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MATURE AND OLD-GROWTH RIPARIAN FORESTS: STRUCTURE, DYNAMICS, AND EFFECTS ON ADIRONDACK STREAM HABITATS

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Abstract. Riparian forests regulate linkages between terrestrial and aquatic ecosystems, yet relationships among riparian forest development, stand structure, and stream habitats are poorly understood in many temperate deciduous forest systems. Our research has (1) described structural attributes associated with old-growth riparian forests and (2) assessed linkages between these characteristics and in-stream habitat structure. The 19 study sites were located along predominantly first- and second-order streams in northern hardwood–conifer forests in the Adirondack Mountains of New York (USA). Sites were classified as mature forest (6 sites), mature with remnant old-growth trees (3 sites), and old-growth (10 sites). Forest-structure attributes were measured over stream channels and at varying distances from each bank. In-stream habitat features such as large woody debris (LWD), pools, and boulders were measured in each stream reach. Forest structure was examined in relation to stand age using multivariate techniques, ANOVA, and linear regression. We investigated linkages between forest structure and stream characteristics using similar methods, preceded by information-theoretic modeling (AIC).

Old-growth riparian forest structure is more complex than that found in mature forests and exhibits significantly greater accumulations of aboveground tree biomass, both living and dead. In-stream LWD volumes were significantly ($\alpha = 0.05$) greater at old-growth sites (200 m^3/ha) compared to mature sites (34 m^3/ha) and were strongly related to the basal area of adjacent forests. In-stream large-log densities correlated strongly with debris-dam densities. AIC models that included large-log density, debris-dam density, boulder density, and bankfull width had the most support for predicting pool density. There were higher proportions of LWD-formed pools relative to boulder-formed pools at old-growth sites as compared to mature sites. Old-growth riparian forests provide in-stream habitat features that have not been widely recognized in eastern North America, representing a potential benefit from late-successional riparian forest management and conservation. Riparian management practices (including buffer delineation and restorative silvicultural approaches) that emphasize development and maintenance of late-successional characteristics are recommended where the associated in-stream effects are desired.

Key words: Adirondack stream habitats (New York, USA); canopy gaps; debris dams; forest management and restoration; forest structure; northern hardwoods; old-growth; riparian forests; stand development; stream geomorphology; stream habitat; woody debris.

Introduction

In the northern forest region of the eastern United States, protection and establishment of riparian buffers, either through restoration efforts or delineations of extant forest, are increasingly used to mitigate land-use impacts on freshwater systems, such as alteration of hydrologic regimes, pollutant and sediment movement, and loss of high-quality habitats for aquatic biota (Kondolf and Micheli 1995, Endreny 2002, Sweeney et al. 2004). Such measures are occurring across a range of ownerships, public and private, although riparian management standards vary (Lee et al. 2004). Unlike the U.S. Pacific Northwest (see Gregory 1997), riparian management objectives in the northern forest region of eastern North America typically are not linked to a desired successional stage or development of specific structural attributes (Brinson and Verhoeven 1999). Instead, a more general objective of maintaining continuous forest cover is usually recommended, primarily to stabilize banks and to filter pollutants (Endreny 2002). For this reason many eastern U.S. states allow forestry practices, such as diameter-limit and selection harvesting, that periodically remove the largest trees within riparian buffers (see, e.g., VT DFPR 1987, Sheridan et al. 1999, Lee et al. 2004). These practices limit the development of those structural characteristics that are most likely to affect stream systems, such as development and recruitment of large

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woody debris (LWD, Gore and Patterson 1985, Mladenoff and Pastor 1993, Hale et al. 1999, McGee et al. 1999, Crow et al. 2002, Angers et al. 2005, Keeton 2006).

Forested landscapes and associated riparian corridors in the northeastern United States have changed profoundly in the last 300 years (Foster et al. 1998, Cogbill 2000). Land-use history has shifted age-class distributions from an old-growth forest dominance (pre-European settlement) to a current condition dominated by young to mature (e.g., 50–100 year old) forests (Lorimer 2001, Lorimer and White 2003). Restoration and management for old-growth forest characteristics is of increasing regional interest across a range of ownerships (Bennet 2005), but many of the presumed ecological values of this approach, such as riparian functions, are not well understood (Nislow 2005). Managers now face a dilemma where secondary riparian forests have recovered or are being restored, raising questions such as whether they should: (1) allow conventional timber harvesting that has the potential to limit further stand development, or (2) promote continued late-successional development via alternative approaches, such as passive management or restorative silvicultural practices (e.g., Singer and Lorimer 1997, Keeton 2006). Consequently, an important area for investigation is the extent to which late-successional riparian functions, such as provision of LWD to stream channels, are provided by the currently dominant mature northern hardwood forests. Do riparian-forest influences on streams change with structural development into an old-growth condition (Hunter and White 1997, Franklin et al. 2002), and are these linked to structural characteristics that could be promoted through management?

Comparatively more is known about the old-growth structural characteristics of upland eastern deciduous and mixed hardwood–conifer forests than about lowland and riparian forests (Woods and Cogbill 1994, McGee et al. 1999, Angers et al. 2005). Old-growth northern hardwood–conifer forests differ structurally from young to mature forests (Tyrell and Crow 1994*a*, Goodburn and Lorimer 1998, Ziegler 2000). They exhibit a wider range of age classes and tree diameters, elevated densities of large trees, larger canopy gaps, greater vertical differentiation of the canopy, and higher volumes of LWD, including snags and downed wood. The extent to which structural characteristics found in upland northern hardwood–conifer old-growth forests also occur in riparian old-growth forests has not previously been investigated. Riparian forests can have different disturbance regimes (e.g., flooding), compositional dynamics, and site productivity (due to nutrient enrichment) compared to uplands (Gregory et al. 1991, Hughes and Cass 1997); these are likely to either enhance or retard late-successional structural development.

Riparian forests regulate or influence important ecological linkages between terrestrial and aquatic systems (Gregory et al. 1991, Naiman et al. 1998, Pusey and Arthington 2003, Sweeney et al. 2004). Relationships between riparian forest structure and in-stream aquatic-habitat characteristics have been well established in some ecosystems, such as temperate coniferous forests in the Pacific Northwest (Naiman et al. 2000). Similar relationships are hypothesized for other ecosystems (Ward et al. 2002), but in the deciduous and mixed deciduous–coniferous ecosystems of the eastern United States researchers have primarily investigated the riparian influences of relatively young, secondary forests (e.g., Osterkamp and Hupp 1984, Thompson 1995, Zaimes et al. 2004). Many relationships between forests and in-stream habitats documented in the U.S. Pacific Northwest involve very large trees and other late-successional structural characteristics, such as high LWD volumes, associated with some of the most structurally complex, temperate forests in the world (Spies et al. 1988, Van Pelt et al. 2006). LWD inputs are known to influence biocomplexity and stream geomorphology in many river systems throughout the world (Gurnell et al. 2005, Naiman et al. 2005*a*). However, it remains uncertain how riparian-forest influences on streams change with processes of stand development in many temperate deciduous and mixed hardwood–conifer forest ecosystems, particularly those for which less is known about late-successional development, structure, and dynamics. This limits our ability to determine how riparian forest management approaches may affect stream ecosystem processes.

Most studies of the riparian influences of late-successional forests have been conducted in the western United States, where clear linkages have been established between forest structure, stream geomorphology, and in-stream habitat characteristics (Bilby and Ward 1991, Richmond and Fausch 1995, Berg et al. 1998, Naiman et al. 1998, 2000). In other regions the scarcity of old-growth forests has restricted opportunities for similar evaluations, with a few notable exceptions in the southeastern United States. (Hedman et al. 1996, Valett et al. 2002), including Southern floodplain systems (Lockaby et al. 1997). Most research in eastern North America has focused on relatively young (e.g., $<$100 year old), secondary forest influences upon pollutant and sediment transport into streams (Peterjohn and Correll 1984, Endreny 2002, Zaimes et al. 2004) and influences on hydrologic regimes (Gore and Shields 1995, Johnson et al. 1995). Moreover, it should not be presumed that late-successional forests in eastern North America necessarily affect stream systems the same way they do in other temperate regions. For instance, previous research in Adirondack streams with early-mature riparian forests suggested that pool formation was driven to a much greater degree by boulders rather than by LWD, reflecting the distinct surficial geology of the region (Kraft et al. 2002, Warren and Kraft 2003). Thus, an important question remains whether riparian functions change in relation to late-successional forest development across a range of temperate forest ecosystems.

