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Landuse legacies and small streams: identifying relationships between historical land use and contemporary stream conditions

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Abstract. The concept of landscape legacies has been examined extensively in terrestrial ecosystems and has led to a greater understanding of contemporary ecosystem processes. However, although stream ecosystems are tightly coupled with their catchments and, thus, probably are affected strongly by historical catchment conditions, few studies have directly examined the importance of landuse legacies on streams. We examined relationships between historical land use (1944) and contemporary (2000–2003) stream physical, chemical, and biological conditions after accounting for the influences of contemporary land use (1999) and natural landscape (catchment size) variation in 12 small streams at Fort Benning, Georgia, USA. Most stream variables showed strong relationships with contemporary land use and catchment size; however, after accounting for these factors, residual variation in many variables remained significantly related to historical land use. Residual variation in benthic particulate organic matter, diatom density, % of diatoms in *Eunotia* spp., fish density in runs, and whole-stream gross primary productivity correlated negatively, whereas streamwater pH correlated positively, with residual variation in fraction of disturbed land in catchments in 1944 (i.e., bare ground and unpaved road cover). Residual variation in % recovering land (i.e., early successional vegetation) in 1944 was correlated positively with residual variation in streambed instability, a macroinvertebrate biotic index, and fish richness, but correlated negatively with residual variation in most benthic macroinvertebrate metrics examined (e.g., Chironomidae and total richness, Shannon diversity). In contrast, residual variation in whole-stream respiration rates was not explained by historical land use. Our results suggest that historical land use continues to influence important physical and chemical variables in these streams, and in turn, probably influences associated biota. Beyond providing insight into biotic interactions and their associations with environmental conditions, identification of landuse legacies also will improve understanding of stream impairment in contemporary minimally disturbed catchments, enabling more accurate assessment of reference conditions in studies of biotic integrity and restoration.

Key words: disturbance, water chemistry, coarse woody debris (CWD), particulate organic matter (POM), macroinvertebrates, fish, diatoms, metabolism.

Research identifying environmental drivers of catchment-scale stream conditions has garnered much attention over the past 30 to 40 y (Hynes 1975, Richards et al. 1996, Allan and Johnson 1997). Most of these studies have focused on the influence of land use on instream processes, with the ultimate goal of assessing the linkage between contemporary land use and stream impairment. However, streams are tightly linked to their catchments (Hynes 1975), and catchment alterations by

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human activity might last for centuries to millennia (Koerner et al. 1997, Dupouey et al. 2002), so historical disturbance might influence instream conditions for periods long after disturbance has ceased. Such prolonged effects of historical land use (i.e., legacies) have been widely documented in terrestrial systems (Foster et al. 2003), whereas only a few cases exist for streams (Harding et al. 1998, Zimmerman and Covich 2003, Burcher and Benfield 2006). One possible reason for the limited demonstration of stream legacies is related to the scale of observation. Unlike the traditional measures used in terrestrial legacy studies conducted at the site or plot scale (e.g., Compton et al. 1998, Bellemare 2002), corresponding approaches in streams often require data at much broader scales (whole catchments). Moreover, identification of legacies in terrestrial studies has been done largely through comparison of recovered to reference (relatively undisturbed) sites (e.g., Burke et al. 1995, Bossuyt and Hermy 2001); however, this approach might be intractable in streams because of the difficulty in obtaining a sufficient number of reference or disturbed catchments showing recovery.

Potential influences of historical land use on contemporary conditions in small heterotrophic streams are strong. In heterotrophic streams, allochthonous inputs strongly influence instream structure and function (Fisher and Likens 1973, Vannote et al. 1980), so recovery of such functions will occur only after catchment recovery. For example, abundance of instream coarse woody debris (CWD), which stabilizes channels and provides habitat for benthic biota (Smock et al. 1989, Wallace et al. 1995), results from inputs by surrounding vegetation that could be decades to centuries old (Hyatt and Naiman 2001, Wallace et al. 2001). CWD is dead wood from surrounding catchments, so recovery to predisturbance conditions can occur only after sufficient woody biomass has accumulated in the catchment. Furthermore, channel incision resulting from agricultural and urbanization practices (Ireland et al. 1939, Paul and Meyer 2001) might take centuries or longer for recovery or restabilization. Moreover, although streamwater chemistry can return to predisturbed levels within 10 to 15 y (Likens et al. 1978, Lynch and Corbert 1991), elevated streamwater Ca^+ and NO_3^--N concentrations can persist for ~20 y after forest harvest (Swank et al. 2001).

Limited data exist documenting legacy effects on stream periphyton, microbial, and macroinvertebrate communities (i.e., basal producer and consumer trophic levels), yet each of these groups is affected by landscape perturbation (Resh et al. 1988, Paul and Meyer 2001, Iwata et al. 2003); thus, the potential for legacy effects on these trophic levels is high. Evidence for legacy effects on fish assemblages is more common because fish are widely reported to be negatively affected by past human activity (Pflieger and Grace 1987, Rahel 2000). Unfortunately, low numbers of studies directly addressing the effects of historical land use on contemporary stream biota have led to conflicting results (Harding et al. 1998, Sutherland et al. 2002), so additional work is needed to increase our understanding of the prevalence and relative importance of historical vs contemporary land use on stream ecosystems.

Recent studies at Fort Benning, Georgia, have explored causal relationships between contemporary land use and stream biotic and abiotic variables. Results of these studies show decreased instream habitat (relative abundance of CWD, suspended solids concentration, streambed stability) and decreased streamwater nutrient concentrations (dissolved organic C [DOC], soluble reactive P [SRP]) with increasing contemporary disturbance in the catchment (Maloney et al. 2005, Houser et al. 2006). In addition, increased contemporary disturbance was linked to altered benthic macroinvertebrate (Maloney and Feminella 2006) and fish assemblages (Maloney et al. 2006), and decreased whole-stream respiration (Houser et al. 2005, Mulholland et al. 2005). These studies are informative descriptions of contemporary land use–instream linkages, but they did not examine influence of historical land use on contemporary conditions nor the relative importance of historical and contemporary influences on contemporary stream conditions. Our study builds on these previous studies by incorporating historical land-cover data into an analysis assessing the degree to which historical land use explains patterns in contemporary stream conditions after removing variation from contemporary land use and natural landscape variables.

