Spatial characteristics of canopy disturbances in riparian old-growth hemlock – northern hardwood forests, Adirondack Mountains, New York, USA

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Abstract: Gap dynamics in temperate, late-successional forests influence important riparian functions, including organic matter recruitment and light environments over streams. However, controls on gap dynamics specific to riparian forests are poorly understood. We hypothesized that (*i*) gaps are larger and more frequent nearer streams, (*ii*) gaps cluster at within-stand scales, and (*iii*) tree damage type and gap fraction vary among riparian landforms. All gaps within four 6–9 ha plots in riparian old-growth eastern hemlock (*Tsuga canadensis* (L.) Carrière) – northern hardwood forest in the Adirondack Mountains, New York, USA, were mapped and measured. We recorded species, damage type, and diameter at breast height for gapmakers and dominant perimeter trees. Spatial distribution was assessed with Ripley's *K*. Spatial autocorrelation in gap area and tree damage type were assessed using Moran's *I*. Linear regression analysis defined relationships between proximity to streams and gap area and frequency. Expanded gap fraction ranged from 28.3% to 47.6%. Gaps were randomly distributed at scales ≤25 m and clustered at scales of 63–122 m. Distribution patterns were not consistent at other scales. Convergent and divergent landforms significantly influenced gap fraction, tree damage type, and species distributions. Positive correlations between convergent topography and gap area suggest an interaction between low-order riparian landforms and gap formation dynamics in late-successional forests.

Résumé : La dynamique des trouées dans les forêts tempérées en fin de succession influence d'importantes fonctions riveraines, dont le recrutement de matière organique et l'environnement lumineux au-dessus des cours d'eau. Cependant, les facteurs qui contrôlent la dynamique des trouées propre aux forêts riveraines sont peu compris. Nous avons posé les hypothèses suivantes : (*i*) les trouées sont plus grandes et plus fréquentes près des cours d'eau, (*ii*) les trouées sont regroupées à une échelle plus petite que celle du peuplement et (*iii*) le type de dommages aux arbres et l'ouverture du couvert varient parmi les reliefs riverains. Nous avons cartographié et mesuré toutes les trouées à l'intérieur de parcelles de six à neuf ha établies dans une vieille forêt riveraine dominée par la pruche (*Tsuga canadensis* (L.) Carrière) et les feuillus nordiques et située dans les montagnes Adirondack de l'État de New York, aux États-Unis. Nous avons noté l'espèce, le type de dommages et le DHP des arbres à l'origine d'une trouée et des arbres dominants en périphérie. La distribution spatiale a été estimée à l'aide du coefficient *K* de Ripley. L'autocorrélation spatiale dans la trouée et le type de dommages aux arbres ont été estimés à l'aide du coefficient *I* de Moran. Une analyse de régression linéaire a été utilisée pour établir les relations entre la proximité des cours d'eau et la superficie ainsi que la fréquence des trouées. L'ouverture expansée du couvert variait de 28,3 % à 47,6 %. Les trouées étaient aléatoirement distribuées à des échelles allant jusqu'à 25 m et regroupées à des échelles variant de 63 à 122 m. Les patrons de distribution n'étaient pas cohérents à d'autres échelles. Les reliefs convergents et divergents influençaient significativement l'ouverture du couvert, le type de dommages aux arbres et la distribution des espèces. Des corrélations positives entre la topographie convergente et la superficie des trouées indique qu'il y a une interaction entre les reliefs riverains de rang inférieur et la dynamique de formation des trouées dans les forêts en fin de succession.

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Introduction

Old-growth forests in northeastern North America provide important ecological and riparian functions. Compared with younger forest stands, old-growth northern hardwoods gen-

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erally have more and larger canopy gaps, greater densities of large trees, greater basal area, and more diversity in size and age classes (Dahir and Lorimer 1996; McGee et al. 1999; Ziegler 2000), which result in greater vertical and horizontal complexity (Keeton et al. 2007). Spatial complexity in canopy structure correlates with heterogeneity of heterotrophic versus autotrophic production as measured by periphyton distributions in streams flowing through these forests (Stovall et al. 2009). Thus, spatial variation in stand structure, particularly the distribution of canopy gaps, influences both light-related functions and large log recruitment into streams (Harmon et al. 1986; Franklin and Van Pelt 2004). Despite having important controls on riparian forest functions, horizontal structural variability has not been well

quantified for riparian forests in the northern hardwood region of eastern North America.

Horizontal structural complexity is driven by the interaction of stand development and natural disturbance processes (Franklin et al. 2002). In variants of northern hardwood forest (e.g., eastern hemlock (*Tsuga canadensis* (L.) Carrière) – northern hardwoods) found in northeastern North America, stand-replacing disturbances occur infrequently, with return intervals often >1000 years (Foster and Boose 1992; Ziegler 2002). Instead, relatively high frequency canopy gap creating disturbances dominate the disturbance regime (Runkle 1982; Ziegler 2002). A mean of 5%–10% of the forest canopy is impacted by fine-scale disturbances each decade in hemlock – northern hardwood forests (Ziegler 2002; D'Amato and Orwig 2008). The resulting condition has been described as a "quasiequilibrium," in which the proportion of a forested landscape in different seral stages remains relatively constant over time (Bormann and Likens 1979; Shugart 1989). However, recent research, such as Ziegler's (Ziegler 2002) work in hemlock – northern hardwood forests, has noted that periodic pulses of more severe, although partial, disturbances can result in nonequilibrium dynamics at sublandscape scales in these systems.

Windthrow is an important driver of structural heterogeneity in riparian forests (Naiman et al. 2005) as evidenced by the diversity of variably sized canopy gaps (Runkle 1982; Franklin and Van Pelt 2004) and the influences that these gaps may have on the aquatic environment of low-order streams. Some research is available on disturbance regimes specific to riparian old growth northern hardwood – conifer forests, but it is limited mostly to middle- and high-order streams with little attention to forest structure (Johnson et al. 1995; Hughes and Cass 1997). Research in old-growth riparian forests in the Zoar Valley along Cattaraugus Creek (a sixth-order, low-gradient river) in New York shows an association between prevailing wind direction and orientation of large woody debris (Pfeil et al. 2007) but did not further explore relationships among topography, wind disturbance, and forest structure within this ecosystem.