Our research addresses this question using northern hardwood–conifer forests in the Adirondack Mountains of upstate New York (USA) as a case study (see Fig. 1). We followed Gregory et al.'s (1991:540) functionally derived definition of riparian areas as "three-dimensional zones of direct interaction between terrestrial and aquatic ecosystems" and "comprised of mosaics of landforms, communities, and environments." This definition was most appropriate because distinct boundaries or compositional differences with "upland communities" (e.g., see alternative definition of riparian areas in Naiman et al. [2005*b*:2]) are not always evident within low-order riparian corridors in our study region. We report on a dataset that is unique because (1) previous studies of old-growth riparian forests in the eastern United States made categorical comparisons without specifically assessing forest structure (Hedman et al. 1996, Valett et al. 2002), (2) our analysis evaluates a relatively large number of old-growth sites, and (3) this is one of the first investigations of old-growth riparian forests in the northern forest region.

Our research (1) describes structural attributes associated with late-successional riparian forests and (2) assesses linkages between these characteristics and indicators of in-stream habitat structure, specifically, LWD, debris dams, and pools. These features are known to influence aquatic biota (Wallace et al. 1995, Gowan and Fausch 1996, Roni and Quinn 2001, Pusey and Arthington 2003), sediment retention (Bilby and Likens 1980, Bilby and Ward 1991, Diez et al. 2000), and biogeochemical processing of nutrients and organic carbon (Steinhart et al. 2000, Valett et al. 2002, McClain et al. 2003). We hypothesized that old-growth riparian forests are more structurally complex (higher biomass, variation in canopy closure, LWD volume, tree height diversity, etc.) than mature forests and have strongly associated effects on LWD accumulations in streams. If this linkage with in-stream habitat is substantiated, we hypothesized that in-stream woody-debris levels would positively correlate with other stream habitat characteristics, such as debris-dam and pool densities. Boulders and stream size also influence variability of in-stream structure, especially pool formation (Kraft et al. 2002, Warren and Kraft 2003). Thus, to test the latter hypothesis we needed to explore interactions between in-stream attributes related to forest structure and site-related geomorphic factors. An important goal throughout this study was to inform riparian forest management, such as determination of structural-development objectives and associated silvicultural approaches.

METHODS

Study areas and sites

Our study was conducted in the western portion of the Adirondack State Park of upstate New York (USA), which contains one of the largest known areas of old-growth forest (estimated at >80 000 ha.) remaining in the northeastern United States (Leopold et al. 1988, Davis 1996). Because old-growth in this region is extensive and well distributed, old-growth sites are not anomalous in terms of biophysical representation or site productivity (McMartin 1994). Our study sites are a statistical sample of late-successional northern hardwood–conifer forests in the Adirondack region. However, late-successional forests in the Adirondacks (Leopold et al. 1988, Woods and Cogbill 1994, McGee et al. 1999, Ziegler 2000) share many structural and compositional characteristics found throughout the northern hardwood region of the eastern United States (Gore and Patterson 1985, Foster 1988, Tyrell and Crow 1994*a*, Hunter and White 1997, Hale et al. 1999, Crow et al. 2002) and Canada (Angers et al. 2005). Thus, while our study sites are most representative of Adirondack ecosystems, they have broader relevancy to issues of old-growth forest recovery and riparian management in eastern North America.

Study sites were located in three areas: a 20 200-ha privately owned preserve, the Five Ponds state wilderness area, and the Pigeon Lakes state wilderness area. Each of these areas is located within a different 4th-order watershed separated by >40 km. We selected these areas due to their high concentrations of primary (i.e., never logged; not burned by historical fires), old-growth forests. We selected sites from the available known occurrences (B. Kershner, 2002 *unpublished map* of old-growth forests in New York; *available online*)[4] of old-growth and proximate, comparable secondary forests based on site-matching criteria. These ensured similarity in (1) forest cover type (northern hardwood–conifer); (2) average age of dominant canopy trees (>80 yr); (3) geographic representation (wide distribution within the western Adirondack region); (4) disturbance history; (5) stream size (bankfull width 2–16 m); and (6) reach length (150–300 m). Reach lengths varied due to upstream/downstream constraints, such as abrupt changes in cover type (e.g., intervening swamp) or stream geomorphology. The mature, secondary stands originated from logging (primarily selection for pulpwood) and subsequent fires in the late 19th and early 20th centuries (Ziegler 2000, Latty et al. 2004). Sites selected for this study have had little or no logging since establishment due to their protected status, allowing us to control for variability associated with management history.

Data collection

We collected data in summer 2002–2004 from a total of 19 sites (Table 1) along primarily 1st- and 2nd-order stream reaches. Riparian vegetation was dominated by mixed northern hardwood–conifer forest. Canopy species included *Betula alleghaniensis* (yellow birch), *Fagus grandifolia* (American beech), *Picea rubens* (red spruce), and *Tsuga canadensis* (eastern hemlock), with minor components of *Acer rubrum* (red maple), *A. saccharum*

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[4] ⟨http://www.championtrees.org/oldgrowth⟩

FIG. 1. Illustrations of northern hardwood–conifer forests in the Adirondack Mountains of upstate New York, USA. (Top left) Remnant old-growth yellow birch tree (age >400 yr) and downed large log persisting within a mature riparian stand (Pigeon Lakes Wilderness). (Top right) Debris dam in an old-growth forest stream (Little Moose Lake Outlet). (Bottom left) Interaction of large woody debris and boulders in an old-growth forest stream (Five Ponds Wilderness). (Bottom right) Old-growth northern hardwood–conifer forest in a riparian area (Little Moose Lake Outlet). An old-growth eastern hemlock tree (age >350 yr) is at center. Note the generally continuous vertical distribution of foliage. (Photo credits: W. S. Keeton.)

(sugar maple), and *Abies balsamea* (balsam fir). Scattered remnant old-growth *Pinus strobus* (eastern white pine) occurred at some sites.

Sites were classified into three age/structural classes: mature forest (6 sites), mature with scattered remnant old-growth trees (3 sites), and old-growth (10 sites). Definitions of old-growth northern hardwood and mixed northern hardwood-conifer forests vary, but generally use a combination of age (more than ~150 years), human-disturbance history, and structure (Dunwiddie et al. 1996, Hunter and White 1997). Our classifications were based on structural criteria (e.g., density of live trees >50 cm diameter at breast height [dbh]; "large tree" threshold based on protocol from previous studies of old-growth northern hardwoods [e.g., McGee et al. 1999]) and the average age of dominant trees. The age criteria defined "mature" sites as dominated by canopy trees 80 to 150 years of age, "old-growth" sites as dominated by trees >150 years of age, and "mature with remnants" as having a dominant

TABLE 1. Descriptive information for the 19 study sites in the western portion of the Adirondack State Park (New York, USA).

