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Title: Response of stream metabolism to coarse woody debris additions along a catchment disturbance gradient

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Abstract— We evaluated the ecological effectiveness of an in-stream restoration project involving coarse woody debris (CWD) additions to streams along an upland soil and vegetation disturbance gradient at the Fort Benning Military Installation near Columbus, GA. We examined short-term (immediate effectiveness) and longer-term (sustainability) responses to CWD additions by measuring ecosystem metabolism rates in 8 streams quarterly over a 6-year period; including 3 years before (2001-2003) and 3 years after (2004-2006) CWD additions were made to half of the streams. Ecosystem respiration (ER) rates in most CWD-addition streams increased relative to control streams from spring 2004 through autumn 2005, suggesting heterotrophic bacteria were the initial responders to CWD additions. Gross primary production (GPP) rates remained low (typically < 0.3 g O_2 m^{-2} d^{-1}) but increased in some CWD-addition streams relative to control streams in spring 2004 and 2005. The magnitude of ER increases in CWD-addition streams during the first two years post-addition increased with catchment disturbance intensity, indicating that more heavily disturbed streams responded most strongly to restorations—an important consideration when targeting future restoration locations. Because restorations did not address actual upland disturbance, continued high erosion rates resulted in 32 – 77% of the added CWD being buried by year two and a corresponding return of GPP and ER rates to pre-CWD addition levels by year three. If restoration projects do not adequately address the source of catchment disturbances, CWD additions will provide only short-term increases in streambed structure and stability, hydrodynamic complexity, and nutrient and organic matter processing and retention.

Keywords: catchment disturbance, stream restoration, ecosystem respiration, primary production, course woody debris, seasonal patterns, inter-annual variability, nutrient uptake, organic matter, hydrodynamics

Introduction

Stream ecosystems are strongly influenced by inputs of water, sediment, nutrients, and organic material from their surrounding catchments (Hynes 1975). Changes in catchment land use affect the rate at which these important constituents are delivered to streams as well as the quality of in-stream habitats (e.g., abundance of course woody debris) and biological community composition (Omernik 1976, Richards and others 1996, Huryn and others 2002, Allan 2004). For example, deforestation can affect the amount and timing of the delivery of water (Webster and others 1990), sediment (Gurtz and others 1980), and nutrients (Likens and others 1970, Aust and Blinn 2004) to streams. Catchment land-use changes have been pervasive with only ~2% of the 5.3 million km of rivers in the conterminous United States remaining relatively unimpacted by human activities (Abell 2000, Palmer and others 2007). The riparian zone can play an important role in mitigating some of the impacts of land use on stream ecosystems and disturbances to these areas can have particularly large deleterious effects on streams (e.g., Lowrance and others 1984, Gregory and others 1991, Richards and others 1996, Aust and Blinn 2004). However, much less is known about how localized, intense disturbances of upland areas affect streams with intact riparian zones.

The natural input of coarse woody debris (CWD) from the surrounding catchment influences stream ecosystems in a variety of ways (Harmon and others 1986). CWD dams can shape channel morphology (by altering water velocity and streambed erosion patterns, and dissipating energy), increase hydrological heterogeneity (by creating backwaters and eddies), facilitate the deposition and retention of organic matter (Naiman and Sedell 1979, Bilby and Likens 1980, Smock and others 1989), and provide habitat surfaces for biofilm algae and microbes and larger organisms (Gregory and others 2003). Nutrient uptake rates (retention) tend to be higher in association with CWD than other stream habitats (Munn and Meyer 1990, Hoellein and others 2009) and increase after experimental wood additions (Wallace and others 1995, Roberts and others 2007b) but not in all cases (e.g. Hoellein and others 2012). The effects of CWD removal on nutrient uptake rates are less straightforward, with studies finding decreased (Ensign and Doyle 2005) or increased nutrient uptake (Warren and others 2013) with CWD removal. High erosion rates associated with upland disturbances lead to high sediment loads being transported downstream and increased flashiness of catchment streams (Lake and others 2007). These two factors often result in decreases in CWD abundances in streams (Maloney and others 2005) which, in turn, can lead to decreases in ecosystem metabolism (Houser and others 2005) and nutrient uptake (Roberts and others 2007b) rates.

Stream restoration projects have the potential to mitigate some of the negative impacts of catchment-scale disturbances on stream ecosystem processes. Despite billions of dollars currently being spent on over 37,000 stream and river restoration projects in the United States alone, the effectiveness of most projects is difficult to assess since adequate post-restoration monitoring is often lacking (Bernhardt and others 2005). In order for restoration projects to be ecologically successful, they must attempt to restore function as well as structure to streams (Lake and others 2007, Craig and others 2008, Palmer 2009, Palmer and others 2014). Within the last decade, a number of studies have examined the effectiveness of restoration efforts at enhancing nitrogen (N) removal in the stream channel and adjacent floodplains (e.g., Bukaveckas 2007, Roberts and others 2007b, Kaushal and others 2008, Sudduth and others 2011, Roley and others 2012, Arango and others 2015, Johnson and others 2016). However, studies that quantitatively monitor stream processes both pre- and post-restoration are rare (e.g., Colangelo 2007, Roberts and others 2007b, Entrekin and others 2009, Roley and others 2012). It is clearly important to assess the effectiveness of restoration projects immediately after the restoration has been completed, but it is perhaps even more important (and less common) to assess the ecological effectiveness beyond the immediate post-restoration period because only then can it be known if restorations are sustainable.

Ecosystem metabolism constitutes the processes (gross primary production [GPP] and ecosystem respiration [ER]) controlling nutrient cycling and organic matter processing in stream ecosystems. Changes in ecosystem metabolism rates are an integrated response to catchment disturbance and land use and have therefore been advocated as useful measures of stream health (Bunn and others 1999, Fellows and others 2006, Young and others 2008). For instance, the ecosystem metabolism method has recently been used to examine rates of GPP and ER in agricultural (Griffiths and others 2013, Roley and others 2014) and urban (Sudduth and others 2011, Beaulieu and others 2013, Reisinger and others 2017) streams. Ecosystem metabolism has also been used to assess restoration effects in streams (Sudduth and others 2011, Hoellein and others 2012, Roley and others 2014, Kupilas and others 2017), but these studies are much less common than those evaluating nutrient uptake responses to restoration. Because ecosystem metabolism constitutes an integrative measure of nutrient and organic matter processing in streams, it represents an optimal assessment tool of the ecological effectiveness of restoration efforts. However, GPP and ER are temporally dynamic processes (Bernhardt and others 2018) and therefore seasonality in stream metabolism should also be captured in ecological assessments of restoration.

In this study, we evaluated the ecological effectiveness of an in-stream restoration project involving CWD additions to several streams along a well-studied (Houser and others 2005, Maloney and others 2005, Houser and others 2006, Roberts and others 2007b) upland disturbance gradient at the Fort Benning Military Installation (FBMI) near Columbus, GA. We measured ecosystem metabolism rates in 8 streams at FBMI seasonally over a 6-year period, including 3 years before (2001-2003) and 3 years after (2004-2006) CWD additions were made to half of the streams. This design allowed us to examine both the short-term (immediate effectiveness) responses that are occasionally assessed and the longer-term (sustainability) responses that are very rarely assessed in restoration projects. Several studies have shown that stream metabolism is strongly related to streambed stability, particularly in sand-bed streams (Grimm and Fisher 1984, Uehlinger and others 2002, Atkinson and others 2008). Therefore, we hypothesized that the increased streambed stability from CWD additions and the CWD additions themselves would provide stable substrates for the development of algal biofilms, resulting in increased rates of GPP. We also hypothesized that the organic matter trapping ability resulting from CWD additions would increase rates of ER in these streams. Finally, we hypothesized that streams with greater catchment disturbance intensity would benefit more from CWD additions and therefore exhibit stronger responses in ER and GPP following manipulation.