Topographic variability can influence natural disturbance susceptibility and the resulting patterns of forest ecosystem structure and function (Foster and Boose 1992; Kulakowski and Veblen 2002). Relationships between coarse-scale topography, such as aspect and elevational variation, and susceptibility to high-intensity wind storms, such as hurricanes, have been described for northern hardwood forests (Foster and Boose 1992). Likewise, topography interacts with flood disturbances in influencing vegetation distribution and structure (Van Pelt et al. 2006). Proximity to streams also has been shown to influence gap pattern in spruce–fir (*Picea–Abies*) forests in the Adirondacks (Battles et al. 1995) that at high elevations, are highly susceptible to wind (Worrall et al. 2005; Kulakowski and Veblen 2002). Limited data are available for other types of disturbances.

Our primary research objective was to determine whether riparian landforms in old-growth hemlock – northern hardwood forest interact with natural disturbances to influence gap pattern and forest structure. To do this, we first described the structural characteristics of riparian hemlock – northern hardwood forest along low-order streams in the Adirondack Mountains of upstate New York, USA. Secondly, we examined the spatial pattern of gaps at different scales. Lastly, we assessed the relationships between proximity to streams and gap size, proximity to streams and gap frequency, and expanded gap fraction and convergent landforms (depressions). We hypothesized that interactions between riparian landforms and wind may increase forest susceptibility to windthrow near streams, resulting in more frequent and larger gaps nearer to streams based on previous research in other systems (Battles et al. 1995). We also predicted that gaps in close proximity to one another would be exposed to wind in a similar manner and, consequently, would exhibit similar spatial and structural characteristics (e.g., size) as well as spatial clustering at within-stand scales (<10 ha). Lastly, we expected the distribution of tree damage types (e.g., snapping vs. uprooting) to correlate with topographic concavity, as indicated by convergent and divergent landform classifications (Dietrich et al. 1993). Divergent areas (landforms such as hilltops or slopes that are convex, causing surface water flow to diverge) typically remain unsaturated even during large precipitation events, whereas convergent landforms (depressions or convex landforms where surface water flow converges) correlate with hydrologic convergence and soil moisture accumulation (O'Loughlin 1986; Dietrich et al. 1993). This landform classification approach has been shown to be predictive of tree survivorship patterns after high-intensity forest fire (Keeton and Franklin 2004), but we know of no previous research linking it with fine-scaled canopy gap dynamics.

Methods

Study area

Our study was conducted in the Adirondack State Park of upstate New York, USA. The region's surficial geology is dominated by erosion-resistant anorthosite and gneiss. Mean summer temperatures were between 17 and 23 °C; winter mean temperatures vary between –11 and –6 °C. Mean annual precipitation ranges between 100 and 130 cm (Leopold et al. 1988). Study sites were located on Ampersand Mountain in the High Peaks Region of the central Adirondack Mountains (three sites) and in a 20 200 ha privately owned reserve in the southwestern Adirondacks (one site; Fig. 1). From a pool of 19 sites identified by Keeton et al. (2007), we selected a subset of sites intended to be representative of old-growth hemlock – northern hardwood forest in the Adirondack region. We chose sites in an unbiased manner by applying selection criteria, which required that sites have relative ease of access and an unbroken (i.e., by human development, roads, or intervening young forest or wetlands) old-growth forest cover extending ≥150 m to each side of a first- or second-order stream reach ≥200 m in length. Our criteria for old-growth classification required at least 20 trees/ha with a diameter at breast height (DBH) ≥50 cm, a dominant cohort >150 years old, uneven-aged class structures, and basal areas >30 m²/ha (Leopold et al. 1988; McGee et al. 1999). Of the initial pool, only four sites met all of our selection criteria: Dutton Brook (DB; 44°14′57″N, 74°14′15″W), Melonberry Brook (MB; 44°14′34″N, 74°15′03″W), McKenna Brook (MK; 44°14′23″N,