Methods

Study site

Our study was conducted on the Fort Benning Military Installation (FBMI), an ~735-km^2 military base in the Southeastern Plains ecoregion of Chattahoochee and Muscogee counties, Georgia, USA (Fig. 1). FBMI has a mild, humid climate, with warmest temperatures in July and August (maximum and minimum temperatures of 37 and 15°C, respectively) and coldest temperatures in January and February (15.5 and −1°C, respectively), with precipitation occurring throughout the year (average = 105 cm/y). Vegetation at FBMI consists mostly of coniferous (i.e., longleaf [*Pinus palustris*], short leaf [*Pinus echinata*], and loblolly pine [*Pinus taeda*]) and mixed deciduous (mostly *Quercus* spp.) species. Streams are low gradient

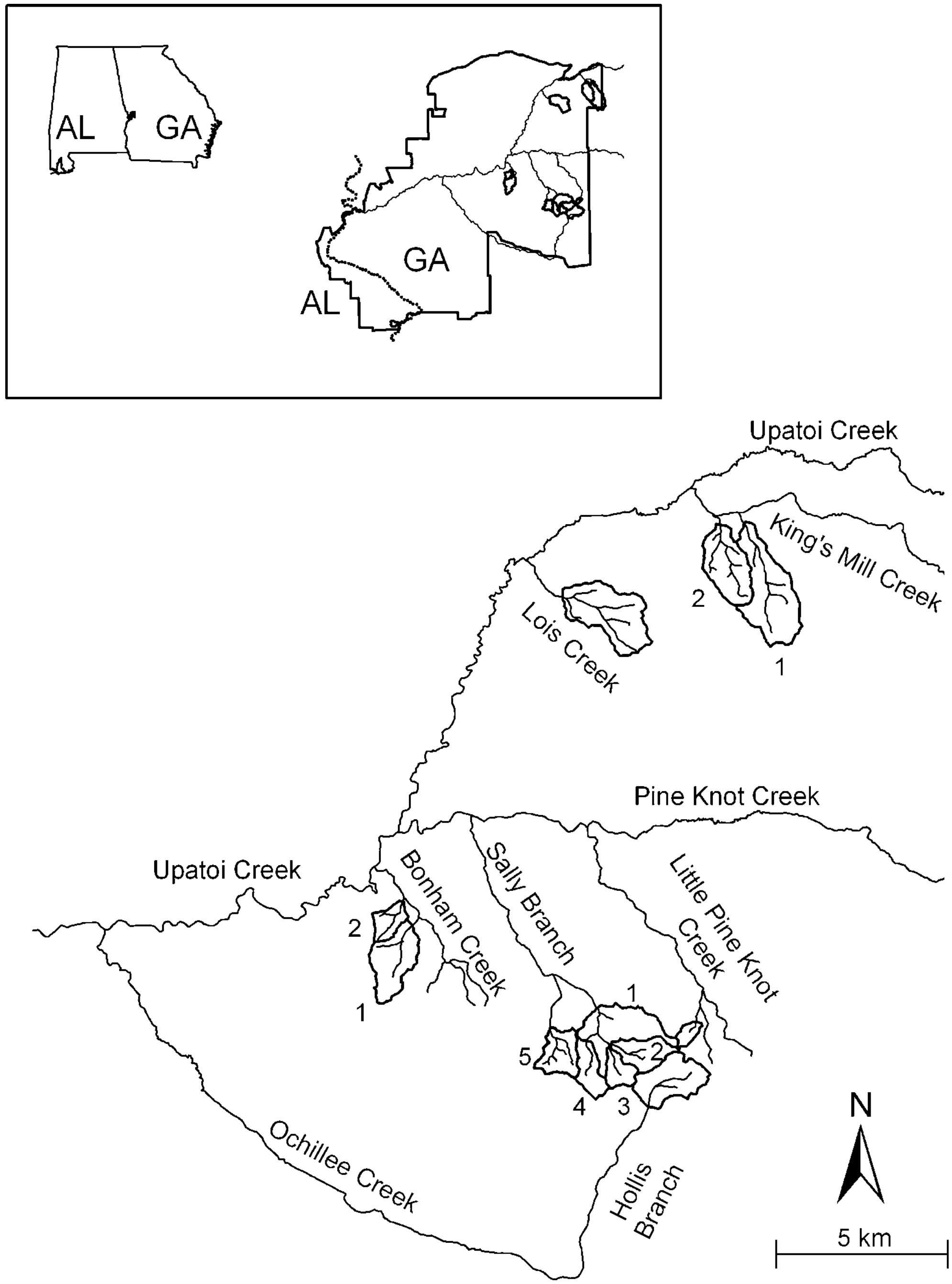

FIG. 1. Locations of study catchments (polygons) within Fort Benning Military Installation, Georgia. Dotted line in inset represents the Chattahoochee River separating Alabama (AL) and Georgia (GA). Numbers in the main figure identify catchments on the same stream (e.g., 1 and 2 on the King's Mill Creek represent King's Mill Creek tributaries 1 and 2 [KM1 and KM2], respectively).

and sandy bottomed with large amounts of CWD (3–12% coverage of streambed) and other organic matter (i.e., leaf detritus), and channels are highly sinuous with intact riparian zones and broad flood plains dominated by black gum (*Nyssa sylvatica*). The main contemporary disturbance to streams is an influx of sediment from upland disturbance related to historical agriculture and contemporary military training practices. Sediment typically reaches streams through ephemeral channels.

The US military had purchased the portions of FBMI addressed in our study by 1942. Before purchase, landuse practices were primarily agriculture and silviculture, which persisted from the early 1800s up to the time of military purchase (Hilliard 1984, Frost 1993, Kane and Keeton 1998). After purchase, the land was used for infantry and mechanized-equipment training with associated heavy equipment vehicles (tanks, armored personnel carriers, light- and heavy-wheeled vehicles). Training dramatically alters the landscape by disrupting surface soil layers and vegetative cover (USAIC 2001, Dale et al. 2002). However, large areas of FBMI are used solely for infantry training, and thus, they are allowed to revegetate and serve as contemporary reference areas (Dale et al. 2002). Established military compartments at FBMI segregate training activities, so we were able to select catchments that varied in their level of contemporary disturbance from military training and that were under different levels of catchment revegetation from historical agricultural disturbance. In addition, controlled burning (2–3-y cycle) and selective timber harvesting are used frequently and are well documented at FBMI (USAIC 2001), and provide additional sources of contemporary disturbance.

We studied twelve 2nd- and 3rd-order catchments (catchment area = 0.33–5.43 km^2) on the eastern part of FBMI (Fig. 1, Appendix). Study sites were typical sandy Southeastern Plains streams (Maloney et al. 2005); our contemporary low-disturbance sites were mostly within compartments reserved for light-infantry training, whereas contemporary high-disturbance sites were mostly within compartments reserved for heavy-tracked vehicle training.

General sampling design

Within each study catchment, we identified a 100- to 120-m stream reach that was long enough to encompass several run–pool sequences, where we quantified a suite of physical, chemical, and biological response variables (see *Physical, chemical, and habitat variables* and *Stream biota* below). During initial visits, we identified and marked 4 permanent sites/reach with similar flow (runs) and habitat (sand substrate). We sampled a total of 13 reaches over 3 y; however, not all variables were measured at every reach in every year (Appendix).