Site identification	Age class	Dominant tree age (yr)	Tree type (%)†		Total basal area (m^2/ha)	Total aboveground biomass (Mg/ha)	Mean bankfull width (m)	Stream gradient (%)
			Conifer	Hardwood				
Pigeon	mature with remnants	85	84	16	32.1	155	4.1	4.3
Combs	mature	106	13	87	26.3	167	4.2	5.4
Oxbow	mature	109	34	66	25.5	146	12.4	2.9
LMT3	mature	110	88	12	27.8	117	‡	0.3
Darby	mature	114	19	81	28.7	179	3.2	3.7
Panther Trail	mature with remnants	124	29	71	31.7	204	2.2	8.9
Otter	mature	132	32	68	34.8	195	5.0	0.8
Constable	mature with remnants	144	61	39	31.8	167	5.9	2.0
WH2	mature	145	45	55	33.3	181	3.4	6.4
LimekilnTrib.	old-growth	205	14	86	31.7	184	1.9	6.6
WH1	old-growth	254	34	66	33.7	201	6.6	2.5
LMT5	old-growth	270	68	31	39.2	224	‡	0.8
CLK2	old-growth	315	29	71	41.7	237	2.5	7.9
LM Outlet	old-growth	315	43	57	41.1	259	9.5	1.2
LMT1	old-growth	345	44	56	36.4	221	2.9	1.2
Sylvan	old-growth	350	59	45	45.3	279	‡	0.2
Panther Brook	old-growth	360	70	30	59.0	366	‡	4.5
CLK Outlet	old-growth	370	36	64	39.0	249	8.0	3.2
Limekiln	old-growth	410	33	67	46.3	274	16.0	0.9

Notes: Study sites are a sample of late-successional northern hardwood–conifer mature to old-growth sites in three areas, each located within a different fourth-order stream watershed. We define "dominant trees" as the largest trees in the primary upper canopy, with crowns occupying the majority of the growing space in the upper canopy and, with the exception of emergent trees, having the greatest access to light above the canopy.

† By basal area.

‡ Data not available.

mature cohort with scattered, morphologically distinct, remnant old-growth trees (see Fig. 1: top left). In most cases, sites in the latter category appeared to have originated from stand-replacing disturbance events (logging, fire, and/or windthrow) that left residual structure or "biological legacies," including remnant living trees (see Keeton and Franklin 2004, 2005). We used increment borers to determine age at breast height for 4–6 (proportionate to reach length) *B. alleghaniensis*, *P. rubens*, or *T. canadensis* at each site. We did not core *F. grandifolia* due to the prevalence of beech bark disease (*Nectria coccinea* var. *faginata*) and associated heart rot; minor species also were not cored. Cored trees were randomly selected from among the larger canopy dominants (excluding remnant trees). Therefore, stand ages used in this study are weighted toward the maximum achieved in the dominant cohort. Ages were estimated in the field following McGee et al. (1999). One unfragmented core per site was randomly selected and returned to the laboratory for analysis under a dissecting microscope in order to assess field error (mean = ±8 yr; SD = ±4 yr; no relationship found with tree diameter).

At each site, five transects were placed parallel to the stream channel: one along the channel center and two on each side. Forest transects were located 5 and 30 m, respectively, from the channel edge. All transects ran the entire length of each reach. Measurements of diffuse non-interceptance (DIFN) were taken with a LI-COR 2000 plant canopy analyzer (LI-COR, Lincoln, Nebraska, USA) at 15–30 (proportionate to reach length) randomly selected points along transects. LI-COR readings were post-processed to calibrate "below canopy" measurements against ambient "above canopy" light measurements taken by a remotely placed meter (LI-COR 1992). DIFN integrates mean leaf angle and leaf-area index (LAI), the latter of which is itself highly predictive of light attenuation through forest canopies (Welles and Cohen 1996). DIFN represents "percentage visible sky" and is thus strongly indicative of both canopy gap frequency and "canopy light absorption" (LI-COR 1992). Large woody debris (LWD; downed logs ≥10 cm in diameter at intercept, ≥1m length) volume was measured along each transect using a line-intercept method. In-stream transects followed the channel center to correct for dislocation of logs from the thalweg. The stream survey protocol followed Warren and Olsen (1964) and previous stream studies (Vallett et al. 2002) to ensure that logs were not double counted, etc.

Additional attributes of forest structure and composition were inventoried using 6–10 (proportionate to reach length) variable-radius (2.3 metric basal-area factor) prism plots randomly placed within 30 m of the stream bank (well distributed, even ratio per side). The heights of all sampled trees (>5 cm dbh) were measured in alternating plots (i.e., 50% of plots per site) with an Impulse 200 laser rangefinder (Laser Technology, Englewood, Colorado, USA). In-stream structures, including logs >30 cm diameter (hereafter referred to as "large logs"; size threshold based on protocol from stream studies in the northern hardwood region [e.g., Kraft et al. 2002]), woody debris dams, boulders >1 m median diameter, and pools >10 cm residual depth were counted and mapped using high-precision global positioning systems (GPS). For each in-stream feature, data were recorded describing dimensions, size, and function. Pools were defined using residual pool-depth criteria in Pleus et al. (1999), and pool area was determined by measuring the length and width of each pool. The dominant pool-forming element was also recorded for each pool. Debris dams were defined as an accumulation of multiple pieces of smaller woody debris between 0.5 and 1 cm in diameter against or around at least one key piece of LWD >10 cm in diameter (with a minimum debris-dam volume of ~0.5 m^3). Debris dams were classified as such if they "obstructed water flow" as per Bilby (1981), but this did not necessitate pool formation. Bankfull width, wetted channel width, and stream gradient were measured every 10 m at 15 to 30 locations (proportionate to reach length) along each channel.

Data analysis

Forest inventory plot data were input into the Northeast Ecosystem Management Decision Model (NED-2, Twery et al. 2005) to generate forest-structure metrics, including aboveground biomass estimates based on species-specific allometric equations developed by Jenkins et al. (2003). Relative-density calculations followed Curtis (1982). These were combined into a data matrix of forest structure and in-stream habitat characteristics arranged by site. Departure from normality was tested for all variables using the Wilk-Shapiro test (Zar 1996). Variables (e.g., pool density) exhibiting a non-normal distribution ($\alpha = 0.05$) were log transformed for tests requiring an assumption of normality. Equal-variance assumptions were confirmed using tests of variance (F tests). To quantify vertical structure we calculated a tree-height diversity index for plots with measured tree heights. The index used the formula for the Shannon-Wiener diversity index, substituting average stem density within 1 m vertical strata for species abundance (Staudhammer and LeMay 2001). LWD volume was calculated following Warren and Olsen (1964) as modified by Shivers and Borders (1996).

Sample sizes varied by statistical test. Evaluations of forest structure and most aspects of in-stream structure utilized data from all study sites ($n = 19$ sites). However, sample sizes for tests involving in-stream LWD varied from 17 to 19 sites depending on whether it was appropriate to include: (1) one site with a history of wood removal from the stream, and (2) another site where physical processes, such as ice flows, appeared to have removed most logs from the stream channel (one site with evidence of less severe ice flow was included in the analyses). Sample sizes were lower ($n = 15$ sites) for tests of variables related to pools, bankfull width, and DIFN due to inconsistencies in data collection at some sites (e.g., equipment malfunction or loss).

We used both categorical and continuous analytical methods because these offer different yet complementary perspectives. Both the former (McGee et al. 1999) and the latter (Ziegler 2000) have been used for analyses of forest structure/age relationships in the Adirondack region. Continuous analyses explored the relative predictive power of independent variables across the spectrum of conditions sampled. Categorical comparisons tested a-priori hypotheses contrasting the differences between mature and old-growth sites. Specific tests were associated with the two primary hypotheses.

Hypothesis 1. *Old-growth riparian forests are more structurally complex than mature forests and increase LWD accumulations in streams.*

Relationships between structural characteristics (independent variables) and the age of dominant trees (dependent variable) were examined using classification and regression tree (CART) analysis with S-Plus software (Statistical Sciences 2002). CART is a robust, nonparametric, binary procedure that partitions variance in a dependent variable through a series of splits based on values of the independent variables (Breinman et al. 1984). Cost-complexity pruning was used to eliminate nonsignificant nodes. We did not use CART to establish definitive thresholds of the predictor variables. Rather, CART provided a way to identify the structural characteristics most strongly associated with forest development along a spectrum of forest ages. It is this sequence (in relation to values of the dependent variable) and the hierarchy of predictor variables that were of primary interest. We used single-factor ANOVA and post-hoc Bonferoni multiple comparisons to test for significant differences ($\alpha = 0.05$) between forest age classes.