Fig. 1. Map of study sites in upstate New York. The solid line is the boundary of Adirondack State Park. The shaded areas show the New York State Forest Preserves.
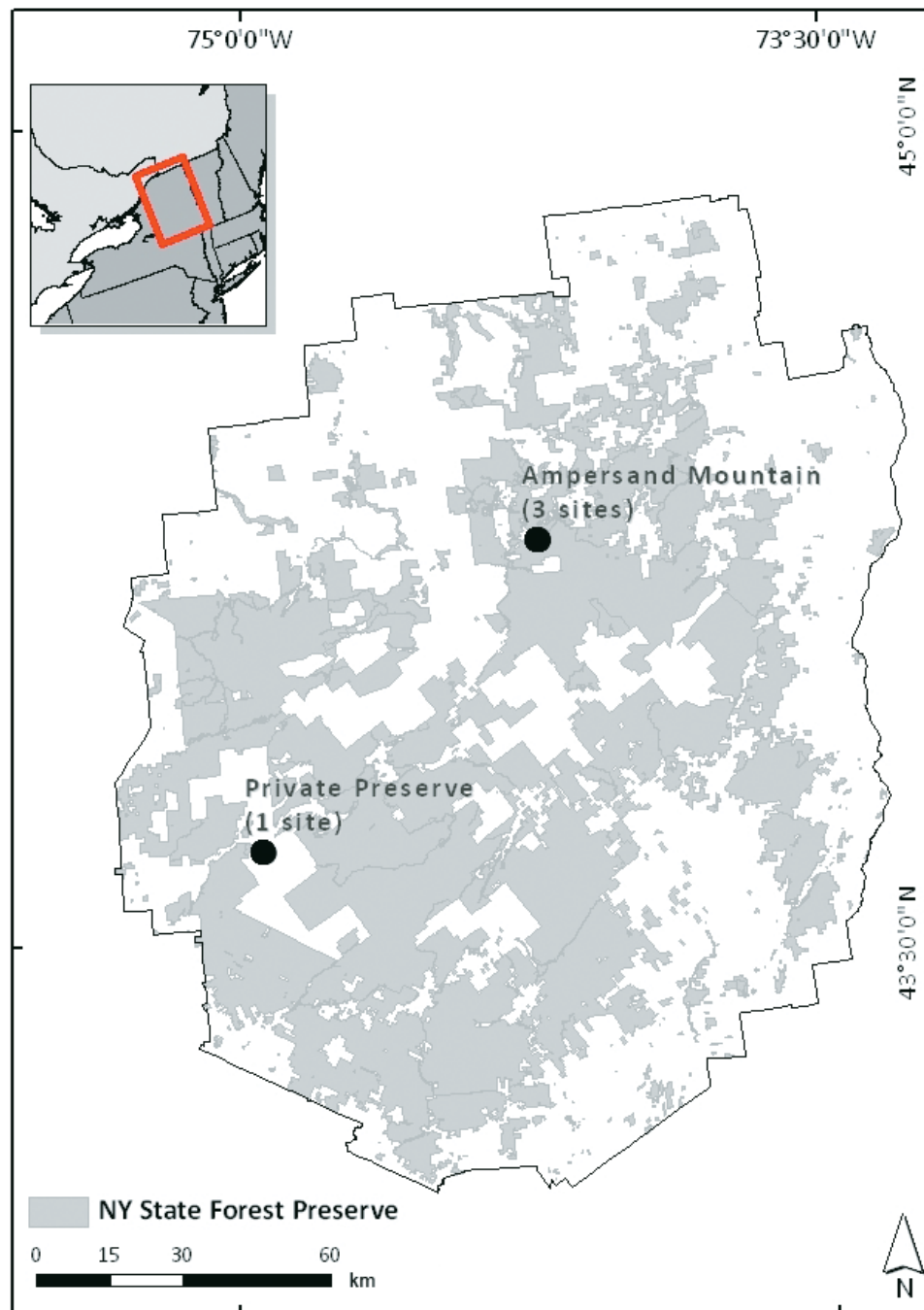
74°13′39″W), and Little Moose Outlet (LMO; 43°40′33″N, 74°56′22″W).

Eastern hemlock, *Fagus grandifolia* Ehrh. (American beech), *Acer saccharum* Marsh. (sugar maple), and *Betula alleghaniensis* Britton (yellow birch) dominated the forest canopies at each study site, although *Picea rubens* Sarg. (red spruce) and *Acer rubrum* L. (red maple) were also present. Stream bank-full width ranged from 2.2 to 6.7 m. Three of the stream reaches were 300 m in length; the fourth was shorter because of geographical constraints including spruce bogs and rocky outcroppings. The study sites had little or no evidence of logging and were most likely unaf-

fected by the logging-related fires in the early 1900s (McMartin 1994). Forests disturbed by the derecho winds that hit the Adirondack Park in 1995 (Jenkins 1995) were excluded from this study. The nearest climatological station with hourly data, Saranac Regional Airport (approximately 16 km distant), indicates the dominant wind direction for storms during summer and autumn months ranges from southwest to northwest (National Climate Data Center 2007).

Field methods

Inventory plots were used to sample forest structure (trees >5 cm DBH), composition, and dominant tree age

and were placed within 30 m of the stream to meet requirements of a related study described in Keeton et al. (2007). These were distributed within a single, large canopy gap survey plot (see below). At each site, we established 6–10 variable radius plots centered on coordinates randomly generated in a geographic information system and located with a Trimble Pro XRS global positioning system. Random, well-distributed plot placement resulted in an inventory spanning the range of canopy conditions, including open and closed canopy conditions. The sample of trees included in each plot was determined using a 2.3 metric basal area prism. The heights of all sampled trees were measured in alternating plots with an Impulse 200 laser rangefinder (Laser Technology, Englewood, Colorado). Estimates of tree age were made in the field from cores extracted with increment borers. Only dominant species were cored; *F. grandifolia* were excluded from coring because of the high incidence of heart rot. Tree cores were extracted at breast height (1.37 m) from four to six of the largest canopy trees. Tree rings were counted to acquire an estimate of age at breast height; they were not cross-dated. For a description of field error estimation, see Keeton et al. (2007).

At each site, a large 6–9 ha canopy gap survey plot was established. Gap survey plots were centered on stream reaches and extended 150 m to each side of bank-full width. Bank-full width was measured across the streambed to include all areas where morphological changes due to stream flow occur. Edaphic gaps, canopy openings resulting from a change in soil or substrate, occurred at two sites in particularly marshy areas, but they covered <1% of the land surface sampled and were excluded from consideration. Our survey was restricted to "developmental gaps," which were defined as those gaps created by a fallen tree or "gapmaker" (Lertzman et al. 1996). A canopy gap was identified as any opening in the canopy >10 m² created by one or more trees greater than 10 cm DBH and having within-gap regeneration <50% of the surrounding canopy height (Runkle 1992; Worrall et al. 2005). If part of a gap had regeneration >50% of the surrounding canopy height, this portion of the opening was assumed to be from an older gap and was considered closed. In the case of a single, large opening (0.69 ha) at one site, eight patches of remnant trees existed within the boundary of the opening. The area occupied by patches with three or more remnant trees was excluded from the area calculated for the canopy opening. Only those gaps with a centerpoint (intersection of two perpendicular lines across the widest and longest stretches of the gap) within the established plot were counted (adapted from Runkle 1992). This method of identifying gaps reduces the probability of bias towards finding a greater abundance of larger gaps. Within each gap survey plot, all canopy gaps were identified and mapped with a Trimble Pro XRS global positioning system. We measured and characterized gaps based on slope, aspect, the number of gapmakers, and the species and DBH of eight perimeter trees. The species, DBH, direction of fall, and decay stage (1–5) were recorded for each gapmaker. The type of damage (snap, uproot, or standing dead) was also recorded. An unknown portion of snapped trees may have died prior to snapping, so the mortality agent for this damage category was unclear.