Landuse classification

We quantified land use in study catchments with ArcView© 3.2 software (Environmental Systems Research Institute, Redlands, California) and the ArcView© extension Analytical Tools Interface for Landscape Assessments (Ebert and Wade 2000). We derived contemporary landuse data from 1999 satellite imagery (Landsat 28.5-m resolution, July and December 1999), but we digitized historical land use manually from 1944 aerial photographs (1-m resolution, March 1944). We standardized resolution of landuse coverages by generating a 30-m grid coverage of the 1944 cover data. We used digital elevation models (DEMs; 1:24,000, 10-m grid size, 1993) in conjunction with each landuse grid coverage to calculate the following landuse conditions in each catchment for the 1944 and 1999 periods: 1) disturbed land (D) as the proportion of bare ground and recently abandoned fields on erodable soils (slopes $>$5%) summed with the proportion of unpaved road cover, and 2) recovering land (R) as the proportion of land with shrubs and sparse vegetation on erodable soils (slopes $>$5%). We used 5% slopes as our threshold value because examination of the relationship between the calculated Universal Soil Loss Equation and catchment slope indicated that slopes $\geq$5% showed high potential for increased annual soil loss in our study area (GASWCC 2000). The 1944 land use data reflected agricultural activities at the time this portion of FBMI was purchased by the military; therefore, D44 included recently abandoned agricultural lands, whereas R44 included lands recovering from fields abandoned prior to 1944 (Fig. 2). The 1999 landuse data reflected land use under military ownership for $\sim$55 y; thus, D99 included heavy machinery and munitions military training, whereas R99 included land recovering from historical agricultural and silvicultural practices, as well as historical military training (Fig. 2). Impervious surfaces (e.g., from paved roads and lots) were mostly absent in catchments (present in only 4 of 12 catchments, and always $<$1.0% coverage), so we excluded this land use from analyses.

Physical, chemical, and habitat variables

We estimated streambed instability by quantifying the change in streambed height between sampling periods using 5 leveled cross-stream transects in 10 streams (Appendix). We constructed each transect of 2 pieces of rebar anchored on opposite sides of the stream bank. During deployment, we used a chalk line and line level to mark level locations on metal bars with plastic cable ties for subsequent measurements. We measured the distance between the horizontal transect and the stream bottom (i.e., bed height) in January 2003 and July 2003 at 20-cm intervals along each transect using a fiberglass tape. We estimated streambed instability as the mean absolute change in streambed height over the study (Maloney et al. 2005).

We estimated stream flashiness, defined as the magnitude of hydrologic response by a stream channel to a storm event, by calculating 4-h recession coeffi-

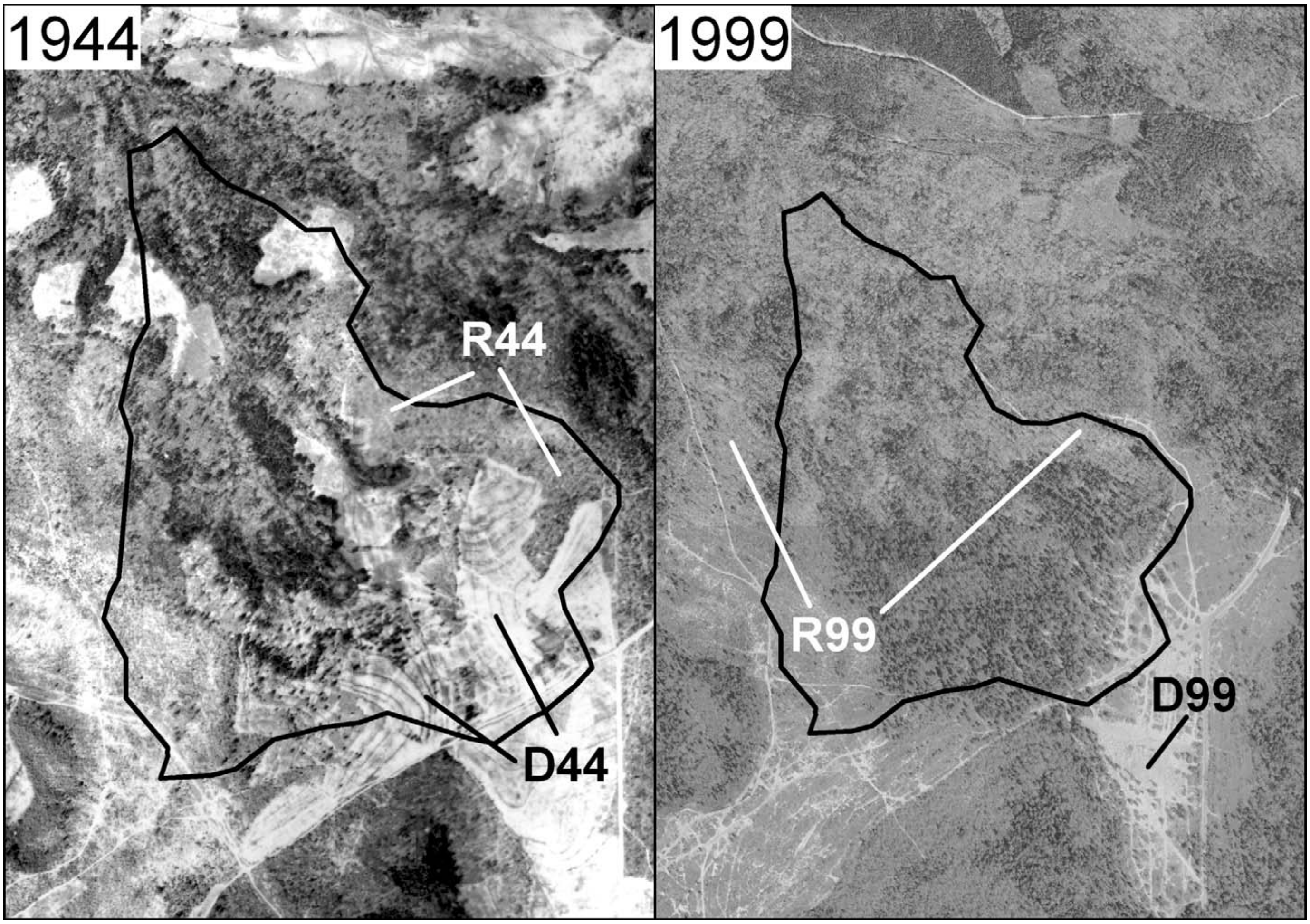

FIG. 2. Aerial photographs of example catchment SB3 showing land use in 1944 and 1999. D44 = recently abandoned fields in 1944, R44 = recovering areas in 1944, D99 = disturbed areas in 1999, R99 = recovering areas in 1999.

cients of the receding limb of storm hydrographs in 9 streams (Rose and Peters 2001). We measured discharge (Q) for storms using an ISCO ultrasonic flow sensor (model 750; ISCO, Lincoln, Nebraska) and portable sampler (model 6700), and we calculated recession coefficients as the slope of the regression of ln(Q) measured at ½- to 1-h intervals over the first 4 h after peak Q (Maloney et al. 2005).