We used linear-regression modeling to explore relationships among (1) continuous variables identified as significant in CART and ANOVA and (2) in-stream LWD accumulations. Alternative curve-fitting techniques were employed. Logarithmic, polynomial, and negative exponential curves (transformation of the dependent variable) were fitted where nonlinear relationships were evident.

Hypothesis 2. *In-stream woody debris abundance is positively correlated with the density of two key stream-habitat features: debris dams and pools.*

We used a different analytical technique for analyses of pool density because we were specifically interested in the interaction of in-stream LWD and stream geomorphic variables. To test this hypothesis it was also necessary to determine the relative predictive strength of independent variables across all sites, rather than for partitioned subsets of sites (as in CART). We constructed 20 models (based on alternative variable combinations) relating in-stream structural (large-log density, LWD volume, and debris-dam density) and geomorphic variables (boulder density, bankfull width, and stream gradient) to pool density. Individual models employed either varying combinations of these variables or single

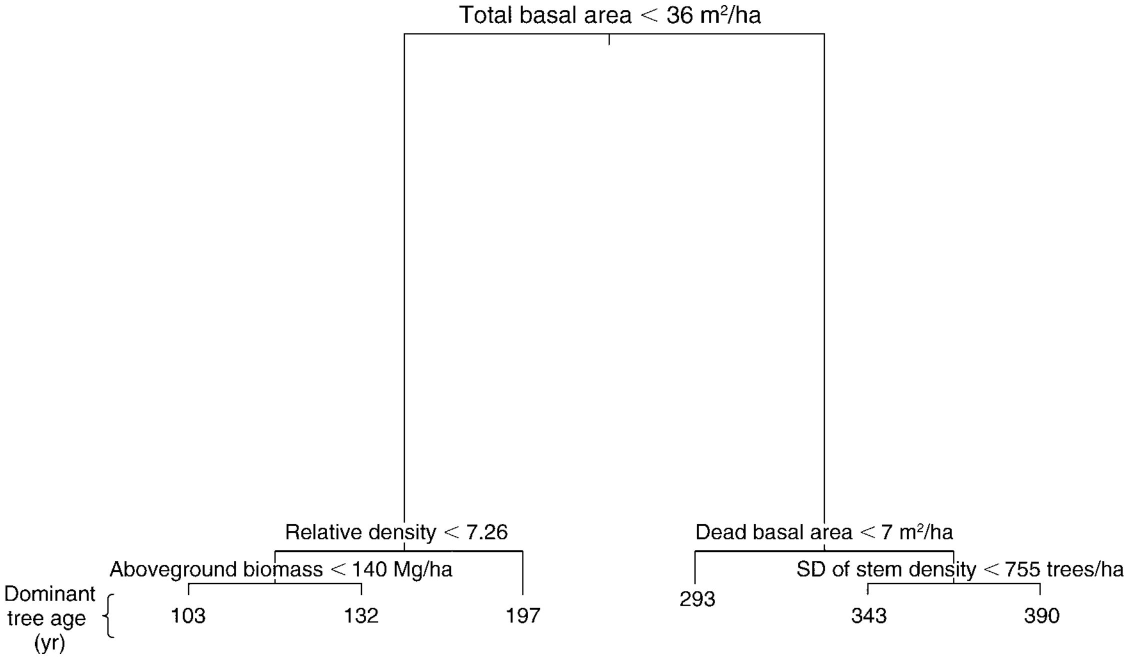

FIG. 2. Classification and regression trees, showing independent variables selected, split values, and partitioned mean values (bottom) of the dependent variable (age of dominant trees). The figure ranks variables by predictive strength (top to bottom) and in sequential order of importance as tree age increases (left to right). The length of each vertical line is proportional to the amount of deviance explained. Independent variables were selected from an initial set of 17 variables. Minimum observations required for each split = 4; minimum deviance = 0.01.

variables, so that the number of variables per model ranged from one to five. Generalized least-squares regressions were run in S-Plus for each model to generate maximum-likelihood estimates. The models were then compared using the information-theoretic method, or Akaike's information criterion (AIC) (Burnham and Anderson 2002). The AIC model-selection approach also allowed us to evaluate information from multiple models, rather than a single strongest model, which was important given our interest in a number of specific forest-structure and stream geomorphic variables. Log likelihood estimates were input into an AIC program developed by B. R. Mitchell (University of Vermont; 2005 *unpublished model-selection software*). Due to a relatively modest sample size and to avoid 2nd-order bias we used a corrected ($\mathrm{AIC_c}$) modeling structure. $\mathrm{AIC_c}$ scores for each model were compared to the best (or most parsimonious) model (i.e. model with the lowest $\mathrm{AIC_c}$ score), such that $\Delta_i = \mathrm{AIC}_{\mathrm{c},i} - \mathrm{AIC_c}$. Ranked models having a Δ_i value of 4.0 or less were selected as having the most strength of evidence (Burnham and Anderson 2002), and inferences were based on these top-ranked models. Akaike weights [w_i, $w_i = \exp(-\Delta_i/2)/\Sigma$ (min, $r = 1$; max, R) $\exp(-\Delta_r/2)$] were generated to estimate the probability of a model being the strongest among a set, and R^2 values were examined to assess variability explained by individual models.

We used additional statistical tests to explore relationships between the variables identified in the strongest AIC models. Linear-regression analysis with alternate curve fitting was used to assess relationships between LWD accumulations and debris dams. We also used regressed geomorphic attributes (independent variables) against in-stream structure (dependent variables). We used a log-likelihood ratio, goodness-of-fit (*G* test) to test for significant differences between observed density of pools formed by boulders and pools by LWD at mature vs. old-growth sites. The *G* test approximates the χ^2 statistic, but is more robust than the chi-squared goodness-of-fit test when, as with our data, certain conditions are met (Zar 1996).

RESULTS

Riparian forest structure

The results strongly supported our first hypothesis. Forest-structure characteristics indicative of greater stocking and utilization of growing space (e.g., basal area, relative density, and biomass), large woody debris (LWD) recruitment (e.g., dead tree basal area), and horizontal complexity (e.g., spatial variation in stem density) increase with dominant tree age based on classification and regression tree (CART) results (Fig. 2). This is demonstrated by the sequential ranking of variables by predictive strength for subsets of sites ordered by increasing tree age (viewed left to right in Fig. 2). Collectively, these suggest a relationship between stand age and greater complexity of specific stand-structure attributes (as per Franklin and Van Pelt [2004]).

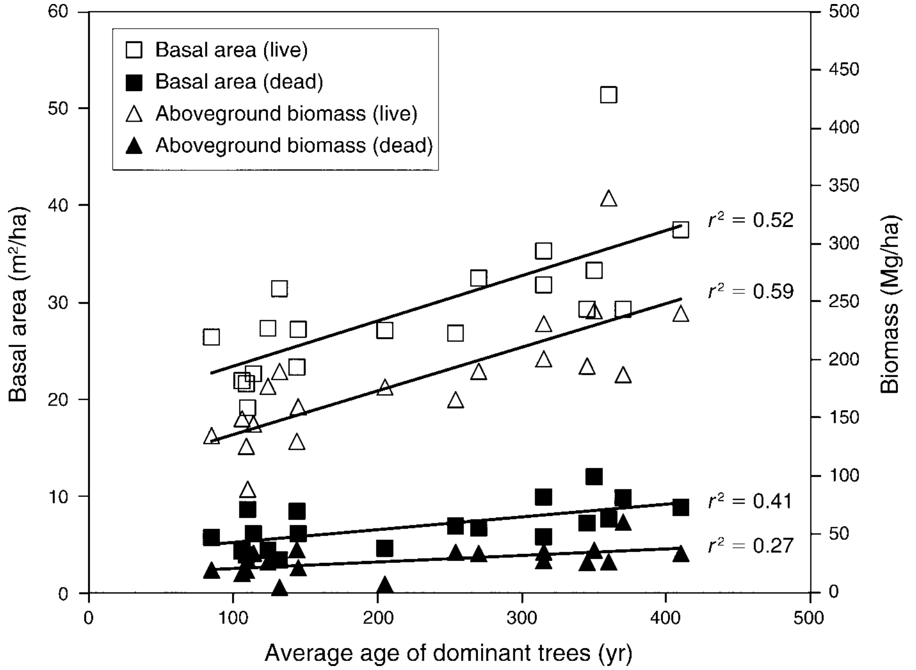

FIG. 3. Linear-regression relationships between basal area (by live tree and dead tree) or aboveground biomass (by live and dead tree) and the average age of dominant trees at study sites.