Because the expanded gap more accurately captures the altered light environment associated with canopy openings (Runkle 1982; Canham 1988; Dahir and Lorimer 1996), we measured expanded gaps in the field. This method uses the stems of bordering trees to estimate gap area as defined by Runkle (1982). To establish expanded gap area we first defined the centerpoint of each gap. The centerpoint lay at the intersection of two hypothetical lines, one crossing the widest portion of the gap, the other crossing the longest portion of the gap. From the centerpoint we measured the distance to the stems of dominant trees in the gap perimeter in eight cardinal directions with an Impulse 200 laser rangefinder (Lertzman 1992; Dahir and Lorimer 1996).

Multiple methods for measuring and reporting gap area exist in the literature. Unfortunately, this limits comparisons among studies employing different methods. To allow comparison of our data with that reported from other studies, we also surveyed "actual" gap area within 20 randomly selected gaps from among those previously measured gaps at three sites. To measure the actual gap area, the distance from the gap center to the edge of the canopy opening (edge of overhanging branches) was measured in eight cardinal directions with a laser rangefinder and prism (Lertzman 1992). We used linear regression to develop an algorithm correlating actual gap size and expanded gap size. The algorithm was then used to predict actual gap area from expanded gap area measurements. Residuals were checked for normality.

Data analysis

We used the Northeast Ecosystem Management Decision Model (NED-2; Twery et al. 2005) to calculate forest structure metrics. Aboveground biomass estimates were based on species group-specific allometric equations developed by Jenkins et al. (2003). We compared structural characteristics at the four sites to determine if fundamental differences in structure might explain differences in gap frequency and patterns or if variation might be explained by site characteristics and, potentially, disturbance history.

To describe gap spatial patterns, we used a maximum expanded gap area of 2009 m² (Runkle 1982). Only two openings were excluded from our spatial analysis because they exceeded the 2009 m² threshold. Large openings are not appropriate for point pattern analysis because they are not adequately represented by a single point. One opening occurred at MB and occupied 0.69 ha. In particular, this opening appeared to have been caused by a single, severe wind event and the area affected was almost linear in shape, so it could not be accurately described by a spatial analysis based on point pattern. These openings were included in calculations of expanded gap fraction.

We analyzed the spatial distribution of gap centerpoints using Ripley's K analysis (Ripley 1979, Haase 1995) run in S+SpatialStats (Insightful Corp., Seattle, Washington). Centerpoints were generated based on the intersection of hypothetical lines across the widest and longest portions of each gap. S+SpatialStats calculate $L(t) = \sqrt{K(t)/\pi}$. $L(t)$ is a transformation of Ripley's K function for analyzing spatial point patterns, where K is the number of points within distance t (Ripley 1979). This is a common transformation of K that allows comparison of results with a line representing the completely random Poisson distribution (Haase 1995).

Points falling below the Poisson distribution indicate spatial regularity or dispersion up to that particular scale. Conversely, points above the Poisson distribution indicate a clumped distribution. Results were assessed with a 95% confidence interval computed with 99 Monte Carlo simulations. No edge correction was performed. Haase (1995) tested multiple methods of edge correction and concluded the slight improvement in results did not warrant the intensive field work required.

Spatial autocorrelation in gap area and the proportion of gapmakers within each tree damage type was assessed using Moran's I in S+SpatialStats (Insightful Corp., Seattle, Washington). Autocorrelation occurs when observations at given distances in time or space are not independent because of some underlying relationship (Diniz-Filho et al. 2003). Moran's I tests spatial autocorrelation by providing a mean of local spatial variations and defining the proportion of covariation to overall variation (Fortin and Dale 2005). A spatial neighbor object was generated with S+ to use with Moran's I analysis. Spatial processes are modeled by predicting the outcome for each region partially on its dependence on neighboring regions. For each site, spatial neighbor objects were created using nearest neighbors within set distance increments. Spatial neighbor objects were created for each site with maximum distances of 50, 100, and 150 m. Spatial analyses are limited by the shortest dimension of the stands, hence the upper threshold of 150 m. Spatial autocorrelation was initially assessed at intervals of 10 m, but all variation was captured within the 50 m thresholds described above.

Digital elevation models with 10 m resolution were obtained for all sites from the national elevation dataset maintained by the US Geological Survey. These models were used to assess two major influences on canopy gap processes: aspect and curvature. The area of each site facing each of eight aspects was calculated in ArcMap (ESRI, Redlands, California). Next, the gap frequency (gaps/ha) and mean gap area (m^2) for each aspect was calculated for each site individually and tested for significant differences among aspects with one-way analysis of variance (ANOVA). The curvature analysis tool in ArcMap (ESRI, Redlands, California) was used to estimate the area of each 6–9 ha plot that was composed of convergent, divergent, or planar landforms. Curvature was assessed on a cell by cell basis with each cell encompassing 100 m^2. The curvature value for each cell is defined by its relationship with the surrounding eight cells as described in Keeton and Franklin (2004). We further related the location of all canopy gaps within these plots to the type of landform on which they occurred.

Comparisons among sites were made using one-way ANOVA and post hoc Bonferoni multiple comparisons (α = 0.05). For these analyses, our statistical population was defined as the population of spatially heterogeneous patches within each site. Thus, for comparison of within-site structure or gap characteristics, sample plots or surveyed gaps were treated as independent data points, an approach consistent with previous old-growth forest studies (e.g., Guariguata et al. 1997; Woods 2004). The influence of distance from the nearest stream on gap size, mean gap area, and gap frequency was assessed with linear regression. All variables were tested for normality with the Shapiro–Wilks goodness-of-fit test (Millard and Neerchal 2001).