We used replicate sediment cores (2.01 $cm^2 \times 10$ cm long polyvinyl chloride tubing) to sample benthic particulate organic matter (BPOM) in the thalweg at the first 3 permanent sites in 12 streams every 2 mo from August 2001 to May 2003. We estimated BPOM as ash-free dry mass (AFDM), determined as the difference between dried (80°C, 2–3 d) and combusted (550°C, 3 h) mass. We quantified stream-specific CWD in April 2002 and March 2003 using fifteen 1-m-wide transects (spaced 5 m apart). We quantified all submerged CWD >2.5 cm in diameter within the 1-m-wide band at each cross-stream transect and expressed this value as a proportion of total streambed sampling area (Maloney et al. 2005). One stream (BC1) had an unusually large flood plain and a large amount of woody vegetation within and near stream channels, which resulted in a large number of live roots in the stream channel and an abnormally high CWD level and probably increased retention of BPOM. Therefore, we excluded BC1 in CWD and BPOM analyses.

We collected streamwater samples (1-L Nalgene bottles) for water-chemistry analysis near the downstream end of each reach ~8 times/y from September 2000 to September 2003 during nonstorm-flow conditions in 12 streams (Houser et al. 2006; Appendix). We shipped samples on ice to the Oak Ridge National Laboratory, Oak Ridge, Tennessee, where we filtered (Whatman glass-fiber filters [Whatman Inc., Florham Park, New Jersey]) them and analyzed SRP (molybdate-blue method using a spectrophotometer with a 10-cm light path), NO_3^--N (colorimetrically using a Seal Analytical Auto Analyzer III; Seal Analytical, Inc., Mequon, Wisconsin), and DOC (high-temperature combustion using a Shimadzu Model 5000 TOC analyzer [Shimadzu Corporation, Kyoto, Japan] after acidification and purging to remove inorganic C). Last, we measured streamwater pH (Beckman model 200 pH meter; Beckman Coulter, Inc., Fullerton, California) on unfiltered water samples.

Stream biota

Diatoms.—We quantified benthic diatoms at the first 3 permanent sites in 11 streams twice (spring, summer) between September 2001 to May 2002. We sampled diatoms by inserting an inverted 4.7-cm-diameter Petri dish randomly into the streambed surface, positioning a masonry trowel beneath the dish and underlying sandy substrate, removing the sand-sediment sample, and then transferring sample contents to a Whirl-pak® bag (Nasco, Fort Atkinson, Wisconsin). We transported samples to the laboratory on ice, where they were homogenized, preserved in 2% glutaraldehyde, digested with H_2O_2 and HNO_3, and then slide-mounted with Naphrax™ (Northern Biological Supplies Ltd., Martlesham Heath, Ipswich, UK) (Barbour et al. 1999). We counted 300 to 400 diatom valves/season (at 1000× magnification) per stream and identified them to the lowest possible taxonomic level. We estimated density of the entire diatom assemblage and the percentage of the assemblage as *Eunotia* spp., the dominant taxon in these streams (24–91% of total cells identified; Miller 2006).

Macroinvertebrates.—We sampled benthic macroinvertebrates at each of the 4 permanent sites 3 times/y (spring, summer, winter) from 2000 to 2003 using Hester–Dendy (HD) multiplate samplers (each HD unit $= 0.34$ m^2) in 11 streams (Maloney and Feminella 2006; Appendix). We incubated HDs for ~8 wk to allow macroinvertebrate colonization, and then we retrieved and transported samples to the laboratory for sorting and identification of macroinvertebrates (usually family or genus). In addition, we took 2 D-frame sweepnet samples (250 μm), one sample upstream and one sample downstream of HD stations, to collect macroinvertebrates from additional habitats not sampled by HDs (e.g., snags and pools). We estimated the percentage of the macroinvertebrate assemblage that cling to hard substrates (% clingers) as an indicator of stable substrate availability (Barbour et al. 1999); the number of dipteran taxa in the family Chironomidae (chironomid richness) as an indicator of taxa generally considered tolerant of sedimentation (Culp et al. 1986, Shaw and Richardson 2001); and the number of taxa in the aquatic insect orders Ephemeroptera, Plecoptera, and Trichoptera (EPT taxa), which generally are considered sensitive to a wide range of perturbations (Barbour et al. 1999). In addition, we estimated total taxon richness and Shannon diversity (H'), and we used a region-specific multimetric index of biotic integrity designed for Georgia streams. This index is a modification of the Florida Stream Condition Index (Barbour et al. 1996) (hereafter the Georgia Stream Condition Index [GASCI]; GADNR 2002).

Fish.—We used a backpack electroshocker (2 passes; LR-24; Smith–Root, Vancouver, Washington) and block seines placed immediately upstream and downstream of each habitat (Maloney et al. 2006; Appendix) to sample fish in 3 pool and 3 run habitats 3 times (spring, summer, winter) in 2003 at 11 of the study streams. We excluded young-of-year fishes from analysis because of difficulty in their capture and identification. We returned all fish to their collection point after identification (species level) and enumeration except for a few voucher specimens of each species. We calculated stream-specific total richness, H', and density of fish in both runs and pools. Three streams (LPK, KM2, BC1) had an extremely limited fish fauna because of downstream obstructions to fish migration (from waterfalls, subterranean flows), so we excluded them from analyses.

Stream metabolism.—We used a 1-station diurnal O_2 curve approach (Houser et al. 2005) to quantify whole-stream metabolism in 11 streams from summer 2001 through summer 2003. We measured dissolved O_2 (DO) concentrations at 15-min intervals with YSI Model 6000- or 600-series sondes equipped with a YSI model 6562 DO probe (YSI Inc., Yellow Springs, Ohio). We deployed sondes for 7 to 21 d in each stream each season (winter, spring, summer, autumn). We determined reaeration coefficients, stream velocity, and Q in situ with simultaneous steady-state injection of propane gas (volatile tracer) and concentrated NaCl solution (conservative tracer) over reaches ranging in length from 45 to 110 m (Marzolf et al. 1994). We determined the net rate of DO change from ecosystem metabolism at 15-min intervals based on the change in DO concentration over the interval corrected for air–water O_2 exchange. We calculated the rate of air–water O_2 exchange with the reaeration coefficient converted from propane to O_2 and observed % DO saturation. We considered nighttime respiration (Rs) as the sum of net ecosystem metabolism occurring at night, and daytime Rs as the interpolation between Rs rates measured 1 h before dawn and 1 h after dusk. We considered total daily Rs as the sum of nighttime and daytime Rs rates over 24 h (from midnight to midnight), and daily gross primary production (GPP) as the sum of the differences between interpolated daytime Rs rates and net ecosystem metabolism.

Data analysis

We used means of each stream response variable in statistical analyses. We found several significant correlations between historical and contemporary landuse variables (e.g., D44 and D99; $r = 0.65$), a problem reported in other studies of catchment-scale land use on aquatic systems (King et al. 2005). Therefore, we used partial correlation analysis to examine the capacity of historical land use (D44, R44) to account for variation in contemporary stream conditions after removing the statistical influence of contemporary land use (D99, R99) and natural landscape features on response variables (see King et al. 2005).