Methods

Study site

Fort Benning Military Installation provides a unique opportunity to evaluate the effectiveness of in-stream restorations (CWD additions) on stream ecosystems impacted by upland disturbance because of the broad range of disturbance intensities found within a small, relatively homogenous region (e.g., numerous stream reaches of comparable morphology, shading, and discharge). We studied eight 1^{st}- to 2^{nd}-order, typical low-gradient (range = 0.8–5.1%, mean = 2.1%; Maloney and others 2005), sandy Southeastern Hills and Plains streams

(Felley 1992) on the FBMI (Fig. 1, 2a). The study streams had generally intact deciduous riparian canopies (mean summer canopy cover = 94%; Maloney and others 2005) dominated by blackgum (*Nyssa sylvatica*) and other mesic species. The streams drained catchments ranging in size from 33 to 369 ha (Fig. 1, Table 1; Roberts and others 2007b).

The geology and land-use history of the study catchments are detailed in Maloney and others (2005). The forest has been allowed to regrow in many areas of FBMI since it was purchased by the US military in 1918 and 1941/1942 (Kane and Keeton 1998), and land cover in these areas now consists primarily of oak-pine and southern mixed forest compared to row-crop agriculture and pasture which dominated land-use prior to its purchase. The underlying soils are sand, sandy clay loam, or loamy sands (Omernik 1987). Some areas of the FBMI are used for military training involving infantry and heavy-equipment vehicles resulting in some catchments having localized areas with high levels of vegetation and soil disturbance leading to high erosion rates and streams with unstable, organic-poor sediments (Maloney and others 2005). Other catchments have remained essentially undisturbed since their purchase by the military.

Leaf emergence at FBMI usually occurs in late March and leaf abscission is often in early November resulting in the study streams (all with generally intact riparian forests) being strongly shaded throughout the April – October period. Since the riparian forests in the study catchments are almost entirely deciduous, light penetration to the stream surface is significantly higher during winter and early spring. The specific stream reaches studied were chosen to minimize variability in morphology, shading, and discharge among streams along the disturbance intensity gradient. Study reaches were chosen to have minimal lateral inflow with the mean ($\pm$ SE) increase in discharge between the upper and lower sampling stations across all study streams for the 2004-2006 period being 4.2 $\pm$ 0.2% (n = 96) and individual streams ranging between 3.0

(BC1) and 6.2% (LPK). Streamwater nutrient concentrations (dissolved inorganic nitrogen [DIN] and soluble reactive phosphorus [SRP]) were low (20-60 μg N/L and 2-5 μg P/L, respectively) and did not differ between the before and after restoration periods in any stream (Mulholland and Roberts, unpublished data).

Disturbance intensity

Disturbance intensity for each catchment was defined as the % of catchment area covered by unpaved roads or bare ground on slopes >5% as determined by Maloney and others (2005). Unpaved roads are mostly used by tracked military vehicles, and much of the bare ground was created by military training using these tracked vehicles. The areas of soil and vegetation disturbance are generally located in upland areas away from the perennial streams, but these areas become hydrologically connected to perennial streams via ephemeral drainages that discharge to the perennial stream during storms.

The 8 streams included in this study were in catchments that spanned most of this available range (~3.2 – 13.7%; Table 1) in disturbance intensity of the 249 second-order catchments on the FBMI (0 – 17%; excluding the 4 most disturbed catchments). Low vegetative cover in highly disturbed catchments has increased stream flashiness and sediment load and decreased streambank stability, leading to increased burial and export of CWD (Maloney and others 2005). The combined effects of increased burial and export of CWD were that the relative abundance of submerged CWD decreased significantly with increased disturbance in our study streams (linear regression: $r^2 = 0.91$, $p < 0.0001$, excluding BC1, a catchment with a notably broader, flatter forested floodplain that appeared to protect the stream from the effects of upland disturbance and had received some restoration of upland areas prior to the current studies so was not included in regression analyses; Houser and others 2005, Maloney and others 2005). The percent areal coverage of CWD was estimated from measurements of submerged and buried (to 10 cm depth) CWD (> 2.5 cm in diameter) at 15 one-meter-long transects per stream (Maloney and others 2005, Mitchell 2009). CWD coverage in the study streams ranged from ~3.1 to ~8.9% (except in BC1 where % areal coverage ≈ 12.6%; Table 1) before the CWD additions (Roberts and others 2007b).

CWD and stream restorations

CWD was added to streams in 4 of the 8 study catchments (KM1, SB2, SB3, and LPK) that spanned a range of disturbance intensities (~4.6 – 11.3%; Table 1). Riparian trees used for CWD additions (*N. sylvatica* in KM1, SB2, and SB3 and *Quercus alba* in LPK) were felled and sectioned during August 2003 and allowed to dry for 2 to 3 months before deployment. Very few riparian trees were felled per stream and these trees were not located adjacent to study reaches in any stream, thus minimal effects on light availability were expected. On October 25-27, 2003, ten CWD additions (~10 m apart) were made over a 100-m reach in each of the 4 streams. Individual CWD additions consisted of 3 logs (~10 – 20 cm diameter, 1 – 2 m long) anchored in the streambed with rebar stakes (Fig. 2b, c). CWD additions were not intended to create pool environments so logs did not span the entire width of the stream and were positioned in a zigzag arrangement (Fig. 2b, c). CWD additions increased the % areal coverage of CWD by ~3.1% (LPK) to ~5.2% (SB3) and resulted in coverage of ~6.9% (LPK) to ~12.1% (KM1) of the streambed surface area in the restored streams (Table 1). High sedimentation in the two most disturbed streams receiving CWD additions (SB3 and LPK) resulted in significant burial of the CWD added to these streams by the end of the first year after manipulation, so additional CWD

(*N. sylvatica* in SB3 and *Q. alba* and *Carya* sp. in LPK) was added to these streams on November 9, 2004. This resulted in CWD additions every 5 m (instead of 10 m) in the study reach of these two streams.

<u>Ecosystem metabolism rates</u>

Daily whole-stream rates of gross primary production (GPP) and ecosystem respiration (ER) were determined using an open-system, single-station diel dissolved O_2 change approach (Odum 1956, Houser and others 2005, Roberts and others 2007a). Measurements of dissolved oxygen (DO) and water temperature were made at 15-min intervals using YSI model 6000 or 600 series sondes equipped with model 6562 DO probes that were placed in a laterally constrained section of each stream. The sondes were calibrated in water-saturated air before and immediately after deployment. The calibration DO data were corrected for barometric pressure recorded during calibration and consecutive calibrations were used to detect instrument drift during deployment.

Sondes were deployed for approximately 3 weeks in 4 streams (2 control and 2 receiving CWD additions) and then moved to the other 4 streams immediately thereafter because of equipment limitations. However, only DO data collected during similar flow conditions to the deployment date were used to minimize the effect of changing flow on metabolism rates (Houser and others 2005). Winter deployments were during January and February; spring deployments were during March and April; summer deployments were in June, July, and August; and autumn deployments were during October and November. This study includes a total of 6 years of seasonal ecosystem metabolism data (3 years before [Houser and others 2005] and 3 years after CWD additions took place).