Variables not normally distributed, such as mean gap area, were log transformed for tests requiring an assumption of normality. In all cases this was necessary, the log transformation was effective. For each site, the influence of landform types on species composition, tree damage type, and other variables was assessed using the Kolmogorov–Smirnov log-likelihood ratio goodness-of-fit test (or G test; Zar 1998). The G test approximates the χ^2 statistic, but it is more robust when certain conditions are met, as was the case with our data (Zar 1998). We applied the Yates' correction for continuity, which yields conservative estimates of significance and reduces type I error probabilities.

Results

Forest structure

A number of forest structure attributes did not differ significantly among sites. These included basal area, aboveground biomass, mean diameter, and stem density (Table 1). However, we did observe a significant difference in live tree DBH and large tree density among stands (Table 1). Site DB had a significantly greater large tree density than MK (Table 1). Mean expanded gap area also differed significantly among sites: DB had the largest mean gap area, which was significantly greater than both MB and MK (Table 1).

General gap characteristics

A strong linear relationship existed between expanded and actual gap area. This linear relationship, as defined by regression, was used to calculate actual area for all gaps. Initially, we derived three formulas — the first for all sites collectively, the second specific to the three sites at Ampersand Mountain, and the third specific to LMO in the southwestern Adirondacks. However, when the ratio between expanded and actual gap area from the two study areas was examined with t tests, no significant difference existed between the study areas. Therefore, a single formula generated from the full set of 20 gaps was deemed appropriate and explained 85% of the variance in this relationship (Fig. 2).

Mean expanded gap area ranged from 335 to 467 m^2 (181–254 m^2 actual gap area; Table 1). Most gaps fall within the smallest size classes although single, large gaps >0.10 ha) comprised up to 25% of total expanded gap area along two stream reaches (Fig. 3). Only 14 (4.2%) of 332 gaps sampled resulted from the death of a single tree. Gap shapes were highly complex and included abundant residual live and dead trees within and around canopy openings.

Spatial distribution

Canopy gaps at all four sites exhibited a random spatial distribution at scales <25 m; at three sites (DB, LMO, and MK), gaps were randomly distributed at ≤60 m (Figs. 4 and 5). At LMO, MB, and MK, clustering of gaps occurred at scales between 63 and 122 m (Fig. 5). Gaps clustered at DB within this range also but with less significance (p = 0.10).

Gap area was positively spatially autocorrelated at DB, LMO, and MK based on a 50 m nearest neighbor threshold (Table 2, Fig. 4). Use of spatial neighbor objects with maximum distances set at 100 and 150 m produced the same re-
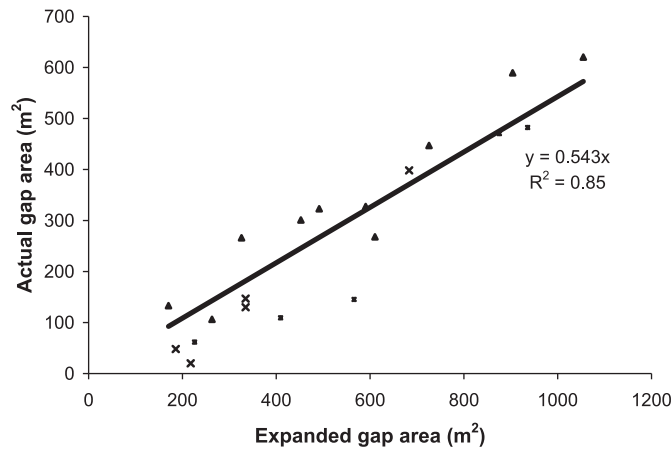
Table 1. Forest structure attributes and gap characteristics for all sites.

Attribute*	DB	LMO	MB	MK	ANOVA results			Multiple comparison ($\alpha = 0.05$)
					MS	F	P	
Basal area (m²/ha)†								
Total	46.2±9.9	41.1±8.6	40.6±7.1	36.7±7.1	127.942	0.906	0.451	
Live	37.9±8.9	35.3±5.4	33.5±6.5	31.2±7.2	67.632	0.568	0.64	
Stem density (no./ha)†	602±399	714±157	791±297	842±334	0.383	0.664	0.581	
Density of large trees (no./ha)	84±21	60±16	60±15	43±14	1572	3.84	**0.021**	DB > MK
Aboveground biomass (Mg/ha)	317.0±73.6	259.4±63.5	268.8±43.2	251.3±46.5	6840.148	1.051	0.386	
Mean live tree DBH	36.3±1.5	35.3±2.1	32.8±1.2	33.1±1.1	1187.319	4.377	**0.004**	DB ≥ MB, MK
Dominant tree age (years)†	300	315	280	280				
Hardwood density (% BA)†	69	43	75	50				
Conifer density (% BA)†	31	57	25	50				
Plot area (ha)	8.3	6.6	9.1	7.3				
Mean expanded gap area (m²)	468.8±62.4	385.1±80.1	374.9±52.6	333.4±44.9	1.612	4.387	**0.004**	DB > MB, MK
Mean actual gap area (m²)	254.6±34.6	209.1±20.9	240.3±21.2	181.0±24.8				
Max. expanded gap area (m²)	1297	2411.5	6900	1693.5				
Max. actual gap area (m²)	704.4	634.5	684.8	919.74				
SD of expanded gap area	282.9	408.5	264.5	220.7				
Mean bank-full width (m)†	6.8	9.5	6.1	5.1				
Total no. of gaps	79	42	97	93				
Gaps/ha	9.5	6.5	10.8	12.7				
Total open canopy (%)	44.6	28.2	47.5	42.5				
Expanded gap fraction (%)	44.6	25.4	43.2	42.5				
Actual gap fraction (%)	24.2	13.7	23.5	23.1				
Convergent expanded gap fraction (%)	47	38.5	53.4	38.3				
Divergent expanded gap fraction (%)	39.4	20.6	40.5	41.3				

Note: ANOVA results are presented for forest structure attributes with replicates within the four sites. Significant results are given in boldface. Calculations for gaps per hectare, mean gap area, and maximum actual gap area only include openings 10–2009 m² in area. Site abbreviations are as follows: DB, Dutton Brook; LMO, Little Moose Outlet; MB, Melonberry Brook; MK, McKenna Brook.