For the partial correlation analysis, we first obtained residuals (ε_y) for each response variable from the contemporary landuse/landscape model:

$$Y_i = \beta_{0,i} + \beta_{1,i}\mathrm{D99} + \beta_{2,i}\mathrm{R99} + \beta_{3,i}Area + \varepsilon_{y,i} \quad [1]$$

where Y_i is the mean value for a particular physical, chemical, or stream biotic variable, $\beta_{0,i}$ is the constant for variable i, $\beta_{1,i}$ is the coefficient of D99 for variable i, $\beta_{2,i}$ is the coefficient of R99 for variable i, $\beta_{3,i}$ is the coefficient of *Area* for variable i, and $\varepsilon_{y,i}$ is the residual variation from each model. D99 is the amount of disturbed land in 1999, R99 is the amount of recovering land in 1999, and *Area* is the catchment area upstream of our downstream-most sampling point. We used *Area* in regression models because it was highly correlated with other natural catchment variables (e.g., Q: $r = 0.87$, stream width: $r = 0.79$) and, thus, provided a reasonable measure of natural landscape variation among study catchments.

Next, we regressed historical land use (D44 or R44) with contemporary land use (D99 and R99) using the formulae

$$\mathrm{D44}_i = \beta_{0,i}^{\mathrm{D44}} + \beta_{1,i}^{\mathrm{D44}}\mathrm{D99} + \beta_{2,i}^{\mathrm{D44}}\mathrm{R99} + \varepsilon_{\mathrm{D44}} \quad [2]$$

and

$$\mathrm{R44}_i = \beta_{0,i}^{\mathrm{R44}} + \beta_{1,i}^{\mathrm{R44}}\mathrm{D99} + \beta_{2,i}^{\mathrm{R44}}\mathrm{R99} + \varepsilon_{\mathrm{R44}} \quad [3]$$

where $\mathrm{D44}_i$ is the amount of disturbed land cover in 1944 in catchments for variable i ($\mathrm{R44}_i$ is amount of recovering land cover in 1944), βs are the same as defined above except that superscripts denote a particular historical landuse model (e.g., $\beta_{0,i}^{\mathrm{D44}}$is the constant for variable i from the D44 model), and the residuals from equations 2 ($\varepsilon_{\mathrm{D44}}$) and 3 ($\varepsilon_{\mathrm{R44}}$) are the unexplained variation in D44 and R44, respectively, after accounting for the influence of contemporary land use (D99, R99).

Last, we obtained partial correlation coefficients by correlating the residuals from equation 1 (ε_y) with residuals from equation 2 ($\varepsilon_{\mathrm{D44}}$) or equation 3 ($\varepsilon_{\mathrm{R44}}$). These partial correlations reveal the amount of variation in each response variable explained by either D44 or R44 after accounting for the effects of contemporary land use (D99, R99) and *Area*. Because of small sample sizes and low power, we assumed that correlations at $p < 0.05$ indicated strong relationships and correlations at $p < 0.10$ indicated weak relationships, to reduce type II error rates (Toft and Shea 1983, Peterman 1990).

Results

Landuse classification

Percent bare ground on slopes >5% was higher in all catchments in 1944 (range 6.61–36.92%, mean = 19.93%) than in 1999 (range 0.14–10.57%, mean = 5.26%; Fig. 3A). Relative changes in % bare ground ranged from −99 to −26% (mean relative change = −74%; Fig. 3A). Depending on catchment, relative changes in % recovering land cover either increased or decreased over this 55-y period (range −37 to 3052%; Fig. 3B); and study-average % recovering land cover increased over this period (mean relative change = 21%). Like % recovering land cover, the relative change in % unpaved road cover either increased and decreased depending on catchment (range −67 to 14%; Fig. 3C); however, unlike % recovering land cover, study-average % road cover decreased over the 55-y period (mean relative change = −26%).

Physical and chemical variables

The contemporary landuse/landscape model explained significant variation in streamwater chemistry (pH, SRP, DOC), organic matter abundance (BPOM, CWD), and bed instability; however, the model did not account for significant variation in stream flashiness or streamwater NO_3^--N (Table 1). After removing the influence of contemporary land use and catchment area, residual variation in many stream physical and chemical variables was explained by historical land use (Table 1). A weak positive relationship ($p < 0.10$) existed between streamwater pH and D99; but after accounting for effects of D99, R99, and Area, pH was strongly positively correlated with D44 ($p < 0.05$), indicating a possible influence of historical land use on contemporary pH levels. Streamwater SRP decreased with increasing D99 and R99, but increased with Area. Partial correlations of residuals from the contemporary landuse/landscape model and the R44 model showed a weak negative relationship with SRP (Table 1), suggesting a possible influence of historical land use on contemporary SRP concentrations. Partial correlation analysis revealed no significant relationship between stream flashiness or streamwater NO_3^--N with D44 or R44 (Table 1). Variation in organic matter variables (DOC, BPOM, CWD) was significantly explained by the contemporary landuse/landscape model because all were negatively correlated with D99. Partial correlation analyses revealed that the only significant correlation between D44 or R44 and the residual variation from the contemporary landuse/landscape models was a negative correlation between BPOM and D44 (Table 1). Streambed instability was weakly explained by the contemporary landuse/landscape model, but residual variation was strongly and positively correlated with R44 (Table 1).

Stream biotic variables

Variation in stream diatom assemblages (as % *Eunotia*, diatom density) was largely explained by contemporary land use and Area; both variables decreased with D99 (Table 1). Partial residuals from the contemporary landuse/landscape models and the D44 models were negatively correlated with % *Eunotia* and diatom density (Table 1), indicating a possible effect of historical land use on contemporary diatom assemblages. The contemporary landuse/landscape model explained significant variation in all macroinvertebrate metrics, and all were negatively related to D99 (Table 1). Partial correlation analysis revealed that D44 was not significantly related to residuals of any macroinvertebrate metric; however, residual variation in Chironomidae richness, H', and total macroinvertebrate richness all were negatively correlated with R44 (Table 1). Residual variation in GASCI was significantly positively related to R44. All fish assemblage metrics were significantly explained by the contemporary landuse/landscape model (Table 1). Residual variation in fish richness was positively related to R44, whereas residual variation was not significantly explained by D44. Residual variation in density of fish in runs (but not pools) was weakly and negatively correlated with D44. Last, whole-stream Rs was only weakly related to the contemporary landuse/landscape model ($R^2_{adj} = 0.42$), and historical land use was not significantly correlated with partial residuals from the contemporary model. GPP showed no relationship with the contemporary landuse/landscape model; however, a significant negative relationship was found between residuals and D44 ($r = -0.75$; Table 1).

