	**0**	**0**	**0**	**0**	**1**	**0.02**	**2**	**0.12**	**1**	**0.01**	**1**	**0.08**	**1**	**0.02**	**0**	**0**	**1**	**0.01**	**0**	**0**	**0**	**0**	**1**	**0.00**	**0**	**0**	**1**	**0.09**
		70	**1**	**0.02**	**1**	**0.17**	**2**	**0.03**	**2**	**0.06**	**3**	**1.21**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0.00**	**2**	**0.04**	**1**	**0.08**	**1**	**0.15**	**1**	**0.10**	**1**	**0.00**	**0**	**0**
		118	**2**	**0.20**	**4**	**0.20**	**6**	**0.48**	**0**	**0**	**0**	**0**	**4**	**0.08**	**2**	**0.33**	**2**	**0.46**	**2**	**0.45**	**0**	**0**	**0**	**0**	**0**	**0**	**2**	**0.10**	**0**	**0**	**2**	**0.10**
Shredders																																
Amphipoda	NI	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	4	0.02	1	0.01	0	0.00	1	0.01	4	0.02	2	0.01	0	0.00	0	0.00	3	0.01	0	0.00	2	0.01	0	0.00	0	0.00	0	0.00	0	0.00
		118	2	0.01	0	0.00	2	0.01	0	0.00	0	0.00	0	0.00	4	0.02	1	0.003	2	0.01	0	0.00	4	0.02	0	0.00	0	0.00	0	0.00	3	0.01
Cambarus bartonii	NI	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	1	7.28	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Molophilus sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.17	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Tipula sp.	D	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.69	0	0.00	0	0.00	0	0.00	0	0.00
Allocapnia sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	1	0.10	1	0.05	0	0.00	0	0.00	0	0.00	1	0.06	0	0.00	0	0.00	0	0.00	1	0.09	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.02	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	1	0.16	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Brocapnia sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	1	0.04	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Nemocapnia sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.12	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Paracapnia sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.16	0	0.08	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Leuctra sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.01
		70	9	0.00	0	1.25	0	0.75	0	0.00	0	0.00	1	0.00	0	0.00	1	0.00	0	0.00	0	0.00	0	0.00	0	4.00	0	0.00	0	0.00	0	0.00
		118	21	1.02	5	0.18	31	1.44	10	0.39	7	0.54	41	2.50	3	0.18	56	4.50	23	1.37	0	0.00	5	0.41	0	0.01	16	0.85	23	1.49	36	1.55
Paraleuctra sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.06	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Zealeuctra sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.37	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Tallaperla sp.	P	14	7	10.34	6	21.3	2	4.63	1	0.04	13	39.3	15	33.9	15	39.7	12	32.57	7	15.46	10	13.7	2	4.25	4	10.3	6	16.95	5	15.9	7	20.9
		70	16	5.75	119	5.50	208	1.50	69	10.5	131	0.75	23	5.50	40	7.25	141	1.75	194	8.75	302	4.50	81	0.50	44	2.25	38	1.50	19	1.00	20	0.00
		118	38	40.71	4	3.00	49	206	25	117	26	189	22	41.7	12	24.2	16	111.5	13	82.29	19	144	13	47.1	13	27.8	14	60.54	5	49.1	10	50.0
Oemopteryx sp.	P	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.21
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Lepidostoma sp.	T	14	1	0.37	5	3.20	3	2.11	1	0.37	1	0.56	1	0.42	1	0.28	1	0.68	0	0.00	1	0.51	2	0.73	1	0.51	2	1.58	2	0.79	1	0.71
		70	3	0.50	1	0.75	1	0.00	0	0.00	1	0.00	4	0.00	1	0.25	1	0.25	0	0.00	0	0.00	2	2.75	1	0.75	0	0.00	1	0.50	1	0.00
		118	4	0.88	11	2.51	13	2.19	5	1.63	12	1.96	3	0.57	1	0.12	19	4.52	12	3.13	4	1.41	0	0.00	0	0.00	4	0.84	4	0.98	10	2.50
Theliopsyche sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.002	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Hydatophylax sp.	T	14	0	0.00	0	0.00	1	0.28	1	0.30	0	0.00	1	0.34	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.19	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Pycnopsyche sp.	T	14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
		70	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	1.15	0	0.00	0	0.00	0	0.00	1	0.25	1	1.63	0	0.00	1	1.87	1	0.47	0	0.00
		118	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	2.28	0	0.00	0	0.00	1	9.34	0	0.00	0	0.00	0	0.00	0	0.00	1	4.66

Appendix B. (cont.)