*Values for basal area (BA), stand density, density of large trees, aboveground biomass, mean live tree diameter at breast height (DBH), gap expanded area, and actual gap area are means ± 95% CIs.

†>50 cm DBH.

Fig. 2. Relationship between expanded and actual gap area for 20 randomly selected gaps in three sites (×, McKenna Brook; ■, Dutton Brook; ▲, Little Moose Outlet). The best-fit linear regression line is shown.

$$y = 0.543x$$
$$R^2 = 0.85$$

Fig. 3. Distribution of expanded gap size classes for all sites collectively.

sults. Additionally, significant spatial autocorrelation occurred in the proportion of uprooted gapmakers within each gap at MK at scales ≤150 m (Table 2). Spatial autocorrelation was not evident in the pattern of uprooted gapmakers at DB, LMO, or MB. Standing dead trees were randomly distributed at each site at most scales with two exceptions. At both LMO and MK, the proportion of gapmakers that died standing was positively spatially autocorrelated, although at different scales (100–200 m and 150–300 m, respectively; Table 2). Both of these sites were also dominated by hardwood species, with *F. grandifolia*, *A. saccharum*, and *B. alleghaniensis* representing >60% of canopy dominants by stem density.
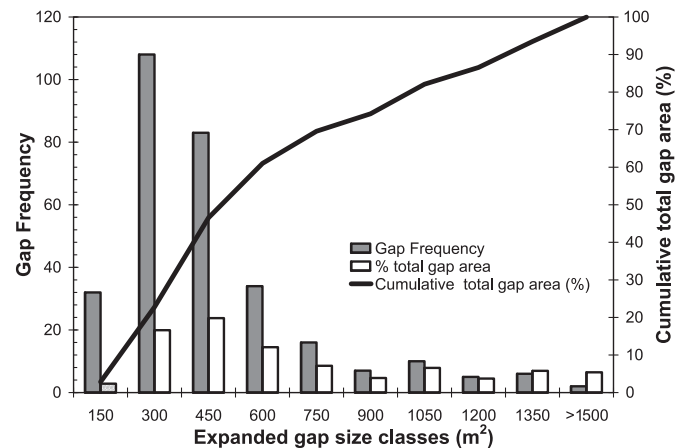
Influence of topography

Distance from the nearest stream did not explain gap size ($r^2 = 0.003$, $p = 0.364$). However, two sites had statistically significant ($p < 0.001$) logarithmic (MB, $r^2 = 0.44$) or negative exponential (DB, $r^2 = 0.43$) relationships between gap frequency (decreasing) and distance from stream (increasing).

The association between gap frequency and concave landforms was also supported by the curvature analysis. Landscape curvature showed a significant relationship with gap processes. Averaged for all sites, gap fraction was greater on convergent (45.0%) landforms than on divergent landforms (36.2%, $t = 2.268$, $p = 0.054$; Table 1). Only one planar landform occurred; thus, there was no association established with gap fraction or other variables. Mean gap area and gap frequency did not differ significantly among different aspects ($F = 1.450$, $p = 0.232$; and $F = 0.491$, $p = 0.832$, respectively).

Convergent and divergent landforms at individual sites showed different patterns with respect to gapmaker species and type of tree damage. Individually, both MK and MB had fewer uproots on convergent landforms, with the number of uproots on convergent versus divergent landforms differing significantly ($G = 6.452$, $p < 0.05$; and $G = 13.723$, $p < 0.01$, respectively). LMO also had more uprooted trees on divergent landforms, but the relationship was not signifi-

cant ($G = 0.154$, $p > 0.05$; Table 3). The number of uproots differed significantly between convergent and divergent landforms at DB ($G = 16.893$, $p < 0.01$; Table 3), but more uproots occurred on convergent landforms.

Additionally, at DB and MB, where canopies were dominated by *T. canadensis*, gapmakers differed in uprooting likelihood on different landform types (Fig. 6, Table 3). At DB, *A. saccharum* ($G = 4.771$, $p < 0.05$), *B. alleghaniensis* ($G = 10.481$, $p < 0.05$), and *T. canadensis* ($G = 8.388$, $p < 0.05$) were all more likely to uproot on convergent landforms. At MB, *P. rubens* was also more likely to uproot on convergent landforms ($G = 8.510$, $p < 0.05$), but *T. canadensis* uprooted more frequently on divergent landforms ($G = 13.841$, $p < 0.001$). At MK and LMO individually, the number of gapmakers by species that uprooted on convergent and divergent landforms was not significantly different from the expected distribution generated based on landform abundance.

Tree species and damage type

At DB, MB, and MK, *F. grandifolia* comprised a disproportionately large part of the gapmaker class (28.6%, 36.8%, and 59.1%, respectively; Fig. 6) as compared with live canopy dominants (11.1%, 5.7%, and 33.2%, respectively). At all sites, *P. rubens* showed a similar trend to *F. grandifolia* with more gapmakers than canopy dominants observed.

Membership of different damage categories differed significantly among species ($F = 5.21$, $p = 0.009$). *Acer saccharum* and *B. alleghaniensis* were more likely to die standing than any other species observed. These two species were also the only species that were more likely to uproot on convergent landforms (Table 3, Fig. 6). *Fagus grandifolia* was the most common species observed among all gapmakers and showed no difference in uprooting between convergent and divergent landforms (Fig. 6). Of the gapmakers that snapped, *F. grandifolia* comprised 47% (84% of all *F. grandifolia* gapmakers snapped). The two coniferous species observed, *T. canadensis* and *P. rubens,* were more likely to uproot than the other species. Of all *P. rubens* gapmakers, 42% uprooted; *T. canadensis* made up 44% of all uprooted gapmakers.