Discussion

Stream physical and chemical variables

Our results suggest that much of the variation in stream physical and chemical variables at FBMI was

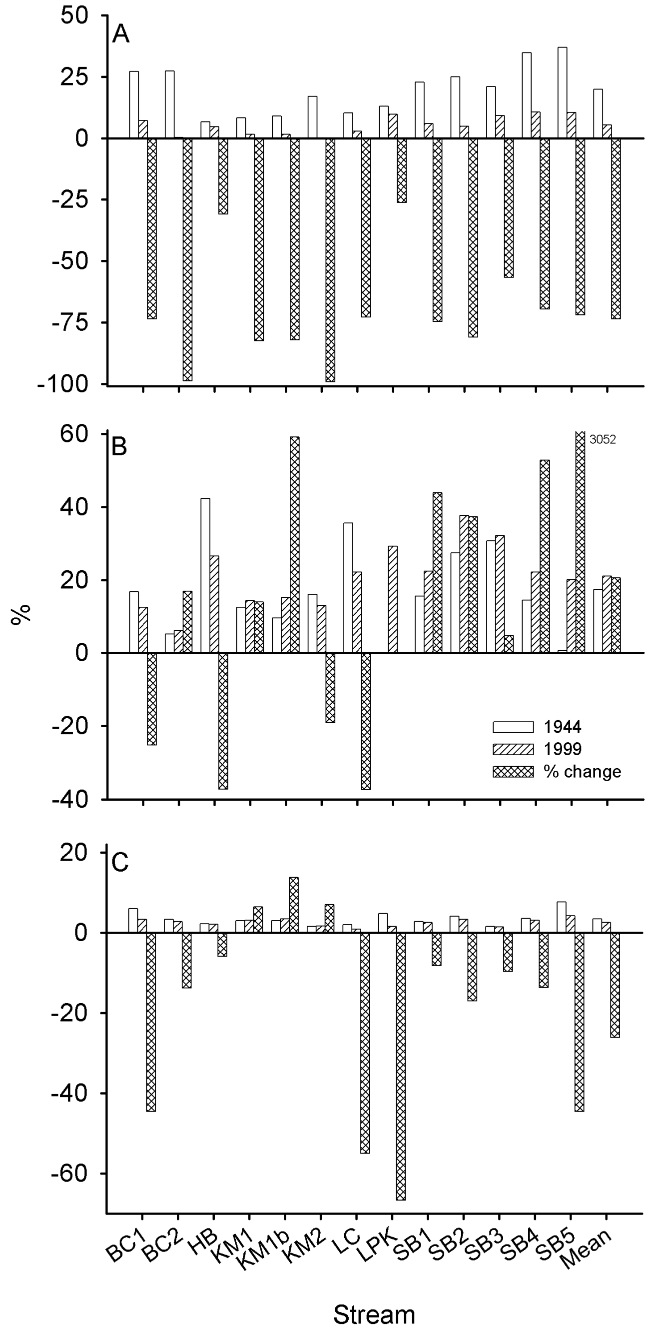

FIG. 3. Land cover classifications of study catchments in 1944 and 1999. A.—Bare ground. B.—Recovering. C.—Unpaved roads. Percent change is the relative % change in each land cover type from 1944 to 1999 (negative values indicate a reduction in that land cover from 1944 to 1999). Disturbed and recovering land covers were restricted to those on slopes >5%. Percent change in recovering land cover could not be calculated for LPK because this site had 0% of this cover in 1944. For site SB5, recovering land cover increased from 0.64 to 19.53%, a 3052% change. Stream abbreviations are given in Appendix.

TABLE 1. Results of multiple regression and partial correlation analyses. Adjusted R^2 (R^2_{adj}) values are from models in which response variables were regressed with % bare ground and % road cover in catchments in 1999 (D99), % recovering land in catchments in 1999 (R99), and catchment area (the contemporary landuse/landscape model). β is the standardized regression coefficient from the models. Partial correlations were calculated as correlations of residuals from the contemporary landuse/area model with residuals from either the model D44 = D99 + R99 or R44 = D99 + R99 (see text for description). SRP = soluble reactive P, DOC = dissolved organic C, BPOM = benthic particulate organic matter, CWD = submerged coarse woody debris, EPT = number insect taxa in the aquatic insect orders Ephemeroptera, Plecoptera, and Trichoptera, H' = Shannon diversity, GASCI = Georgia Stream Condition Index, GPP = gross primary production, Rs = respiration, D44 = % of bare ground and unpaved road cover in a catchment in 1944, R44 = % recovering land in a catchment in 1944. Bold font indicates statistical significance at $p < 0.05$; italic font indicates statistical significance at $p < 0.10$.

	Contemporary landuse/landscape model				Partial correlation coefficient	
Variable	D99 β (partial R^2)	R99 β (partial R^2)	Area β (partial R^2)	R^2_{adj}	D44	R44
Physical and chemical						
pH	*0.53 (0.35)*	0.44 (0.29)	0.18 (0.06)	*0.44*	**0.6**	–0.34
SRP	**–0.41 (0.61)**	**–0.45 (0.67)**	**0.44 (0.66)**	**0.89**	–0.41	*–0.55*
NO_3^--N	–0.02 (0.00)	0.54 (0.27)	–0.21 (0.05)	0.13	–0.20	–0.18
DOC	*–0.58 (0.36)*	–0.16 (0.04)	0.18 (0.06)	*0.38*	–0.18	–0.04
BPOM	**–0.85 (0.60)**	0.02 (0.00)	–0.08 (0.02)	**0.52**	**–0.63**	0.35
CWD	**–0.91 (0.75)**	0.03 (0.00)	0.00 (0.00)	**0.73**	0.5	0.07
Flashiness	*0.79 (0.52)*	–0.13 (0.03)	–0.10 (0.02)	0.39	–0.12	0.23
Streambed instability	–0.28 (0.15)	*0.60 (0.51)*	*–0.66 (0.53)*	*0.56*	0.08	**0.71**
Diatoms						
% *Eunotia*	**–0.78 (0.75)**	0.27 (0.31)	*0.34 (0.38)*	**0.81**	*–0.53*	–0.20
Density	**–0.62 (0.78)**	–0.05 (0.02)	**0.45 (0.66)**	**0.9**	**–0.65**	0.04
Macroinvertebrates						
% clingers	**–0.84 (0.72)**	0.34 (0.32)	0.19 (0.13)	**0.69**	–0.34	0.15
No. chironomid taxa	**–0.67 (0.62)**	0.01 (0.00)	*0.38 (0.36)*	**0.69**	0.15	*–0.59*
EPT	**–0.71 (0.73)**	–0.04 (0.01)	*0.36 (0.42)*	**0.79**	–0.27	–0.14
H'	**–0.69 (0.56)**	0.28 (0.19)	0.35 (0.26)	**0.57**	–0.07	**–0.75**
Richness	*–0.56 (0.43)*	–0.11 (0.03)	0.37 (0.27)	**0.53**	–0.02	**–0.76**
GASCI	**–0.90 (0.79)**	–0.08 (0.04)	–0.05 (0.01)	**0.75**	–0.39	**0.69**
Fish						
Run density	–0.16 (0.11)	**0.71 (0.75)**	*–0.58 (0.63)*	**0.74**	*–0.70*	0.36
Pool density	0.19 (0.12)	*0.60 (0.63)*	–0.42 (0.43)	*0.68*	–0.26	–0.07
Richness	**–0.62 (0.78)**	**0.57 (0.79)**	**0.52 (0.73)**	**0.86**	–0.49	**0.9**
H'	**–0.74 (0.72)**	0.39 (0.47)	0.39 (0.44)	**0.74**	–0.37	0.6
Metabolism						
Rs	*–0.69 (0.43)*	–0.31 (0.16)	–0.20 (0.07)	*0.42*	0.47	–0.23
GPP	–0.18 (0.04)	0.43 (0.23)	–0.53 (0.27)	0.26	**–0.75**	–0.06