Volumetric ecosystem metabolism rates (g O_2 m^{-3}) were determined from the rate of change in DO concentration using the equation $\Delta DO = GPP - ER + E$, where ΔDO is the change in DO concentration, GPP is gross primary production (g O_2 m^{-3}), ER is ecosystem respiration, and E is net exchange of O_2 with the atmosphere between consecutive measurements. E is the product of the O_2 reaeration coefficient (k_{O2}) and the average DO deficit (DO concentration at 100% saturation minus the DO concentration in stream water) over the measurement interval. Reaeration coefficients, discharge, and velocity were determined for each stream using simultaneous, continuous injections for propane gas (volatile tracer) and a concentrated NaCl solution (conservative tracer) prior to each deployment following the methods detailed in Houser and others (2005) and Roberts and others (2007a).

The net metabolism flux for a given measurement interval is equal to $\Delta DO - E$. During the night, GPP is zero, so the net metabolism flux is equal to ER. Daytime ER was determined by interpolating ER averaged over the hour before dawn and the first hour after dusk (Houser and others 2005, Roberts and others 2007a). GPP for each daytime interval was the difference between the net metabolism flux and interpolated ER (see Fig. 3 in Roberts and others 2007a for details). Daily volumetric GPP and ER rates (g O_2 m^{-3} d^{-1}) were calculated as the sum of the 15-min rates over each 24 hour period. Volumetric rates were converted to areal units (g O_2 m^{-2} d^{-1}) by multiplying by the mean water depth. Water depth was calculated from stream width (average of wetted-width measurements taken every 5 m along the reach), discharge, and velocity (both from the NaCl injections) of each stream (Houser and others 2005, Roberts and others 2007a).

Statistical analysis

We quantified the effects of CWD additions on whole-stream GPP and ER rates using a modified before–after control–intervention (BACI; Green 1979) approach. Both control and intervention [CWD addition] locations were replicated (Underwood 1994) in four locations for a total of 8 study streams. During the pre-manipulation period (2001-2003), FBMI streams exhibited strong seasonal differences in stream metabolism and physical parameters yet no significant interannual variation (Houser and others 2005), we therefore averaged all pre-manipulation measurements within each stream to ensure robust estimates and evaluated the effects of CWD additions on a seasonal basis. After:before [A:B] ratios (e.g., ER in winter 2004 divided by mean ER in winters 2001 – 2003 for a given stream) were calculated in each of four seasons (winter, spring, summer, and autumn) in each stream and in each post-treatment year (2004, 2005, 2006). This approach allowed us to examine both the effectiveness of CWD additions as well as the duration over which any effects persisted. Similarly, we calculated A:B ratios for physical variables (i.e., discharge, temperature, and reaeration coefficient) for each stream in each season and post-restoration year. Since ratio data were not normally distributed, all ratios were square root-transformed. The effects of CWD addition on A:B ratios of physical variables and metabolism rates were evaluated in each season using two-way ANOVAs with Holm-Sidak corrections for all pairwise comparisons with treatment (i.e., comparing the transformed A:B ratios of the 4 control streams to the transformed A:B ratios of the 4 CWD addition streams) and post-treatment year as factors.

We also quantified changes in GPP and ER rates over time in each stream in each season by comparing seasonal mean rates before manipulation (2001 – 2003) with seasonal mean rates after manipulation (2004, 2005, and 2006). Since metabolism data were not all normally distributed, changes over time were evaluated using one-way ANOVAs on ranks (Kruskal-

Wallis test) with Dunn's method used for evaluating pairwise comparisons among years. To examine the effect of watershed disturbance on ER and GPP in CWD addition streams, the ER and GPP A:B ratios for all manipulated streams were regressed against % watershed disturbance intensity in each post-treatment year.

All statistical analyses were conducted using either SigmaPlot (version 14.0) or SigmaStat (version 4.0) (Systat Software Inc., Point Richmond, California). Significance was defined as α=0.05, and marginal significance was defined as α=0.10.

Between the autumn 2005 and winter 2006 sampling periods, the least disturbed control stream (BC2) received a drastic disturbance in the form of the construction of a road that crossed the stream ~200 m upstream of the study reach, resulting in a large increase in sediment loading to the reach (Mulholland and others 2009). As a result of this disturbance, data from BC2 were included in all figures but excluded from all analyses in the third year after manipulation (2006).

Results

<u>Physical variables</u>

Most physical variables were similar before and after the CWD additions within each stream. The range of wetted widths (0.90 – 2.07 m) and mean depths (0.04 – 0.15 m) across streams was relatively narrow (Table 1). Discharge rates over the 6 year study period were generally higher in winter and spring (15.2 and 17.4 L/s) than in summer and autumn (8.7 and 9.4 L/s; Table S1). Seasonal differences in discharge were primarily a result of seasonal differences in evapotranspiration rates since rainfall was distributed relatively evenly among seasons. After:before ratios of discharge (Fig. S1, Table S2) varied by year in spring (A:B ratios of discharge were higher in 2005 and 2006 than in 2004) and summer (A:B ratio was higher in

2005 than in 2004 or 2006), but did not differ by treatment (control versus manipulated streams) during any season (Table S2).

Water temperatures were warmer during summer (22.7 $\pm$ 0.2 °C) than in winter (11.2 $\pm$ 0.5 °C) with spring and autumn temperatures being intermediate (Table S1). Similar to discharge, A:B ratios of water temperature (Fig. S2, Table S3) varied by year in spring (A:B ratio of temperature was highest in 2006, intermediate in 2005, and lowest in 2004). There was a significant interaction of treatment and year in summer (Table S3), with the A:B ratio of temperature higher in manipulated streams than control streams in 2004 (Fig. S2). The A:B ratio of water temperature did not differ by treatment (control versus manipulated streams) during any other season (Table S3).

O_2 reaeration coefficient (k_{O2}) did not show any discernible temporal patterns for either the control or manipulated streams in any season (Table S4). Seasonal A:B ratios of k_{O2} (Fig. S3) did not vary by treatment or year (Table S5). Taken together, these findings indicate that these physical variables did not appreciably change in response to the CWD additions.

Stream ecosystem metabolism rates

Daily rates of ecosystem respiration (ER) exhibited a wide range of values (~ 1.0 – 11.5 g O_2 m^{-2} d^{-1}) throughout the study (Fig. S4). All streams were highly net heterotrophic (daily ER rates exceeded daily GPP rates) in all seasons both before and after CWD additions. There was a significant effect of CWD additions on A:B respiration ratios in 3 of 4 seasons that varied by year (Table S6). Differences in A:B respiration ratios between control and CWD addition streams were significant in all seasons of 2004 and 2005 except winter 2004 (Fig. 3) which was the first season after CWD was added to the manipulated streams. In 2006, there were no significant differences in the A:B ratio for ER between control and manipulated streams (Fig. 3). During the first two years after CWD was added, ER rates generally increased in manipulated streams during all seasons (Fig. S4). However, there was considerable among-stream variation in responses and the number of streams in which ER increased varied by season (Table S7) and year. In 2004, the effect of restoration on increasing ER was observed in two manipulated streams in spring, with non-significant trends observed in several streams in other seasons (Fig. S4). In contrast, ER did not increase significantly in any control stream in any season in 2004. The change in ER in CWD addition streams was more consistent in 2005, with 2 (summer), 3 (winter and spring), or all 4 manipulated streams (autumn) exhibiting higher ER rates than in the pre-treatment period for those seasons (Fig. S4). Overall, the largest increases in ER were observed in the two streams with the most highly disturbed catchments (SB3 and LPK with 10.49 and 11.26% of catchment disturbed, respectively) (Fig. S4).