			Single- and Mixed-Species Leaf Litter																											
			L		*A*		*Q*		*R*		*LA*		*LQ*		*LR*		*AQ*		*AR*		*QR*		*LAQ*		*LAR*		*LQR*		*AQR*		*LAQR*	
Taxa	**Order**	**Day**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Total Shredders		**14**	**9**	**11**	**11**	**24**	**6**	**7**	**2**	**1**	**15**	**40**	**19**	**35**	**17**	**40**	**14**	**33**	**8**	**16**	**12**	**14**	**4**	**5**	**5**	**11**	**10**	**19**	**7**	**17**	**10**	**22**
		70	**32**	**6**	**122**	**15**	**210**	**2**	**70**	**11**	**136**	**1**	**32**	**7**	**42**	**8**	**144**	**2**	**197**	**9**	**304**	**5**	**87**	**5**	**45**	**7**	**40**	**3**	**22**	**2**	**21**	**0**
		118	**65**	**43**	**19**	**6**	**95**	**210**	**40**	**119**	**45**	**192**	**66**	**45**	**21**	**27**	**91**	**121**	**49**	**87**	**24**	**155**	**23**	**48**	**14**	**28**	**34**	**62**	**32**	**52**	**59**	**59**
Total Invertebrates		**14**	**76**	**26.2**	**28**	**27.8**	**23**	**8.1**	**15**	**10.9**	**70**	**46.6**	**52**	**48.7**	**45**	**43.6**	**30**	**35.0**	**26**	**26.1**	**37**	**21.4**	**27**	**22.4**	**21**	**12.2**	**30**	**22.3**	**25**	**18.3**	**47**	**26.4**
		70	**167**	**24.8**	**195**	**24.6**	**308**	**22.3**	**136**	**19.7**	**272**	**18.7**	**254**	**15.8**	**163**	**16.3**	**254**	**19.0**	**387**	**38.7**	**393**	**16.7**	**295**	**35.6**	**77**	**10.7**	**150**	**93.6**	**113**	**10.0**	**95**	**13.9**
		118	**175**	**53.6**	**51**	**11.0**	**245**	**230**	**150**	**131**	**97**	**206**	**201**	**57.4**	**117**	**35.0**	**240**	**137**	**162**	**116**	**61**	**166**	**143**	**56.1**	**126**	**46.8**	**159**	**75.5**	**180**	**66.1**	**239**	**78.0**

Appendix C. Denaturing gradient gel electrophoresis images.

Figure 1. Denaturing gradient gel electrophoresis of bacterial communities colonizing leaf litter incubated for 50 d in Ball Creek, Coweeta Hydrologic Laboratory, Macon Co., North Carolina, USA. Lane labels denote individual species litter from single- and mixed-species treatments [red maple, *Acer rubrum* (*A*); tulip poplar, *Liriodendron tulipifera* (*L*); chestnut oak, *Quercus prinus* (*Q*); rhododendron, *Rhododendron maximum* (*R*)] and controls (- CTL = negative control; + CTL = positive control). For mixed-species treatments, the letter after the hyphen represents the individual litter species. Positive control was a reference bacterial culture of *Pseudomonas aeruginosa* PAO1. Separate bands represent discrete bacterial DNA ribotypes.

Figure 2. Denaturing gradient gel electrophoresis of fungal communities colonizing leaf litter incubated for 50 d in Ball Creek, Coweeta Hydrologic Laboratory, Macon Co., North Carolina, USA. Lane labels denote individual species litter from single- and mixed-species treatments [red maple, *Acer rubrum* (*A*); tulip poplar, *Liriodendron tulipifera* (*L*); chestnut oak, *Quercus prinus* (*Q*); rhododendron, *Rhododendron maximum* (*R*)] and controls (- CTL = negative control; + CTL = positive control). For mixed-species treatments, the letter after the hyphen represents the individual litter species. Positive control was a reference fungal culture of *Cortinarius multiformis*. Separate bands represent discrete bacterial DNA ribotypes.

Figure 1.

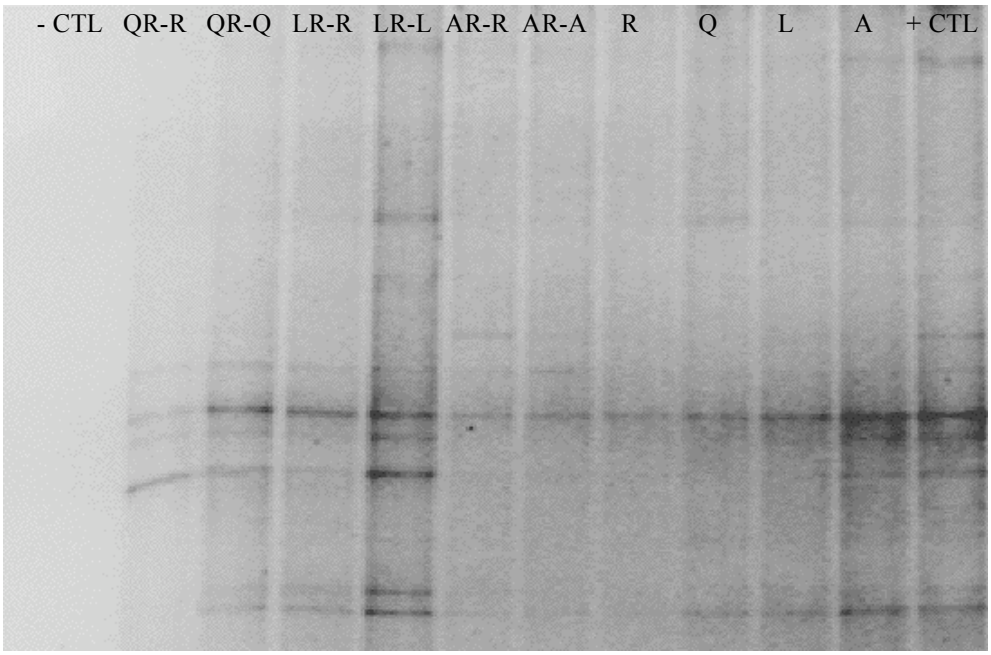

Figure 2.