explained by measures of contemporary land use and catchment area. After 55 y of recovery from landscape disturbance, many forest patches at FBMI are in mid-successional stage, a time when soils have largely recovered from prior agricultural practices (Switzer et al. 1979, Maloney et al., in press). However, after accounting for the influence of contemporary land use and natural landscape features (i.e., catchment area), several contemporary chemical (pH, SRP) and physical variables (BPOM, bed instability) remained significantly correlated with historical landuse conditions.

A strong relationship between contemporary catchment disturbance and streamwater chemistry was not surprising. Changes in water chemistry after disturbance often return to predisturbance levels within 10 y (Likens et al. 1978, Lynch and Corbert 1991), and the 55 y of terrestrial recovery at FBMI was expected to be sufficient for recovery of streamwater chemistry. However, it was surprising that historical land use explained significant residual variation in streamwater pH, SRP, and BPOM; these results suggest that the imprint of historical land use on these variables remains for decades after abandonment. Elevated streamwater Ca^+ and NO_3^--N levels were reported 20 y after forest harvest (Swank et al. 2001); however, our study is the first to report the potential for longer-term influences of historical disturbances on contemporary streamwater chemistry.

The lack of a relationship between contemporary land use or natural landscape conditions and stream flashiness was a consequence of inclusion of an outlier stream (SB4; Maloney et al. 2005). SB4 was the only study stream with an undefined channel and, thus, could be considered a hydrological outlier (i.e., >2 SD from average recession constants for other streams). We retained SB4 in the present analysis to assess whether historical land use might account for the deviation of this site. However, when we removed this site from the analysis, the contemporary landuse/landscape model explained 94% (R^2_{adj}) of the variation in stream flashiness, whereas historical land use explained no significant variation in residuals ($p > 0.05$). Recovery of forests and their soils at FBMI after 55 y of abandonment (Switzer et al. 1979, Maloney et al., in press) is probably associated with reductions in overland flow caused by increased infiltration and uptake by catchment vegetation. The strong relationship between contemporary land use and flashiness might be a consequence of this reduced overland flow.

Streambed instability showed a strong relationship with historical land use. This relationship probably occurred because of the sandy substrate of stream channels. The sand originates from both upland catchment and instream sources. Catchment sediment sources can persist for decades to centuries (Meade 1982, Trimble 1999), whereas sediments originating from incised stream banks are often products of historical land use (Ireland et al. 1939). At FBMI, many of the historical agricultural fields are currently forested and have low erosion rates; however, sediments that eroded during the agricultural period continue to migrate through ephemeral channels toward and through perennial streams. Moreover, sediment input is probably higher from incised stream banks in historically more-disturbed catchments than in less-incised stream banks in historically less-disturbed catchments. High sediment input from legacy erosion and contemporary bank failure to streams in historically disturbed catchments might promote the strong relationship between streambed instability and historical land use.

The absence of a legacy effect on CWD was surprising because CWD residence times in streams often are >100 y (Wallace et al. 2001, May and Gresswell 2003). One reason for this result might have been historical removal of CWD from streams ("cleaning"; Harmon et al. 1986). If this practice occurred at FBMI before 1944, then most instream CWD would have originated after military purchase, and thus, would show stronger relationships with contemporary (cf. historical) land use. Unlike CWD, smaller sized BPOM has a relatively short residence time; this characteristic would explain the strong negative relationship between BPOM and contemporary disturbance level. Moreover, instream BPOM is retained by CWD (Bilby 1981, Wallace et al. 1995); thus, the strong negative relationships of CWD and BPOM with contemporary disturbance levels probably are associated. BPOM showed a surprising negative relationship with increasing historical disturbance. This relationship might be the consequence of separate or combined influences of reduced organic matter and increased inorganic matter input in historically more disturbed catchments.

Stream biota

The strong relationships of contemporary land use and catchment area with contemporary biotic assemblages are not surprising, given the strong relationships of land use and natural variables with associated habitat conditions. In fact, these strong relationships suggest that land use and catchment area probably are controlling influences on contemporary biotic assemblages. However, significant relationships of residual variation in diatom, macroinvertebrate, and fish assemblages and whole-stream GPP with historical land use suggest that contemporary assemblages continue to be influenced by historical land use in these streams. Diatoms within the study streams were numerically dominated by *Eunotia* (range 24.1–90.6%, mean = 63.4%), a group that is acidophilic (taxa usually occurring at pH <5.5; Van Dam et al. 1994) and largely nonmotile (S. A. Miller, Auburn University, unpublished data). However, streams in catchments with high levels of contemporary disturbance had pH values above the optimal level for most *Eunotia*, and streams in historically disturbed catchments had unstable stream beds, in which sediment deposition might bury nonmotile taxa, such as *Eunotia* (Miller 2006, see also Bahls 1993). Thus, diatom assemblages in FBMI streams seem to be subject to the dual controls of contemporary land use, through reduced habitat and nutrient concentrations, and historical land use, through high bed instability.

Contemporary land use and catchment area also explained much of the variability in all macroinvertebrate metrics (EPT, Chironomidae, and total richness, H', GASCI) and most fish metrics (taxon richness, H') evaluated. Strong relationships between these assemblages and contemporary land use are reported commonly, and such relationships underlie the use of benthic macroinvertebrates and fishes in studies of stream biotic integrity (e.g., Barbour et al. 1999). However, our results suggest that the imprint of historical land use remains on contemporary assemblages in FBMI streams. The positive correlations between benthic biotic integrity (GASCI) and fish richness with R44 indicate that both metrics show some, but not full, recovery from historical land use before 1944. Our results also suggest that degraded biotic conditions remain from historical land use because D44 was negatively correlated with residual variation in fish density in run habitats and R44 was negatively correlated with residual variation in Chironomidae richness and overall macroinvertebrate richness and diversity. Landuse legacies have been demonstrated for benthic macroinvertebrates and fishes in streams of western North Carolina (Harding et al. 1998). Streambed instability, which was strongly related to R44, might be the strong driver of the high correlation between R44 and macroinvertebrate and fish response variables. Increased bed instability can reduce available stable habitat for macroinvertebrates and fish spawning (Cordone and Kelley 1961), and also might reduce foraging efficiency of drift-feeding fishes (Ryan 1991).