Daily gross primary production (GPP) rates were low throughout the entire study in all streams with values typically < 0.3 g O_2 m^{-2} d^{-1} except for during late winter-early spring in some years in a few less-disturbed streams receiving CWD additions (Fig. S5). Overall, the addition of CWD to FBMI streams resulted in some significant treatment effects on GPP after:before manipulation ratios, with higher A:B ratios in manipulated than control streams in winter ($p < 0.01$), spring ($p < 0.1$), and autumn ($p < 0.1$) (Table S8). However, this effect also varied by time since restoration. In 2004, there were no significant differences in the A:B ratio for GPP between control and manipulated streams in any season. In 2005, A:B manipulation ratios of GPP rates in streams receiving CWD additions were significantly higher than in control streams in winter and spring (Fig. 4; $p < 0.05$). Although mean A:B ratios always appeared higher in manipulated than in control streams after spring 2005, differences were only marginally significant in winter 2006

($p < 0.1$; Fig. 4). GPP rates in all four control streams were significantly influenced by year in at least one season, but no control stream exhibited a significantly higher rate in the post-treatment than in the pre-treatment period during any season (Fig. S5, Table S9). GPP rates were significantly influenced by year in all four manipulated streams in at least one season (Fig. S5, Table S9). However, the only large stimulation in GPP resulting from CWD additions occurred in the least disturbed stream (KM1) and only in spring 2004 and 2005 with only the 2005 increase being significant (Fig. S5). A significant increase in GPP in stream SB3 was observed in spring 2005, but the magnitude of this increase was small (0.06 v. 0.02 g O_2 m^{-2} d^{-1}) (Fig. S5).

Pre-manipulation disturbance intensity had a significant effect on the magnitude of the response to CWD additions with ecosystem respiration A:B ratio being predicted by prior disturbance intensity in the first two years after restoration (Fig. 5a). The high variability in this relationship results from both stronger responses being observed during the second year after CWD addition (2005; slope = 0.24, $r^2 = 0.36$, $p = 0.01$) than in the first year (2004; slope = 0.12, $r^2 = 0.19$, $p = 0.09$) and seasonal variability (each point per year in Fig. 5a represents the mean in a given season) in the strength of the response to CWD addition. The relationship was not significant in 2006 ($r^2 = 0.09$, $p = 0.26$) (Fig. 5a). In contrast, the magnitude of response in GPP A:B ratios to CWD additions was not predicted by pre-manipulation disturbance intensity in any of the 3 years after restoration (Fig. 5b; $r^2 < 0.15$, $p > 0.15$ in all years).

Discussion

FBMI streams have some of the lowest published GPP rates in the literature (Houser and others 2005) and remained low throughout the post-restoration period regardless of whether the stream received CWD additions or not. FBMI streams exhibit a broader range and showed stronger responses in ER rates with A:B ratios peaking during the second year after CWD addition. Since the study was designed to examine both the short-term (immediate effectiveness) responses that have occasionally been assessed and the longer-term (sustainability) responses that have rarely been assessed in restoration projects, we have organized the discussion by year since CWD addition to better examine how the integrated response of ecosystem metabolism (both GPP and ER) changed with time since manipulation.

First year post-CWD addition

In the first year after the CWD addition, there were modest increases in ER and smaller responses in GPP. The net result of the CWD additions was to make these streams even more strongly net heterotrophic throughout the first year after manipulation. These results are counter to our original hypothesis but consistent with results from the pre-CWD addition period showing that GPP did not consistently vary with CWD abundance but ER was higher in streams with higher CWD abundance (Houser and others 2005).

CWD is important in shaping channel morphology (e.g., increasing streambank and streambed stability), decreasing water velocity, and increasing hydrological (e.g., spatial variation in water velocity) and habitat heterogeneity (Bilby 1981, Trotter 1990, Bilby and Bison 1998). The addition of CWD to FBMI streams quickly (within 1 month) resulted in increased hydrodynamic complexity, including decreased average water velocity and increased importance of transient storage (Roberts and others 2007b). Results from other recent studies also suggest that stream restorations have the potential to positively affect hydrologic residence time (Kasahara and Hill 2006, Bukaveckas 2007, Becker and others 2013, Kupilas and others 2017). The net result of these hydrodynamic changes is that increasing the abundance of CWD increases the potential contact time of sediment-associated biota with dissolved constituents during transit through the stream, thus increasing nutrient uptake (Roberts and others 2007b) and retention and processing of organic matter (this study).

Consistent with the above predictions, we have previously demonstrated that both NH_4^+ uptake (Roberts and others 2007b) and ER (Houser and others 2005) rates decreased (while GPP remained low) as catchment disturbance intensity increased (and CWD abundance decreased) in FBMI streams. Similarly, organic matter availability, both in terms of benthic organic matter (BOM: Maloney and others 2005) and dissolved organic carbon (DOC: Houser and others 2006), decreased with increased catchment disturbance (and decreased CWD). When CWD was added to these streams, organic matter retention (see contrast between 1 month after CWD addition in Fig. 2c and immediately before and after CWD addition in Figs. 2a and 2b) and NH_4^+ uptake rates increased (Roberts and others 2007b). Throughout the first year after CWD was added to FBMI streams, ER rates increased but GPP remained relatively unchanged. Taken together, these results suggest that the initial responders to CWD additions in FBMI streams were heterotrophic bacteria and that NH_4^+ assimilation in these FBMI streams is driven largely by heterotrophic assimilation.

<u>Second year post-CWD addition</u>

The positive effects that the CWD additions had on stream morphology and structure were more clearly observed during the second year after the additions. Maloney and others (2005) previously showed that the FBMI streams with greater abundances of CWD experienced less scouring of the streambed and greater streambank and streambed stability than streams with lower abundances of CWD. In addition, the CWD added to manipulated streams provided more stable substrata for algal and microbial colonization and growth on otherwise shifting, fine-grained streambed sediments; i.e., the logs served as stable substrata and they helped stabilize fine sediments (Roberts and others 2007b). The increased substrata stability corresponded to observations of filamentous cyanobacteria mats (*Lyngbya* sp.; Walter R. Hill, personal communication) forming on logs added to manipulated streams, other wood in these streams, and on the newly formed stable substrata on the streambed during winter and spring of 2005 (BJR, personal observation). However, this increase in cyanobacterial abundance was patchy in distribution (restricted to isolated areas associated with the CWD additions) and therefore only resulted in limited increases in ecosystem-scale rates of GPP in two manipulated streams during spring 2005. As light availability decreased in summer and autumn, the patches of cyanobacteria were no longer observed and GPP rates in all streams were again ≤ 0.3 g O_2 m^{-2} d^{-1}, consistent with the idea that light availability often limits primary production in forested streams (Hill and others 1995, Mulholland and others 2001).

This increase in substrata stability and availability of BOM associated with increased CWD abundance during the second year after CWD addition also corresponded to stronger responses in ER in all streams during all seasons of 2005 than were observed in 2004. The magnitude of the observed increases in ER in 2005 relative to pre- and first year post-CWD addition tended to increase with catchment disturbance intensity in all seasons indicating that the more heavily disturbed streams responded most strongly to the restorations.