Fig. 4. Map of canopy gap locations along low-order streams. The size of the symbol is proportional to the actual area (m²) occupied by each expanded gap and to scale with the map, although the shape and orientation are not realistic with one exception: the mapped perimeter of a 0.69 ha blowdown at MB. Streams and contour lines (10 m intervals) are shown for reference. Site abbreviations are as follows: DB, Dutton Brook; LMO, Little Moose Outlet; MB, Melonberry Brook; MK, McKenna Brook.
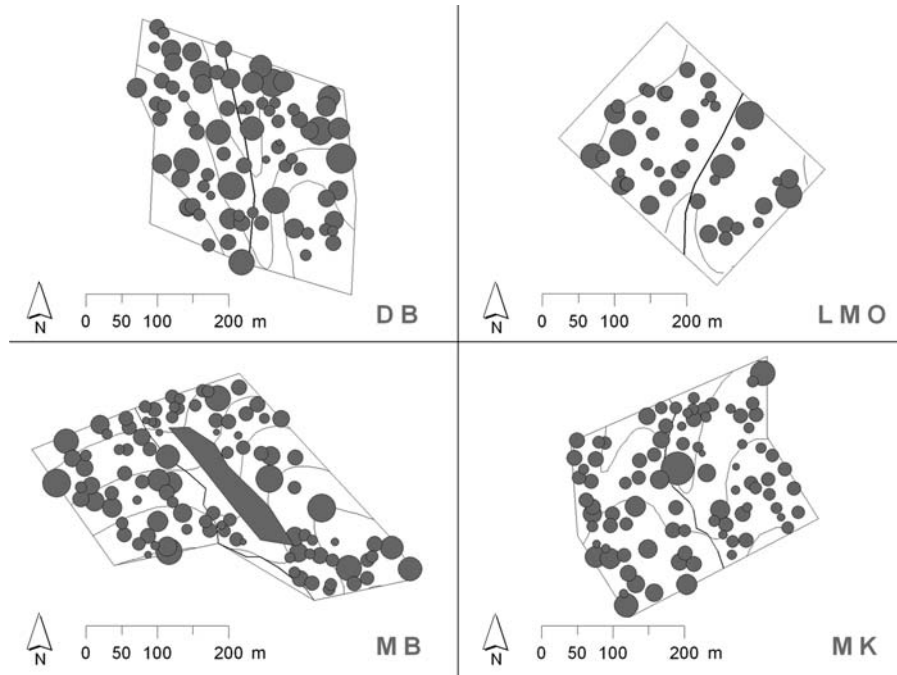
Fig. 5. Spatial clustering for each stream reach, Ripley's *K* analysis. Solid lines show values of *L*(*t*) calculated for distances up to 250 m, depending on the site. The broken lines enclose a 95% confidence interval around the zone for random distribution. *L*(*t*) values above the confidence interval correspond to clustered distributions, whereas values below the confidence interval indicate dispersed distributions. See Fig. 4 for site abbreviations.
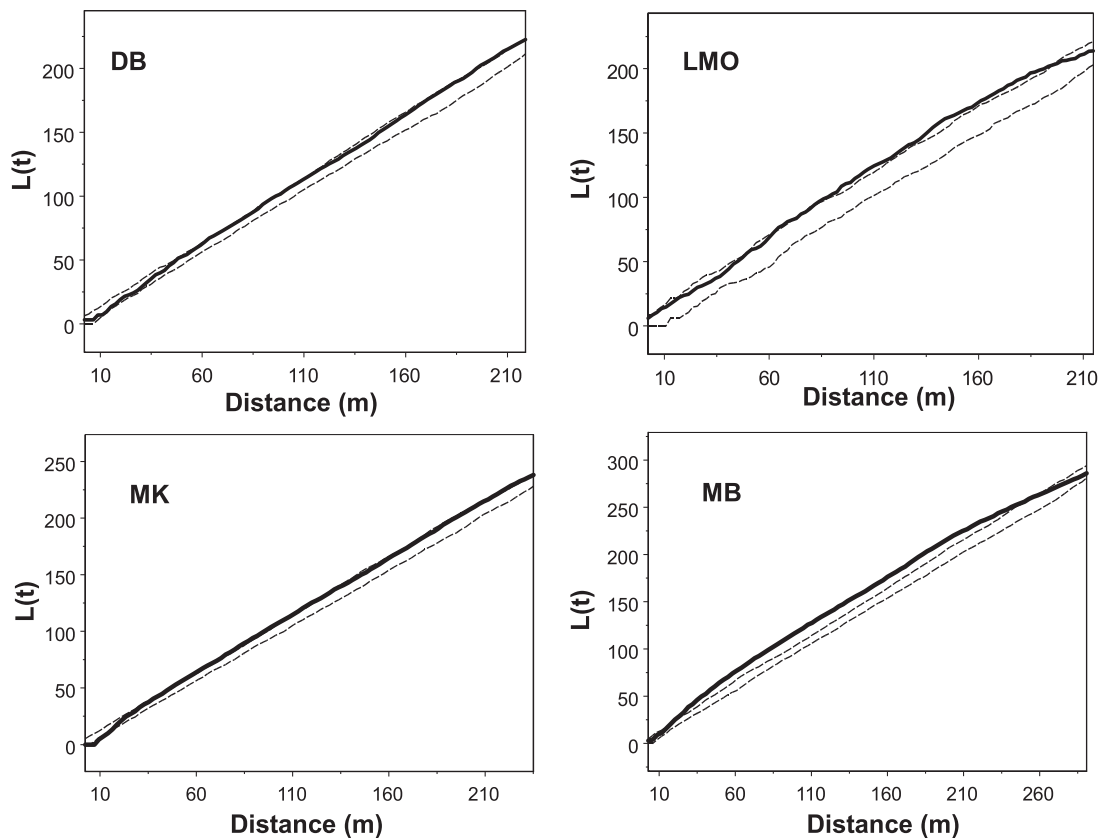
Table 2. Spatial autocorrelation of canopy gap area, uproot occurrence, and standing dead occurrence at different scales. The test statistic shown is a normal statistic derived from Moran's *I* in S+ SpatialStats (Insightful Corp., Seattle, Washington).