Measurements of whole-stream metabolism clearly indicate a potential legacy effect because residual variation in GPP was strongly related to levels of historical disturbance. A potential mechanism for this relationship is streambed instability in historically disturbed catchments, an apparent legacy of agriculture that predates military training at FBMI. High bed instability probably reduces habitat quality for periphytic algae and cyanobacteria, the primary autotrophs in these streams (Miller 2006). Rs was negatively related to contemporary catchment disturbance level, a trend that probably is the result of low availability of labile organic C, CWD, and associated debris dams ("hot spots" for benthic metabolism; Hedin 1990, Fuss and Smock 1996, Houser et al. 2005) in streams in catchments with high levels of contemporary disturbance.

Disturbance legacies and implications for stream ecology and conservation

At FBMI, many contemporary stream physical, chemical, and biological variables continue to be influenced by historical (>55-y-old) agriculture. Estimating full recovery times for these streams from the effects of historical agriculture is not feasible, given the additional contemporary disturbance from military activities, but full recovery times in these streams are likely to be longer than those reported for nearby terrestrial ecosystems (e.g., at middle stage of succession 45–100 y; Switzer et al. 1979). Future stream recovery after cessation (or mitigation) of military activities also is difficult to predict from our results because the focus of our study was on stream recovery after cessation of agriculture. However, military land-use practices are often smaller in scale and often involve better erosion control and land management practices than historical agriculture, so streams might recover more quickly from military disturbances than from agriculture. We suggest doing additional research to quantify the recovery of ecosystems after cessation/mitigation of military practices, especially considering that as much 6% of global environmental degradation is consequent to military land use (Vertegaal 1989).

Incorporating a legacy perspective into ecological studies also might help elucidate potential mechanisms explaining outlier data points (e.g., whole catchments in our study). Such a perspective might provide insight into subtle biotic interactions and their associations with local environmental conditions and aid in identification of reference conditions in studies of biotic integrity and restoration. For example, we were able to use a legacy approach to relate increased streambed instability with historical disturbance and, in turn, with habitat-mediated variability in the dominance of *Eunotia* spp. that was unexplained by contemporary land use. Without quantitatively rigorous approaches designed to assess the potential influence of historical disturbance on contemporary measures one can offer only speculative explanations for high levels of habitat alteration in certain streams and their legacy effects on contemporary biota. Nevertheless, in studies of biotic integrity and restoration, assignment of disturbance levels typically is based on contemporary landuse and catchment conditions, with little or no consideration of prior land use that could manifest as measurable legacy effects. We suggest that failure to recognize legacy effects in systems with minimal contemporary disturbances could lead to misclassification of depauperate systems as being in reference condition.

Last, our results are correlative, so our inferences linking historical land use and contemporary stream conditions are only speculative, and thus, must be strengthened by more research, including studies based on natural experiments. In particular, studies that use whole catchments as replicates and are designed to compare responses among a suite of recovering and reference sites (e.g., contemporary responses of historically disturbed but recovered catchments vs historical reference but currently disturbed catchments) could provide a more direct means of quantifying the prevalence and relative importance of legacy vs contemporary influences on streams. Ironically, identification of multiple reference catchments of similar character might be impractical because of the high degree of historical landscape disturbance in many regions. Another potentially fruitful approach would be to quantify stream conditions within catchments with contrasting levels of recovery. This design might be more feasible than an experimental approach and might elucidate recovery rates of stream processes from historical disturbance, a topic in which stream ecologists lag far behind their terrestrial counterparts.

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Appendix. Site characteristics and years in which each study stream was sampled. Military land uses: IR = infantry/ranger light impact, HM = heavy machinery; CWD = submerged coarse woody debris, BPOM = benthic particulate organic matter, UTM = Universal Transverse Mercator. — indicates not sampled.

Stream	Stream code	UTM	Military land use	Stream order	Catchment area (km^2)	Year contemporary stream variables were sampled: Periphyton	Macro-invertebrates	Fish	Metabolism	Water chemistry	CWD	BPOM	Flashiness	Bed instability
Bonham Tributary	BC1	0710893N 3588286E	IR	2	2.1	2001, 2002	2000, 2001, 2002	2003	2001, 2002, 2003	2000, 2001, 2002, 2003	2002, 2003[a]	2001, 2002, 2003[a]	2000, 2001, 2002, 2003	2003
Bonham Tributary	BC2	0710627N 3588976E	IR	2	0.75	2001, 2002	2000, 2002	2003	2001, 2002, 2003	2000, 2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2000, 2002, 2003	2003
Hollis Branch	HB	0717848N 3583123E	IR	2	2.15	2001, 2002	2002, 2003	2003	2001, 2002	2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2001, 2002, 2003	2003
Kings Mill Creek Tributary	KM1[b]	0720701N 3600036E	IR	2	3.69	—	2001, 2002	—	2001, 2002, 2003	2000, 2001, 2002	2002, 2003	2001, 2002, 2003	2001, 2003	2003
Kings Mill Creek Tributary	KM1b[b]	720897N 3599493E	IR	2	3.35	2001, 2002	—	2003	—	—	—	—	—	—
Kings Mill Creek Tributary	KM2	0719946N 3599991E	IR	3	2.31	2001, 2002	—	2003[a]	2001, 2002, 2003	2000, 2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2001, 2002, 2003	2003
Lois Creek	LC	0715377N 3597908E	IR	2	3.32	2001, 2002	2000, 2001, 2002	2003	2001, 2002, 2003	2000, 2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2000, 2001, 2002, 2003	2003
Little Pine Knot Tributary	LPK	0719223N 3585421E	HM	2	0.33	2001, 2002	2000, 2001, 2002	2003[a]	2001, 2002, 2003	2001, 2002, 2003	2002, 2003	2001, 2002, 2003	—	2003
Sally Branch Tributary	SB1	0716349N 3585850E	HM	3	5.43	—	2000, 2001, 2002	2003[a]	—	2000, 2001	2002	2001, 2002	—	—
Sally Branch Tributary	SB2	0716808N 3584787E	HM	2	1.23	2001, 2002	2002, 2003	2003	2001, 2002, 2003	2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2001, 2002, 2003	2003
Sally Branch Tributary	SB3	0716673N 3584684E	IR	1	0.72	2001, 2002	2002, 2003	2003	2001, 2002, 2003	2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2001, 2002, 2003	—
Sally Branch Tributary	SB4	0716005N 3584889E	HM	1	1	2001, 2002	2002, 2003	2003	2001, 2002, 2003	2001, 2002, 2003	2002, 2003	2001, 2002, 2003	2001, 2002, 2003	2003
Sally Branch Tributary	SB5	0714935N 3585249E	HM	2	1.27	2001	2001, 2002	—	2001, 2002, 2003	2001, 2002, 2003	2002	2001, 2002	—	—

[a] Data from site not included in analyses (see Methods for explanation

[b] Fish and periphyton samples for KM1 collected at a site located upstream from other samples (labeled KM1b)