Of 17 independent variables used in an initial model, 5 variables were included in a final CART model. Basal area was the most important predictor of overall forest age in CART models, with sites falling below a threshold of 36 m^2/ha generally having dominant trees <250 years of age, and sites above that threshold having dominant tree ages extending above 300 years of age. The CART model identified several secondary predictor variables explaining lesser amounts of variance among sites after these were partitioned into two subsets based on basal area, which explained a significantly greater proportion of deviance. Values for two attributes of aggregate overstory structure, aboveground biomass (trees only), and relative density (a metric integrating basal area and quadratic mean diameter), were selected as partitioning points for variance among mature to early old-growth (e.g., 150–200 years of age) streamside forests. The basal area of dead trees and the standard deviation of stand density explained partitioning points among the oldest stands evaluated in this study, which were >250 years of age (Fig. 2).

A significant positive relationship was found between dominant riparian forest tree age and total basal area ($r^2 = 0.67$), live basal area ($r^2 = 0.52$), and dead tree basal area ($r^2 = 0.41$) (Fig. 3). This result was also supported by observed significant differences in numerous forest structure metrics as a function of forest age class; these metrics included basal area (total and live tree), aboveground biomass (total and live tree), relative density (live tree), q factor (ratio of tree densities between successively larger size classes), medial diameter, large-tree density, tree height diversity index (as an indicator of vertical structure), and canopy height (Table 2). For these metrics statistical significance was due to differences between old-growth and mature age classes based on multiple comparisons. The volumes of downed large woody debris (LWD) on the riparian forest floor were significantly larger ($P = 0.036$) in old-growth riparian forest sites (mean = 164 m^3/ha) compared to the mature riparian forest sites (mean = 86 m^3/ha). Dead-tree basal area and large-dead tree density, identified in CART as significantly correlated with stand age (continuous variable), were not statistically significant at the 95% confidence level when sites were grouped by age class (categorical variable). Mean stem density (total, live, or dead trees) showed no relationship with stand age in ANOVA analyses (Table 3). No significant differences in species composition (hardwood vs. conifer) were observed between the age classes.

Mature sites with remnant old-growth trees were intermediate in structure for some variables, but not for others (Table 2), and our ability to detect significant differences was limited by low sample size ($n = 3$ sites). Multiple-comparison results for this category were variable, with significant differences evident only when compared to old-growth sites. While mean values for the mature-with-remnants age class were, for a number of variables, close to those for old-growth sites in absolute terms, no statistically significant differences were found between the mature age class and sites categorized as mature with remnant old-growth (Table 2).

Table 2. Descriptive statistics and ANOVA results for forest structural variables grouped by age class.

Forest-structure variable	Values (mean ± 95% CI), by age class			ANOVA results		
	Mature, M	Mature with remnants, MR Forest-structure variable	Old-growth, OG	$F_{2,16}$	P	Multiple comparisons ($\alpha = 0.05$)
Stocking (live and dead)						
Basal area (m^2/ha)						
Total	29 ± 4	32 ± 1	41 ± 1	7.833	**0.004**	OG > M
Live	24± 5	26 ± 5	33 ± 5	5.3	**0.017**	OG > M
Dead	5 ± 2	6 ± 5	8 ± 2	2.912	0.083	
Aboveground biomass (Mg/ha)						
Total	164 ± 23	175 ± 29	250 ± 20	8.578	**0.003**	OG > M OG > MR
Live	144 ± 27	148 ± 29	221 ± 16	6.399	**0.009**	OG > M
Dead	21 ± 8	28 ± 10	33 ± 11	1.745	0.206	
Stem density (no. trees/ha)						
Total	956 ± 275	1139 ± 1182	1189 ± 263	0.823	0.457	
Live	777 ± 209	981 ± 875	1005 ± 249	1.065	0.368	
Dead	179 ± 151	159 ± 326	183 ± 55	0.059	0.943	
Relative density (no. trees/ha)	5.35 ± 0.70	5.97 ± 0.87	7.27 ± 0.70	7.065	**0.006**	OG > M OG > MR
Tree diameter distributions						
q factor †	1.51 ± 0.08	1.50 ± 0.18	1.39 ± 0.07	5.206	**0.036**	OG < M
Medial diameter (cm)	31.3 ± 3.5	33.3 ± 4.6	38.3 ± 3.1	6.732	**0.008**	OG > M
Quadratic mean diameter (cm)	20.1 ± 3.1	18.8 ± 6.8	21.3 ± 3.3	0.502	0.615	
Large-tree structure ‡						
Large tree density (no. trees/ha)‡						
Total	13 ± 7	19 ± 20	45 ± 14	8.699	**0.003**	OG > M
Live	11 ± 5	12 ± 19	37 ± 12	8.275	**0.003**	OG > M OG > MR
Dead	2 ± 2	7 ± 2	8 ± 4	3.312	0.063	
Composition, by basal area (%)						
Conifer	38.50 ± 28.10	58.00 ± 68.62	43.00 ± 12.79	0.78	0.475	
Hardwood	61.50 ± 28.10	42.00 ± 68.62	56.90 ± 12.90	0.774	0.478	
Canopy height (m)	28.33 ± 2.94	25.00 ± 6.57	31.00 ± 1.12	9.539	**0.002**	OG > MR
Tree height diversity index	4.23 ± 0.37	4.51 ± 1.82	5.03 ± 0.32	5.870	**0.012**	OG > M
Downed large woody debris, LWD						
Forest LWD volume (m^3/ha)	86.16 ± 33.89	144.48 ± 187.37	163.63 ± 39.57	4.14	**0.036**	OG > M

Note: Boldface is used to highlight significant *P* values.

† The *q* factor is the ratio of the number of trees in each size class to the number of trees in each successively larger size class.

‡ Trees >50 cm dbh.

Measurements of diffuse non-interceptance (DIFN) over stream channels were positively related to bankfull width, with decreasing overhead foliage and canopy closure as streams widened ($r^2 = 0.42$, $P = 0.030$). DIFN increased most precipitously for streams wider than 9 m bankfull width. When our analysis was restricted to streams <9 m wide, mean DIFN over stream channels (channel transects only) was not significantly different for old-growth stands (DIFN = 0.018) compared to mature stands (DIFN = 0.083) or mature stands with remnants (DIFN = 0.075). For DIFN measured within adjacent riparian forests, rather than over stream channels, there also was no significant difference between age classes (mean per site = average of four forest transects). However, the standard deviation of DIFN was significantly greater ($P = 0.038$) over old-growth stream channels compared to younger sites.

In-stream structure

Large woody debris.—Our hypothesis of an association between old-growth forests and LWD accumulations in stream reaches was supported by the results. A

Table 3. Best AIC_c models ($\Delta_i < 4.0$) predicting pool density.

Rank	Model covariates	Log likelihood	AIC_c	Δ_i	w_i	R^2
1	Bankfull width, boulder density, debris-dam density	2.4957	6.3420	0.0000	0.3935	0.72
2	Bankfull width, boulder density, large-log density	2.2872	6.7589	0.4169	0.3195	0.66
3	Bankfull width, boulder density	−0.5713	8.9887	2.6467	0.1048	0.60
4	Bankfull width, boulder density, debris-dam density, large-log density	2.8622	9.7302	3.3882	0.0723	0.73

Note: Not shown are the 16 alternative models (rejected) that had Δ_i values >4.0; $\Delta_i = AIC_{c,i} - AIC_c$; w_i = Akaike weight.