<u>Third year post-CWD addition</u>

The large increases in ER (and modest increases in GPP) rates observed in most restored streams throughout the second year after CWD addition were not observed in 2006. Areas denuded of almost all vegetative cover in highly disturbed FBMI catchments resulted in increased stream flashiness and sediment load and decreased streambank stability, leading to increased burial of (the already lower standing stocks) of CWD (Maloney and others 2005). Since the current restoration effort was not designed to address the impacts of the upland disturbances themselves, a significant percentage of the added wood was buried (e.g., Fig. 2d) in all manipulated streams by the end of the second year, with the KM1, SB2, SB3, and LPK streams experiencing 32, 68, 77, and 59% burial of added CWD, respectively (Mitchell 2009). By the end of the second year post-CWD addition, the increases in hydrodynamic complexity (decreased water velocity and increased size and importance of transient storage zones) and NH_4^+ uptake observed 1 month after CWD addition (Roberts and others 2007b) were no longer observed (Roberts, unpublished data). Annual precipitation rates for both the before and after CWD addition periods spanned the range of observations at FBMI since 1950; with 2005 and 2003 being among the wettest, 2004 and 2002 being intermediate, and 2006 and 2001 being among the driest years on record. This combined with the fact that the two most heavily disturbed catchments that received CWD addition required augmentation by the end of the first year post-addition (an average rainfall year) suggests that the observed burial of CWD additions (and loss of effectiveness of the restoration) was likely the result of a gradual process that would occur even faster if the streams had been exposed to unusually large storm events. The net result of these findings is that throughout the third year after CWD addition, the study streams behaved similarly to the pre-manipulation period.

Implications for stream restorations

The addition of CWD to FBMI streams provided stability and structure to the streambed, increased the hydrodynamic complexity, and led to nearly immediate (within 1 month) increases in organic matter retention and nutrient (NH_4^+) uptake rates (Roberts and others 2007b) and increased ER rates (within the first year). This is consistent with the findings of other recent studies that suggest stream restorations influence stream hydrologic residence times (Kasahara and Hill 2006, Bukaveckas 2007, Becker and others 2013, Kupilas and others 2017). Additionally, several other stream restorations have shown relatively quick increases in N uptake; including the creation of riffles to enhance hyporheic exchange (Kasahara and Hill 2006), channel naturalization through creation of stream meanders and pools and riffles to create diverse flow conditions (Bukaveckas 2007), and geomorphic restoration involving hydrologic reconnection of a stream to its floodplain (Kaushal and others 2008). While these studies have each looked at relatively short-term (<1 to a maximum of 2 years post-restoration) responses in a single system, they contribute to a growing literature indicating the incorporation of ecological theory into the design of stream restorations greatly improves the likelihood of observing effective ecosystem-scale responses (Lake and others 2007).

The fast responses in nutrient uptake (Roberts and others 2007b) and ER rates combined with a lack of any corresponding increases in GPP indicates that the initial responders to stream restorations (CWD additions) in FBMI streams were heterotrophic microbes and that NH_4^+ assimilation in FBMI streams is driven largely by heterotrophic assimilation. These findings are consistent with the stream microbial community following the “rubber band” model of community recovery (Sarr 2002) in which recovery may be relatively quick once suitable habitat is rebuilt (Lake and others 2007). This recovery trajectory usually requires the disturbance to be stopped so that the habitat can be rebuilt, but in this case, suitable habitat (CWD) was added directly to the stream as part of the restoration. It takes longer for enough stable substrate to be created (especially in these streams within catchments of highly erodible sediments; Houser and others 2005) so that increases in photosynthesis rates in isolated patches of the stream (associated with CWD additions) can translate into a large enough increase in autotrophic biomass to produce an ecosystem-scale increase in GPP rates. Therefore, stream algae seem to follow a slower, non-linear recovery trajectory more similar to Sarr's (2002) "broken leg" model (Lake and others 2007) than that of heterotrophic microbes. It appears to take even longer for the impact of CWD additions to effectively progress up the food web to invertebrates and fish (Mitchell 2009). Taken together, these findings seem to suggest that different components of the stream community may follow highly diverse degradation-recovery pathways.

Many ecological restoration projects aim for rapid progress to bring a system from a degraded state toward a specific target endpoint but consequently the longer-term prognosis for the system is often neglected (Hilderbrand and others 2005). Longer-term monitoring of wetland restoration projects suggests that it will likely take many restored wetlands decades to resemble pre-disturbance conditions (Zedler and Callaway 1999, Wilkins and others 2003, Hilderbrand and others 2005). While stream restorations lack similar long-term monitoring information it is likely that the development or reestablishment of full community structure and ecosystem function in stream ecosystems will often take much longer (years to decades) than the duration of planned monitoring of project effectiveness (if there is post-restoration monitoring). As longer-term post-restoration monitoring of stream restorations begins to occur, the relevant degradation-recovery pathways (Lake and others 2007) will be more easily identified and restoration sustainability more accurately assessed.

The ultimate failure of the FBMI restoration effort illustrates the importance of designing for resilience in restoration projects in order to maximize the opportunity for sustained effectiveness (Hilderbrand and others 2005). It is not possible to anticipate all future events and environmental conditions, but restorations can be conducted in ways that allow for ecosystem variability (Molles and others 1998) and uncertainty (Hilderbrand and others 2005) which may require increases in the scale of future restoration efforts. For example, if FBMI stream sedimentation and ultimately CWD burial rates were better understood prior to the initiation of the current project, CWD may have been added to experimental reaches that were much longer than 100 m. It is difficult to predict whether these longer “restored” reaches would have resulted in a significantly longer duration of observed effectiveness. However, it is also important to consider that as the spatial scale increases, so does the temporal scale over which restoration effects may proceed (Lake and others 2007). As a result, an even longer time span of post-restoration monitoring will be required to assess the effectiveness and sustainability of restoration activities.

In order for future restoration projects to be ecologically successful (Palmer and others 2005), they must adequately address the source of catchment disturbances that are impacting streams (e.g., Bohn and Kershner 2002, Lake and others 2007), not simply attempt to restore the structure of streams. The restoration of stream structures may provide immediate improvements to stream ecosystems, however, only with reductions in disturbance intensity are restored conditions likely to persist. So, if the disturbance was historical (meaning erosion has since been controlled), simply adding wood back to streams may restore ecosystem processes and stream functions to their pre-disturbance state. However, if the disturbance still persists today (as seen in FBMI streams), adding wood will only provide transient improvements to the stream.

Similary, many urban restorations aimed at restoring highly eroded stream channels suffer similar failures because the driver (flashy hydrography) and root cause (impervious surfaces) of the problem are not addressed (Hilderbrand and others 2005). At FBMI and similar sites, restoration efforts must include re-vegetation of uplands to reduce sediment loads to the streams so that added wood will not simply be buried. If this condition is met, the addition of woody debris should provide stability and structure to the streambed and increase hydrodynamic complexity which will allow nutrient and organic matter retention and processing (i.e., nutrient uptake and ecosystem metabolism rates) to increase and potentially support a more robust biotic community.

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Table Headings.

Table 1. Selected physical and chemical characteristics of the study-stream reaches.

Table 1.