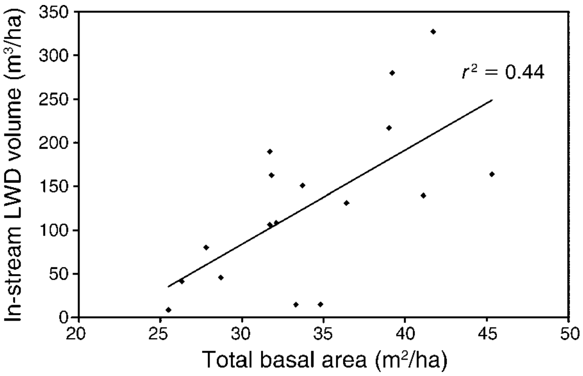

FIG. 4. Linear-regression relationship between the volume of large woody debris (LWD) in wetted stream channels and the total basal area (live plus dead) of adjacent riparian forests.

number of correlations signaled a strong indirect relationship between forest age and in-stream LWD, via stand age-related influence on forest structure (i.e., basal area). LWD volumes in streams were correlated ($r^2 = 0.44$, $P = 0.004$) with the total basal area (live and dead tree) of adjacent riparian forests based on regression results (Fig. 4). The volume of LWD within riparian forests was also predictive ($r^2 = 0.43$, $P = 0.003$) of LWD in stream channels. However, the average volume of LWD in old-growth stream channels was significantly ($P < 0.001$) larger compared to volumes in adjacent riparian forests (164 m^3/ha). Mean in-stream LWD volumes were significantly ($P < 0.001$) larger at old-growth sites (200 m^3/ha) compared to mature sites (34 m^3/ha) or mature sites with remnant old-growth trees (126 m^3/ha). Total in-stream LWD volume was positively correlated ($r^2 = 0.54$, $P < 0.001$) with the density of large logs (>30 cm diameter), as well as debris dams ($r^2 = 0.34$, $P = 0.011$) in stream channels. There was an even stronger positive relationship (Fig. 5) between large log density and debris dam density ($r^2 = 0.64$, $P < 0.001$), a finding that partially supported our second hypothesis regarding LWD effects on in-stream habitat. A statistically significant ($r^2 = 0.52$, $P = 0.026$) trend (negative exponential curve) was found between decreasing LWD volume with increasing bankfull width.

Pools.—Multivariate analyses provided additional support for our hypothesis that in-stream LWD affects other aquatic-habitat characteristics, such as pool density. The results also confirmed our prediction that this relationship is influenced by an interaction between riparian-forest structure and site-specific geomorphology. Of 20 initial AIC_c models including pool density as the response variable, four models had sufficient strength of evidence (or Δ_i values <4.0) to warrant further consideration (Table 3). These were parsimonious models (i.e., 2–4 variables per model), having a combined Akaike weight of 0.89, indicating a high probability that this set included the strongest model. All four models included bankfull width and boulder density, indicating that geomorphic variables are important determinants of pool density in these systems. The lowest ranked alternative models (rejected) included stream gradient, signaling that this geomorphic feature is not strongly predictive of pool density for the range of gradients examined. Debris dam density was included in the top-ranked model, which explained 72% of the variance in pool density. The second- and fourth-ranked models included large-log density but not debris-dam density. Total LWD volume was not included in any of the top-ranked models.

Pool density (log transformed) declined significantly ($r^2 = 0.43$, $P = 0.022$) with increasing bankfull width, for which the most variation was explained by a negative exponential relationship. The average area occupied by individual pools (log transformed) decreased as debris dams increased ($P < 0.001$), but this relationship explained only 15% of the variability in pool area. No significant relationship was observed between pool area and boulder density. For sites with debris dams, dam density was positively and logarithmically correlated with mean residual pool depth ($r^2 = 0.35$, $P < 0.001$), exhibiting diminishing returns at densities greater than ~10 dams per 100 linear meters of stream.

A significantly greater proportion of pools was formed by LWD than boulders at old-growth sites by comparison with mature forest sites ($P < 0.001$), based on log-likelihood ratio tests ($G = 61.06$; the critical value for the G statistic at $P = 0.001$ is 10.83). Along old-growth stream reaches, 49% and 36% of pools were formed by LWD and boulders, respectively, with the remainder not attributable to a specific pool-forming element. The proportions were reversed at mature sites: LWD formed 15.6% of observed pools, boulders formed 66.5%, and other factors were responsible for the formation of other pools. Boulder abundances in old-growth (mean = 11 boulders per 100 m) vs. mature (mean = 12 boulders per 100 m) sites were not significantly different ($P = 0.40$). Based on these findings we infer that LWD inputs represent a subsidy over geomorphic background levels in terms of increasing the amount of pool formation.

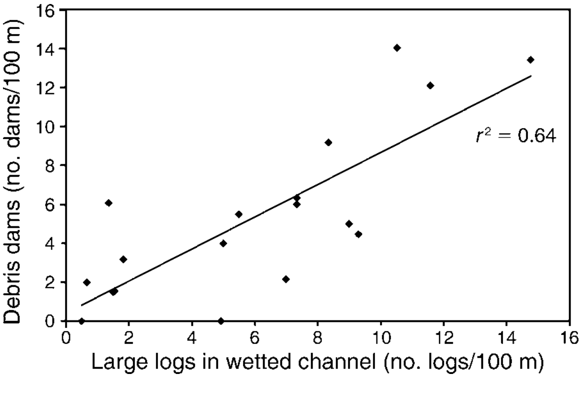

FIG. 5. Linear-regression relationship between debris-dam density and large-log density (number per 100 m of stream reach).

DISCUSSION

Old-growth riparian forests at our Adirondack (New York, USA) study sites exhibited structural characteristics and corresponding influences on stream habits that differed from those associated with mature forests. Riparian forest structure was strongly linked to key in-stream habitat characteristics, including large woody debris (LWD), debris dams, and pools along forested streams generally ranging in width from 2 to10 m. Our hypothesis that old-growth northern hardwood–conifer forests have higher levels of structural characteristics (e.g., basal area, LWD volume, etc.) that correlate with in-stream LWD accumulation was strongly supported. In-stream LWD density was, in turn, related to debris-dam and pool densities as hypothesized, although geomorphic variables were equally important in predicting the latter. Mature riparian forests in these systems have significant potential for continued structural development into an old-growth condition based on the results. Stand development processes leading to increased forest structural complexity (Franklin et al. 2002, Franklin and Van Pelt 2004) will also influence associated linkages with stream systems, such as the abundance of woody debris and pool formation. These considerations will be important for forest and watershed managers as forested landscapes in the northeastern United States continue to mature. Given the scarcity of old-growth forest sites within the eastern United States, our results suggest that these ecosystem processes would be even further enhanced as mature forests and associated streams develop the structural characteristics typical of old-growth forests.

Implications for stand-development models

Our results demonstrate that basal area (live and dead) and aboveground biomass can continue to develop and/or accumulate very late into succession in northern hardwood–conifer forests. Dead-tree basal area and the standard deviation of stem density were selected in classification and regression tree (CART) analysis as the strongest predictors of stand age for our oldest sites. It is likely that the former signals increased mortality and standing dead wood accumulation, while the latter indicates horizontal structural development. Heterogeneous patch mosaics, created by fine-scale canopy disturbances and gap phase dynamics (Bormann and Likens 1979, Runkle 2000), are a defining characteristic of the very latest stages of stand development in temperate forests (Franklin et al. 2002).

Unlike previous studies (Tyrell and Crow 1994*a*, McGee et al. 1999, Ziegler 2000), we did not find a negative relationship between mean stand density and stand age. This is probably due to the very high densities of shade-tolerant species in the understory, primarily red spruce, eastern hemlock, and American beech, encountered at our old-growth sites. These densities were associated with the high frequency of canopy gaps (based on field observations), and in the case of beech, with the prevalence of beech bark disease that is known to promote root sprouting (Gavin and Peart 1993).

The positive relationship between basal area and stand age concurs with previous research in upland old-growth forests in the Adirondack region (Woods and Cogbill 1994, McGee et 1999, Ziegler 2000). Consistent agreement between empirical studies in the Adirondack region suggests a need to reexamine theoretical models of stand development for northern hardwood–conifer systems. These predict peaks in biomass accumulation after about two centuries of development, followed by declining biomass in stands roughly 200 to 350 years of age, and "steady-state" biomass dynamics in stands more than ~350 years of age (Bormann and Likens 1979). In contrast to the Adirondacks, basal area appears to peak somewhat earlier in stand development in the upper Midwest, reaching maximum values in 230–260 yr old forests, with a subsequent decline in older forests (Tyrell and Crow 1994*a*). Generalized models of stand development and biomass dynamics may not adequately capture the full range of variability evident in empirical data sets. If these data represent a trend of continued biomass (i.e., correlated with basal area, see Jenkins et al. [2003]) additions in stands well over 300 years of age (Fig. 3), which cannot be inferred directly from chronosequence comparisons, a leveling off or decline in standing biomass would have to occur later in stand development than previously predicted.

A dynamic view of old-growth riparian-forest structure

Late-successional/old-growth structure is both spatially and temporally variable based on our results. Old-growth riparian forests in the Adirondacks have significantly higher basal areas, relative densities, large-tree densities (live and dead), and downed LWD volumes relative to mature forests. Old-growth forests exhibit greater horizontal variation in stand structure (e.g., open gap and high-density patch mosaics), greater vertical differentiation of the canopy (as indicated by tree-height diversity index), and taller canopies. The oldest stands also have higher basal areas of dead trees based on the CART results. However, these characteristics also vary considerably from site to site, sometimes collectively and other times independently. This suggests the need for multiple, continuous variables to quantify late-successional forest structure.

Rather than emphasizing an archetypical old-growth condition, we suggest that old-growth structure in northern hardwood–conifer systems develops and occurs along a continuum that likely varies with disturbance history, site productivity, and other factors. Disturbance regimes characterized by frequent, fine-scale disturbances are typical of mixed conifer–hardwood forest systems in the northeastern United States (Runkle 2000, Seymour et al. 2002, Ziegler 2002). However, in the Adirondack region these occur with a range of variability that includes infrequent, high-intensity ice storms and windthrow events, such as geographically localized microbursts (Ziegler 2002). Due to these episodic, large-scale disturbances, Ziegler (2002) concluded that three of four old-growth areas studied were not in a "quasi-equilibrium" condition (i.e., as per Bormann and Likens [1979]). Variation in natural-disturbance frequency, type, and intensity, for instance associated with topographic heterogeneity and landscape context (Keeton and Franklin 2004), would result in a range of possible late-successional structural conditions, with only a subset of sites at any one time exhibiting the full complement of pronounced or high-density old-growth structural characteristics. Biological legacies, such as remnant live trees persisting through secondary or post-disturbance stand development, may contribute to a range of intermediate structural variability, although our ability to assess this relationship was limited by low sample size for this condition.

Riparian landforms can increase susceptibility to some disturbances, such as flooding, ice damage, and wind throw (Gregory et al. 1991, Hughes and Cass 1997, Millward and Kraft 2004). This may broaden the range of variability of late-successional structure in riparian forests by comparison with uplands, though we did not investigate this question. Anthropogenic disturbances and land-use history also have had a controlling influence on variability in old-growth forest structure and composition in the northeastern United States (Foster et al. 1998, McLachlan et al. 2000), though this was not a factor at our study sites. The range of variability evident in old-growth riparian forest structure in the Adirondacks is consistent with stand-development models that emphasize both variability in rates and pathways of succession (Franklin et al. 2002, Keeton and Franklin 2005) and the dynamic nature of temperate deciduous old-growth systems at fine scales (Foster 1988, Frelich and Lorimer 1991, 1994, Hunter and White 1997).

Effects of old-growth forests on stream systems

Old-growth riparian-forest structure (e.g., basal area, LWD volume) strongly affects LWD recruitment into stream channels and thus, indirectly, pool density in low-order Adirondack streams. Basal area is positively correlated with stand age in Adirondack northern hardwood–conifer forests based on our results and previous studies (Woods and Cogbill 1994, Ziegler 2000). At our study sites higher basal areas were strongly correlated with accumulations of downed LWD, both within the riparian forest and in the stream channel, a relationship related to LWD recruitment potential. Ziegler (2000) also found a strongly positive correlation between downed-log volume and stand age in upland old-growth forests.

Our AIC results indicate that debris-dam density is an important predictor of pool frequency in low-order Adirondack streams. This result supports observations from the Pacific Northwest (Montgomery et al. 1995), where high in-stream LWD densities correspond with significant increases in pool frequency. However, our results show that geomorphic variables, including boulders and bankfull width, also influence pool frequency. The role of LWD must be considered in this context for Adirondack stream systems, e.g., as a subsidy that increases pool-formation potential. Although boulders also form pools, there are more pools when LWD is abundant. Debris-dam frequency in our study streams was closely linked with in-stream woody debris volume, which in turn was linked to riparian-forest characteristics. LWD recruitment, debris-dam frequency, and associated effects on pool frequency will increase as riparian forests develop towards a late-successional structural condition.

Individual logs and LWD accumulations provide a variety of ecological and geomorphic functions in stream ecosystems. Woody debris and debris dams, in particular, are important for retention of sediment and organic material, which can strongly influence stream nutrient cycling and detritus-dependent biota (Smock et al. 1989, Wallace et al. 1995, Valett et al. 2002, Warren et al., *in press*). Woody debris both directly and indirectly influences stream invertebrate communities (Wallace et al. 1995, Lemly and Hilderbrand 2000, Johnson et al. 2003) and increases habitat complexity in pools, thereby increasing the potential number of fish that can co-occur within a section of stream (Berg et al. 1998, Sundbaum and Naslund 1998, Flebbe 1999, Neumann and Wildman 2002, Rosenfeld and Huato 2003). Warren and Kraft (2003) found that wood manipulations significantly altered abundances of brook trout (*Salvelinus fontinalis*) in Adirondack streams where pool frequency was affected. However, where wood removal did not alter pool formation, brook trout abundances remained largely unchanged. The relationship between LWD and pool frequency found in this study may signal an indirect effect of forest age on fish communities.

The volume of LWD in old-growth stream channels (200 m^3/ha) was substantially larger than in adjacent riparian forests, and is also larger than those previously reported for upland old-growth northern hardwoods in the Adirondacks by Ziegler (2000; 126 m^3/ha) and McGee et al. (1999; 139 m^3/ha). The volume of Adirondack in-stream LWD also exceeds levels reported for upland forests in New Hampshire (Gore and Patterson 1985) and the upper Midwest (Tyrell and Crow 1994*b*, Goodburn and Lorimer 1998), though it is comparable to the average volume reported for old-growth streams in North Carolina by Hedman et al. (1996; 243 m^3/ha) and Valett et al. (2002; 200 m^3/ha). It is possible that LWD accumulations in old-growth streams are greater than in upland forests due to greater disturbances (i.e., increased tree mortality due to flooding and bank undercutting) along forest-stream edges (Gregory et al. 1991), decreased LWD decomposition rates in streams, and/or enhanced forest productivity at riparian sites due to enhanced nutrient and moisture availability.