Width, depth, discharge, and velocity values are means (SD) based on measurements made during quarterly NaCl/propane injections from summer 2001 through autumn 2006 (n = 21). See Fig. 1 for stream abbreviations

								CWD (% areal coverage)	
Stream	Disturbance intensity (% catchment)	Catchment area (ha)	Reach length (m)	Width (m)	Depth (m)	Discharge (L/s)	Velocity (m/min)	Before	After
Control streams									
BC2	3.15	75	45	0.96 (0.11)	0.11 (0.03)	5.34 (2.41)	2.84 (0.87)	8.92	-
HBC	6.62	215	110	1.77 (0.18)	0.11 (0.03)	19.44 (13.29)	5.39 (2.10)	6.34	-
BC1	10.46	210	60	1.25 (0.13)	0.15 (0.03)	9.12 (3.60)	2.80 (0.69)	12.62	-
SB4	13.65	100	80	1.49 (0.42)	0.05 (0.02)	9.72 (5.84)	7.75 (2.42)	3.11	-
Manipulated streams									
KM1	4.63	369	105	2.07 (0.29)	0.14 (0.04)	26.65 (14.97)	5.26 (1.24)	8.60	12.09
SB2	8.12	123	115	1.61 (0.19)	0.08 (0.03)	18.53 (9.15)	8.57 (1.58)	7.30	11.62
SB3	10.49	72	100	1.18 (0.25)	0.07 (0.03)	9.17 (6.23)	6.46 (1.52)	3.70	8.89
LPK	11.26	33	65	0.90 (0.17)	0.04 (0.01)	3.66 (1.38)	5.93 (1.20)	3.79	6.90

Figure Legends

Fig. 1. Study catchments on the Fort Benning Military Installation near Columbus, Georgia. Study catchments include 2 tributaries of Bonham Creek (BC1 and BC2), 3 tributaries of Sally Branch Creek (SB2, SB3, and SB4), 1 tributary of Little Pine Knot Creek (LPK), 1 tributary of Kings Mill Creek (KM1), and Hollis Branch Creek (HBC). Shaded catchments indicate catchments that received coarse woody debris (CWD) additions. GA = Georgia, AL = Alabama.

Fig. 2. Photographs of one of the four study streams that received CWD additions (Sally Branch Creek 3 (SB3); disturbance intensity = 10.49%) in October 2003 a) before and b) after CWD additions were made to the stream, c) one month after CWD addition (November 2003) showing the effectiveness of additions at reducing water velocity and retaining organic matter and other materials, and d) March 2006 showing the extensive burial of added CWD (77% of CWD added to SB3 was buried by January 2006).

Fig. 3. Mean (+ SE) after:before (A:B) CWD addition ratios of ecosystem respiration (ER) rates for control (open bars) and manipulated (gray bars) streams for the a) winter, b) spring, c) summer, and d) autumn sampling periods in 2004, 2005, and 2006. A:B ratio = 1 (dashed lines) indicate no change between the two sampling periods. Significant effects of treatment (control v. manipulated streams) and year on ER rates were assessed using two-way ANOVAs on square-root transformed ratios (F and p values for test of treatment effects are listed for each season). Significant treatment effects for a given year are indicated above bars. **MS** indicates $p < 0.1$, * indicates $p < 0.05$, and ** indicates $p < 0.01$. Note that the y-axis scale on each figure differs.

Fig. 4. Mean (+ SE) after:before (A:B) CWD addition ratios of gross primary production (GPP) rates for control (open bars) and manipulated (gray bars) streams for the a) winter, b) spring, c) summer, and d) autumn sampling periods in 2004, 2005, and 2006. The figure is assembled in same manner as Fig. 3.

Fig. 5. Relationship between pre-manipulation disturbance intensity and after:before (A:B) CWD addition ratios of a) ecosystem respiration (ER) rates a) and gross primary production (GPP) rates for manipulated streams in 2004 (white symbols), 2005 (black symbols), and 2006 (gray symbols). Data points represent season means for each stream by year. A:B ratio = 1 (dashed line) indicates no change between the two sampling periods. Dotted and solid lines indicate statistically significant linear regressions for ER in 2004 ($p = 0.09$; marginally significant) and 2005 ($p = 0.01$); 2006 was not significant ($p = 0.26$). Linear regressions for 2004 and 2005 are: (Respiration A:B) = 0.12 (disturbance intensity) + 0.58 and (Respiration A:B) = 0.24 (disturbance intensity) + 0.06, respectively. Regressions with GPP were not significant.

Fig. 1.

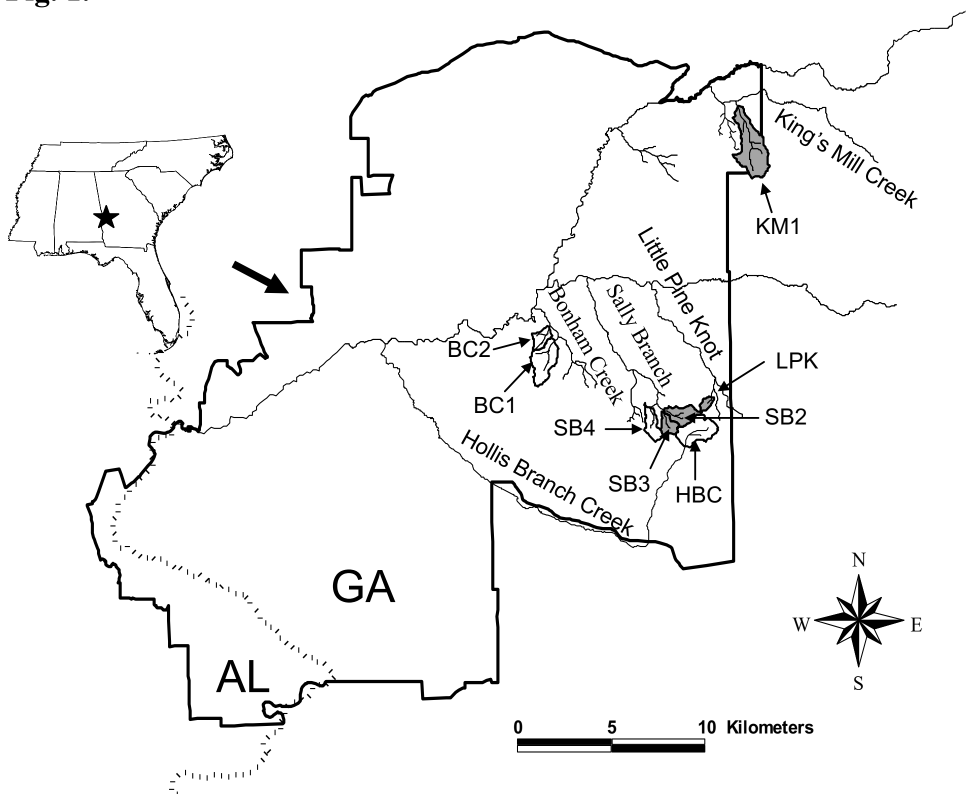

King's Mill Creek
KM1
Little Pine Knot
Bonham Creek
Sally Branch
BC2
BC1
LPK
SB2
SB4
SB3
HBC
Hollis Branch Creek
GA
AL
N
W
E
S
0
5
10 Kilometers

Fig. 2.

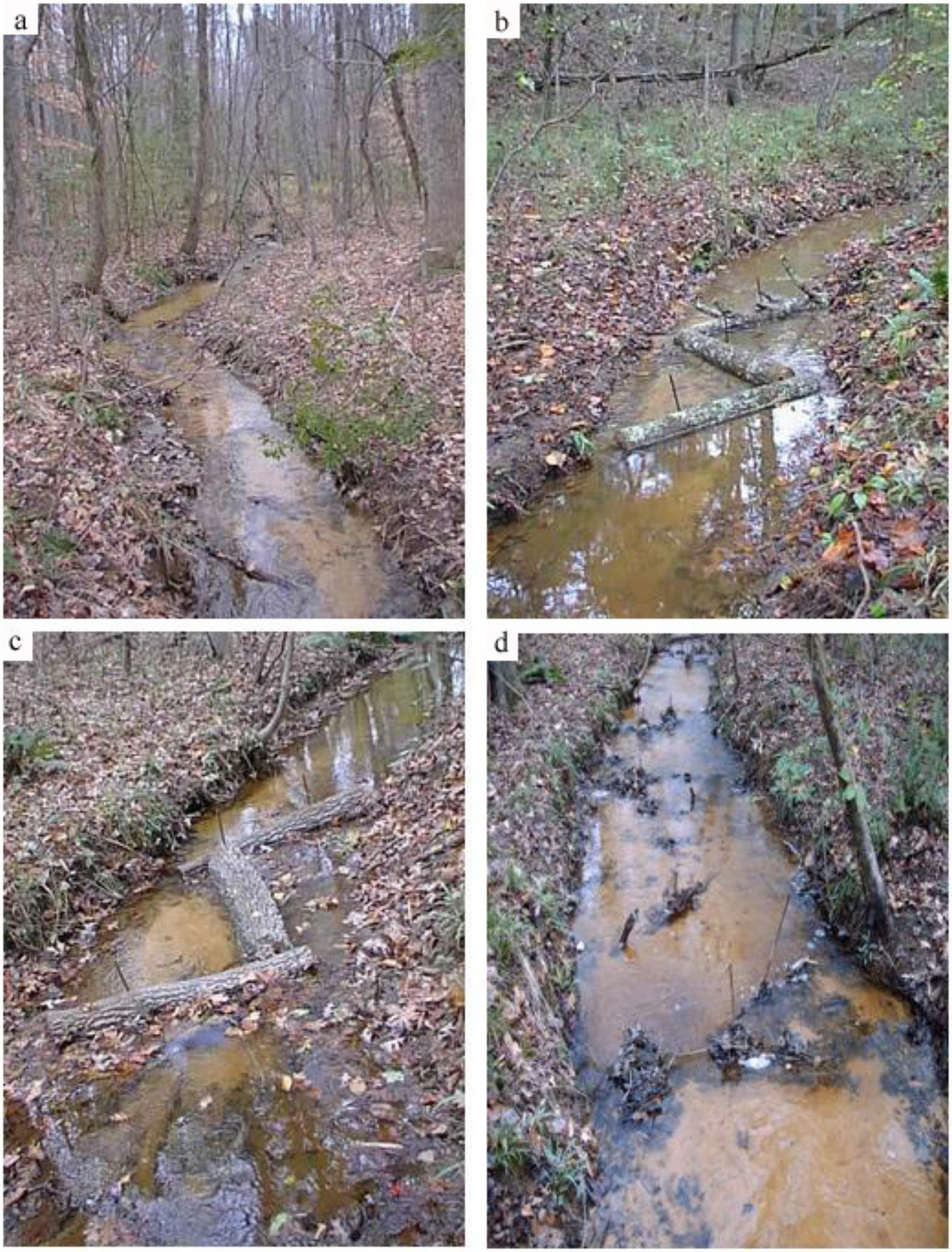
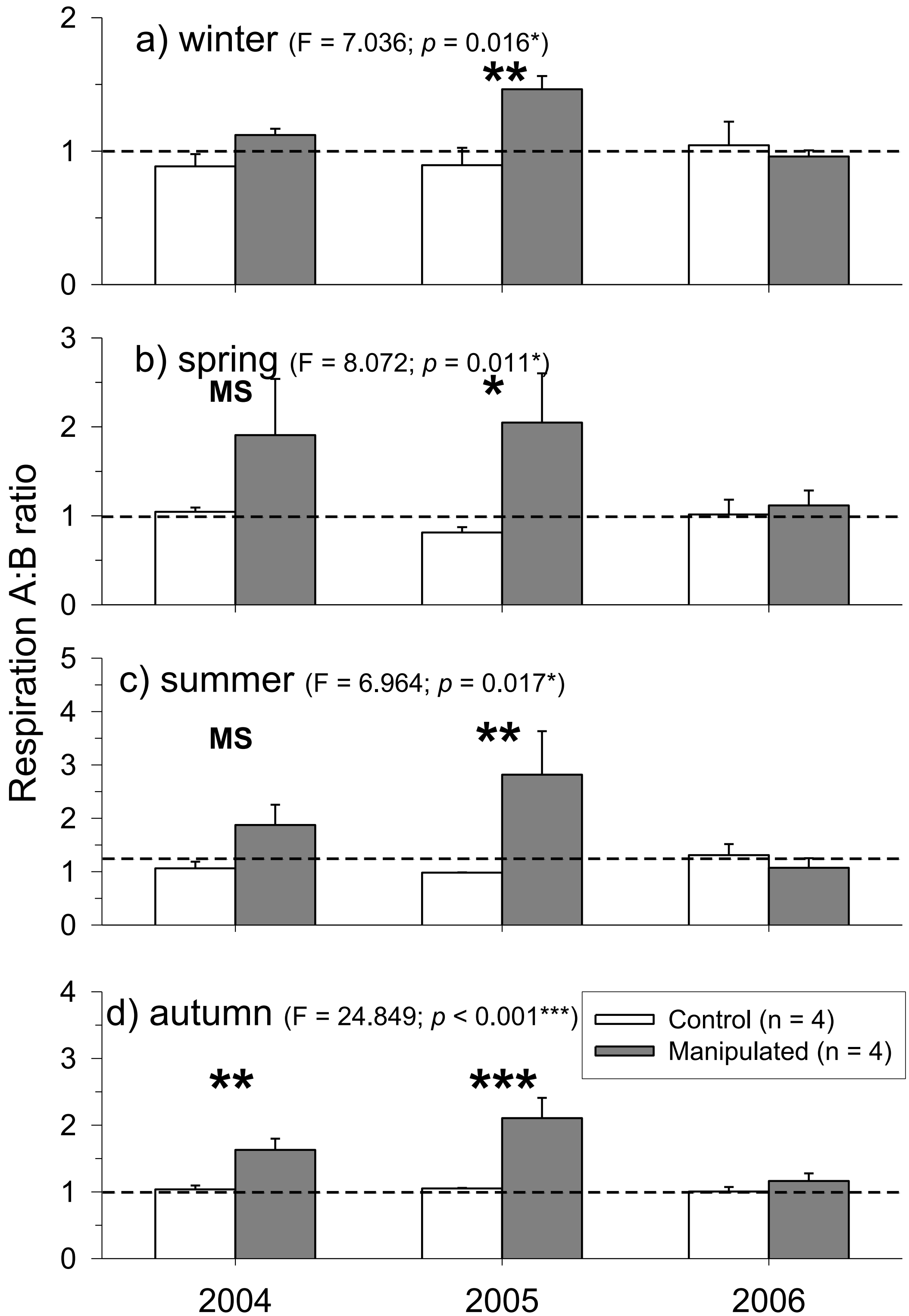
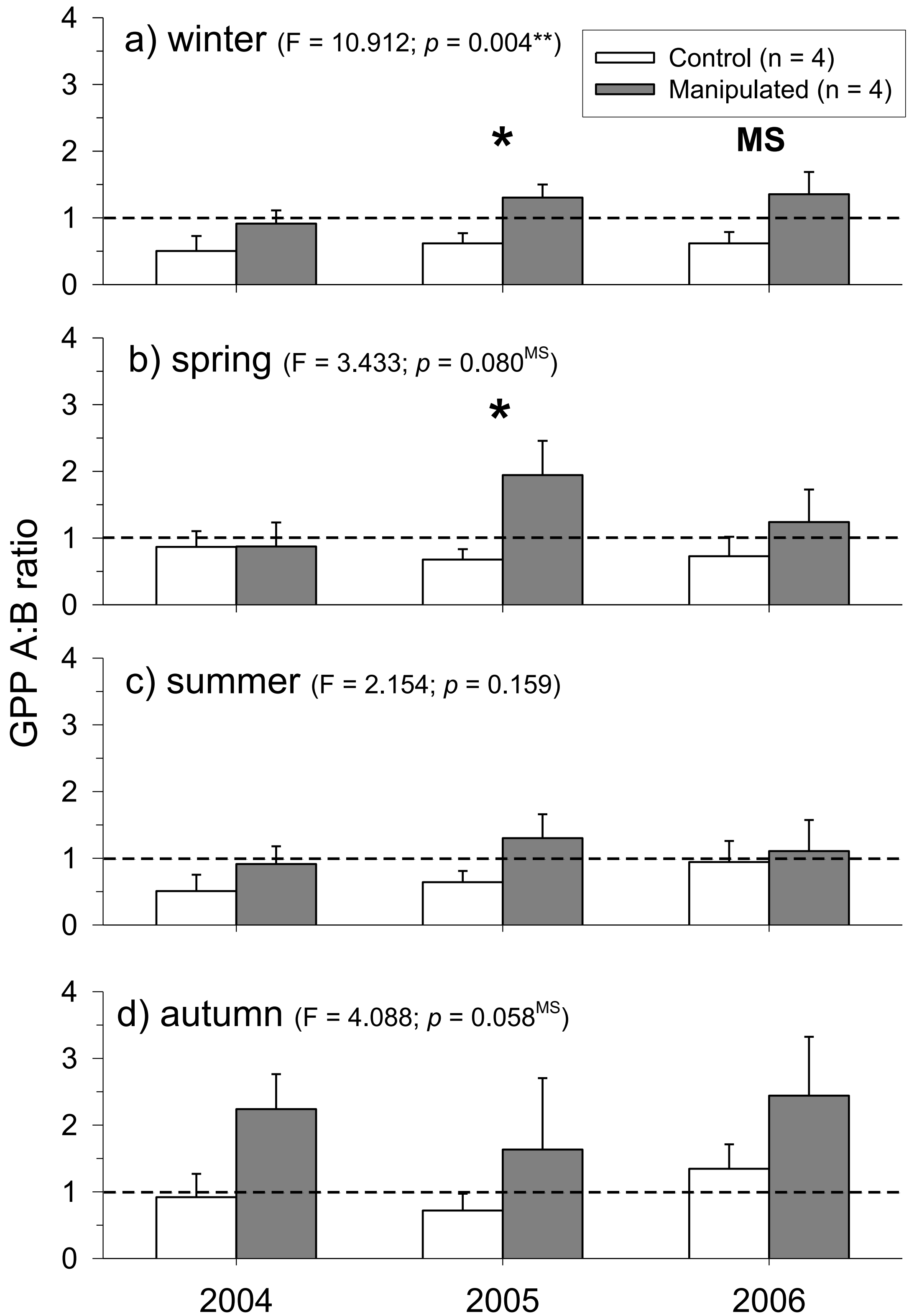