Woody-debris-related riparian influences on streams are limited by mechanisms and rates of LWD transfer to streams (Meleason et al. 2003). Previous research has shown stream LWD inputs in the Adirondack region to be partially episodic in relation to disturbances, such as flooding, ice, and wind (Kraft et al. 2002). Input rates would also be affected by pathogens, such as beech bark disease (McGee et al. 1999), and baseline tree mortality rates—the latter of which are not currently stable in late-successional Adirondack forests (Manion and Griffin 2001). Based on these considerations, it is probable that the functions we found associated with stream LWD, such as debris-dam formation, will vary temporally with the dynamics of LWD recruitment. They would also be negatively affected by management practices within riparian areas that reduce the recruitment potential for large logs.

Interactions between large woody debris and stream geomorphology in pool formation

Our model selection (AIC) and CART results support the hypothesis that pool density involves an interaction among boulders, stream size, and LWD contributed by riparian forests. Debris dams and large logs (LWD $>$ 30 cm), rather than LWD volume itself, were the best predictors of pool density. But boulders are also clearly important as pool-forming elements in streams within young to mature Adirondack forests, based on our findings and previous observations (Kraft et al. 2002, Warren and Kraft 2003). Logs and debris dams play an increasingly important role in pool formation as riparian forests age and develop the capacity to provide LWD to the stream channel. In old-growth streams, boulders and LWD interact in forming large debris dams anchored around large logs, large boulders, or a combination of the two (Fig. 1: bottom left). These debris dams, in turn, increase the probability of pool formation.

In-stream LWD volume was negatively correlated with stream size at our sites, possibly due to increased discharge and possible ice flows (there was evidence of heavy ice flows at one site $>$12 m bankfull width). Increasing bankfull width may also have been correlated with declining pool density due to the proportionate increase in total channel area.

Canopy structure influences on stream processes

For streams $<$9 m bankfull width, our analysis of DIFN (or "percentage visible sky") suggests that canopy closure is more spatially variable (e.g., greater standard deviation of DIFN) and openings are more spatially aggregated in gaps over old-growth stream channels, in comparison with younger forest streams. Variability in DIFN can be attributed to the higher frequency and larger average size of canopy gaps typically found in old-growth northern hardwoods (Tyrell and Crow 1994*a*, Dahir and Lorimer 1996, Runkle 2000) and observed at our sites. Gaps in mature northern hardwood canopies tend to be smaller, on average, due to smaller canopy trees (Dahir and Lorimer 1996).

Heterogeneous canopy structure over low-order, old-growth forest streams may have implications for light availability, stream temperature, and in-stream production. We did not investigate these directly. However, based on the observed variability in DIFN, we can infer that light absorption over old-growth streams may also vary spatially (Van Pelt and Franklin 2000, Cournac et al. 2002). Shifting gap mosaics would make this effect highly dynamic (Frelich and Lorimer 1991, Runkle 2000), with the spatial pattern and distribution of canopy gaps along streams fluctuating over time. In-stream productivity in closed-canopy riparian systems is predominately heterotrophic and driven by allochthonous organic matter (Vannote et al. 1980, Sabater et al. 2000). It is interesting to consider that a more heterogeneous light environment might increase primary productivity in patches receiving more light, while also maintaining cool shaded conditions elsewhere, although net effects on stream temperature and organic matter inputs are uncertain. Forest-structure influences on light variability within individual low order stream reaches have not, to our knowledge, been previously investigated, and such direct ecological influences of canopy gaps on small-stream systems merit further investigation.

Potential sources of error

Three potential sources of error warrant discussion. First, there is uncertainty involved in assigning an "age" to uneven-aged, primary forest stands. Return intervals for large, stand-replacing disturbances can exceed 1000 years for inland, northeastern temperate forests (Seymour et al. 2002). Yet primary northern hardwood forests are highly dynamic at finer scales (Lorimer and White 2003), consequently "stand-age" is more typically defined as some aspect of canopy tree age. We choose to make this calculation based on the oldest, dominant trees in each stand, rather than as a mean of all canopy trees that would include recent recruits. Therefore, our age estimates are best used as a relative measure for comparative purposes. Second, another potential source of error is the line-intercept method used for estimating LWD volume (Warren and Olsen 1964). This method has proven highly accurate when there is a random log orientation (Bate et al. 2004); however, this assumption could be violated in streams due to reorientation of logs by stream flow (Waddell 2002). In a comparison of in-stream line-intercept data with wood-volume estimates derived from three-dimensional log measurements at the same sites, we have observed a close correspondence between these methods ($r^2 = 0.87$) (D. R. Warren, W. S. Keeton, and C. E. Kraft, *unpublished data*). Third, multi-collinearity among variables was addressed through the choice of analytical methods, allowing us to avoid (e.g., variable partitioning in CART) or control (e.g., multiple ranked models as per AIC) for this potential problem.

Conclusions and management implications

Mature northern hardwood–conifer forests do not provide the same type or magnitude of riparian functions associated with old-growth forests. Forest structural complexity can continue to develop very late into succession in these riparian forests. Stand-development models should be modified, where appropriate, to incorporate this potential. Old-growth structure varies continuously, but has strongly associated influences on low-order stream systems, including recruitment of LWD and debris dams and formation of pools. Consequently, old-growth streams have ecologically important in-stream habitat characteristics that are distinct from mature forest streams in the Adirondack region. These findings suggest that relationships among riparian forest development, structure, and effects on streams are likely to occur in a broader range of temperate forest ecosystems than previously documented.

The mature forests that currently dominate the northeastern U.S. landscape do not provide the same riparian functionality that was likely to have been provided, in aggregate, by presettlement forests. Managers can consider promoting late-successional/old-growth forest conditions where the associated in-stream habitat characteristics are desired. Watershed managers can use riparian-forest structure as an indicator of present and future potential riparian functionality. Because riparian old-growth forests provide high-quality stream habitats, riparian buffer systems could be designed to incorporate protected old-growth riparian corridors.

Where old-growth riparian forests are not currently available, mature riparian forests offer a source for future old-growth structure, provided forest management practices are employed that either maintain or enhance, rather than retard, stand-development potential (Keeton 2006). We identified a number of structural characteristics associated with old-growth forests and linked to in-stream habitat that can be directly manipulated. These include biomass, basal area, large-tree (live and dead) density, and, as a function of these parameters, LWD volume and density. A key consideration is retention of some large trees as an alternative to cutting all trees over a given diameter limit, which is typical of the selection systems most frequently employed in riparian northern hardwoods (Keeton 2006). Large-tree retention and/or thinning to "crown release" selected dominant trees (Singer and Lorimer 1997) would maintain recruitment potential for LWD. The significant influence of large pieces of LWD ($>$30 cm) specifically rather than just the volume of LWD in the stream highlights the value of maintaining large trees in the riparian area as the recruitment source for in-stream LWD. Retaining high post-harvest basal areas will similarly help provide the biomass and related structural complexity that appears strongly related to in-stream characteristics. Small-group selection methods, creating openings at scales (e.g., 0.5 ha) similar to those associated with natural disturbance regimes in the region (Seymour et al. 2002), would approximate the patchy canopy structure we found in old-growth riparian forests. These options are now widely applicable given increasing interest in managing for late-successional habitats on many conservation-easement lands, including former industrial timberlands, and among public agencies (Bennet 2005).

Riparian management in many eastern U.S. states employs a zonation system adjacent to surface waters (Lee et al. 2004). In some regions this consists of a thin, unmanaged zone closest to the water body, a wider secondary zone in which low-impact timber harvesting is allowed, and, when abutting agricultural or developed land, a tertiary strip of unmowed grass or meadow. This system could be modified to enhance the provision of old-growth characteristics by (1) widening the unmanaged zone to allow redevelopment of late-successional forests within a broader area and/or (2) emphasizing restorative silvicultural practices in the second zone. Previous research suggests that provision of old-growth characteristics at distances away from low-order streams up to the average maximal height of dominant canopy trees achievable on a given site will maximize the potential for LWD recruitment into the stream channel (Naiman et al. 2000). This would require a modification of buffer-width standards in the northern hardwood region, which tend to be less inclusive—compared to other regions—of site-specific considerations (Lee et al. 2004).

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