Fig. 3.

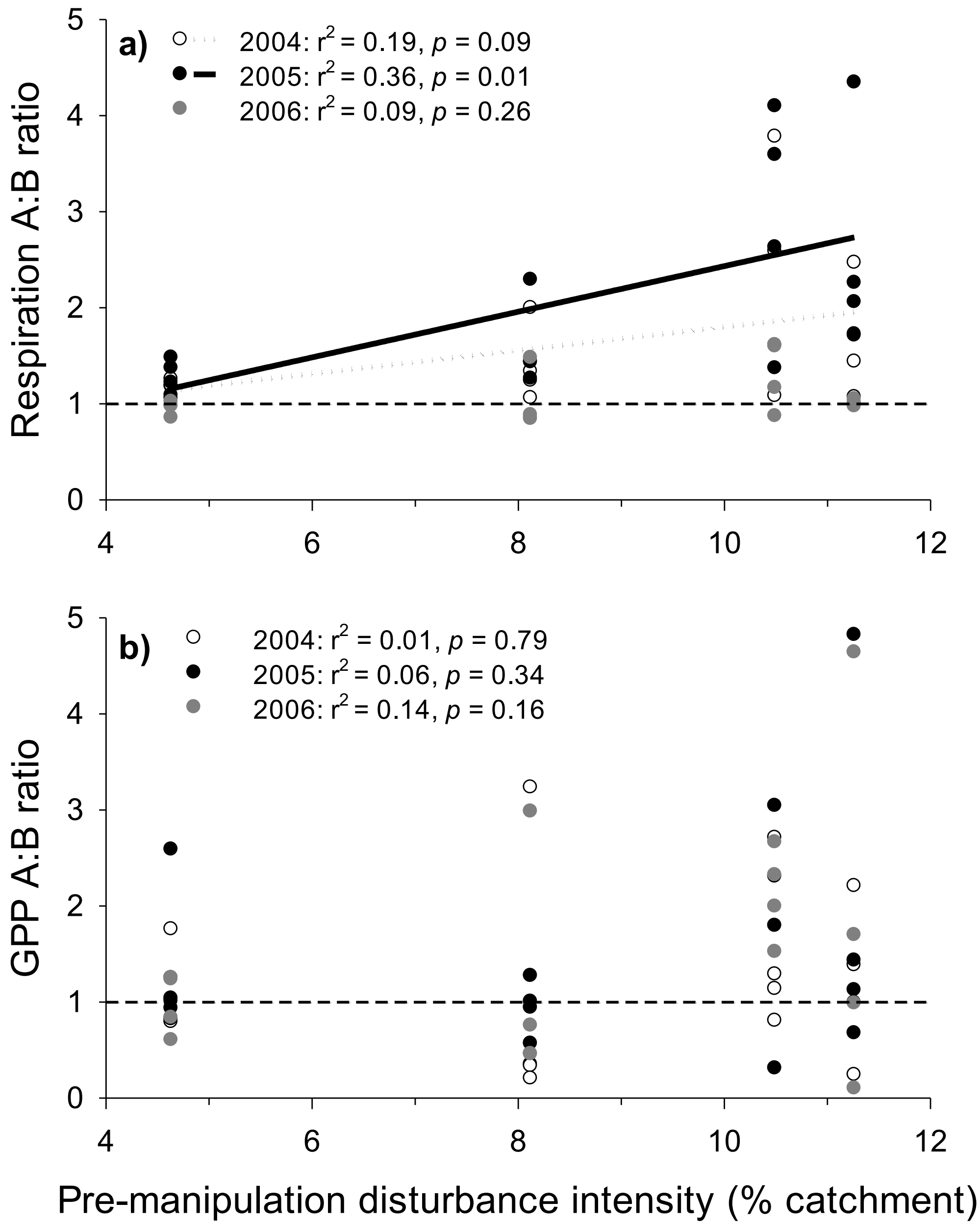

a) winter (F = 7.036; p = 0.016*)
**
b) spring (F = 8.072; p = 0.011*)
MS
*
c) summer (F = 6.964; p = 0.017*)
MS
**
d) autumn (F = 24.849; p < 0.001***)
**
***
Control (n = 4)
Manipulated (n = 4)
Respiration A:B ratio
2004
2005
2006

823 **Fig. 4.**


GPP A:B ratio
a) winter (F = 10.912; p = 0.004**)
Control (n = 4)
Manipulated (n = 4)
*
MS
b) spring (F = 3.433; p = 0.080^MS)
*
c) summer (F = 2.154; p = 0.159)
d) autumn (F = 4.088; p = 0.058^MS)
0
1
2
3
4
2004
2005
2006

824

Fig. 5.


a)
2004: r^2 = 0.19, *p* = 0.09
2005: r^2 = 0.36, *p* = 0.01
2006: r^2 = 0.09, *p* = 0.26
Respiration A:B ratio
b)
2004: r^2 = 0.01, *p* = 0.79
2005: r^2 = 0.06, *p* = 0.34
2006: r^2 = 0.14, *p* = 0.16
GPP A:B ratio
Pre-manipulation disturbance intensity (% catchment)