Site and distance (m)	Normal statistic	*P*
Mean expanded gap area (m²)		
DB		
50	3.949	**<0.001**
100	–0.978	0.328
150	4.369	**<0.001**
200	10.700	**<0.001**
250	6.996	**<0.001**
300	6.032	**<0.001**
LMO		
50	–107.300	**<0.001**
100	7.894	**<0.001**
150	13.700	**<0.001**
200	29.100	**<0.001**
MB		
50	1.327	0.184
100	–0.486	0.627
150	–1.337	0.181
200	–1.659	0.097
250	–1.023	0.306
300	–0.451	0.652
MK		
50	–4.447	**<0.001**
100	0.606	0.544
150	8.267	**<0.001**
200	12.700	**<0.001**
250	–460.000	**<0.001**
Uproots (% gapmakers)		
MK		
50	3.688	**<0.001**
100	1.804	0.071
150	2.636	**<0.001**
200	1.512	0.131
250	1.237	0.216
Standing dead (% gapmakers)		
LMO		
100	3.544	**<0.001**
150	4.428	**<0.001**
200	1.430	0.153
MK		
50	0.487	0.626
100	–0.410	0.682
150	1.757	0.079
200	2.221	**0.026**
250	2.290	**0.022**

Note: Values given in boldface are significant. Negative coefficients indicate negative spatial autocorrelation, meaning that gaps in close proximity to one another at the scale specified have dissimilar values. Coefficients >1.96 indicate positive spatial autocorrelation. See Table 1 for site abbreviations.

Discussion

Forest structure in old-growth riparian forests

Our results indicate that natural disturbance processes strongly influence the horizontal structure and dynamics of old-growth riparian forests. Given that most structural attributes (e.g., basal area and stem density) did not differ significantly among our study sites (Table 1), it is likely that different disturbance histories explain the significant variability in gap characteristics and patterns we observed. However, it is important to note that one of our sites (DB) had both the greatest large tree density and mean gap area (Table 1), a relationship also observed in old-growth hemlock–hardwood forests of the Great Lakes region (Dahir and Lorimer 1996).

Canopy gap sizes reported in this study fall within the range reported for mesic old-growth forest stands across the eastern United States (Runkle 1982). However, mean gap area exceeds previous values reported for old-growth hemlock–hardwood forests in upstate New York (Runkle 1982; Ziegler 2000), in the Great Lakes region (Dahir and Lorimer 1996), and in Maine (Chokkalingam and White 2001). Expanded gap fraction at the three sites on Ampersand Mountain (DB, MB, and MK; Table 1) exceeds a previous estimate of mean decadal canopy disturbance for forests on the same mountain (Ziegler 2002) and is likely attributable to a summer windstorm in 2004. Prior to the 2004 summer storm season, Ziegler (2002) found significant variability in the decadal disturbance rate at other locations in the Adirondacks but concluded that the forest at Ampersand Mountain exhibited "quasiequilibrium" dynamics. Our results suggest that even at this site, intermediate severity wind disturbances (Woods 2004; Hanson and Lorimer 2007) may disrupt quasiequilibrium dynamics at the scale of forest stands.

Process, scale, and pattern in canopy disturbance

Our results supported the hypothesis that canopy gaps in old-growth hemlock – northern hardwood riparian forest stands exhibit a clustered (aggregated) spatial pattern at within-stand scales along low-order streams. We observed random spatial distributions at fine scales (<60 m), but the size of objects (gaps) with which points are associated can affect the distribution of points at fine scales (Koukoulas and Blackburn 2005). Mortality resulting from pathogens, insects, or other biotic factors is frequently distributed in either random or evenly dispersed patterns (Woods 2004; Worrall et al. 2005), whereas wind or other gap-enlargement agents are associated with clustered patterns (Foster and Reiners 1986; Lawton and Putz 1988; Battles et al. 1995; Woods 2004; Koukoulas and Blackburn 2005). Our results also closely resemble patterns observed in old-growth oak woodland in England where gaps were randomly distributed for scales >20 m up to 72 m and clustered beyond 72 m (Koukoulas and Blackburn 2005). Because no peak in the distribution patterns observed in our study was reached, spatial distributions should be assessed at coarser scales to gain a better understanding of topographic influence across the landscape. Positive spatial autocorrelation observed in both gap area and gapmaker types suggests a degree of induced spatial autocorrelation, although the mechanistic relationship is uncertain. Induced spatial autocorrelation occurs when a variable responds to the spatial structure of an external process (Fortin and Dale 2005).

Table 3. Uprooted gapmakers by landform type.

Site and species	n	Observed		Expected		G	p
		Convergent	Divergent	Convergent	Divergent		
DB							
ACSA	13	10	3	6.1	6.9	4.771	<0.05
BEAL	7	7	0	3.3	3.7	10.481	<0.05
FAGR	22	12	10	10.4	11.6	0.463	ns
PIRU	14	10	4	6.6	7.4	3.346	ns
TSCA	95	59	36	44.9	50.1	8.388	<0.05
All	188	117	71	88.9	99.1	16.893	<0.001
LMO							
ACSA	2	1	1	0.9	1.1	0.006	ns
PIRU	6	3	3	2.8	3.2	0.018	ns
TSCA	17	8	9	8.0	9.0	0.000	ns
All	32	14	18	15.1	16.9	0.154	ns
MB							
BEAL	3	2	1	1.5	1.5	0.403	ns
FAGR	21	5	16	10.2	10.8	5.418	<0.05
PIRU	5	5	0	2.4	2.6	7.236	<0.05
TSCA	50	9	41	24.3	25.7	20.299	<0.001
All	117	37	80	56.8	60.2	13.723	<0.001
MK							
ACSA	15	4	11	6.4	8.6	2.886	ns
BEAL	3	1	2	1.3	1.7	0.268	ns
FAGR	26	9	17	11.1	14.9	1.931	ns
PIRU	20	6	14	8.5	11.5	2.711	ns
TSCA	37	12	25	15.8	21.2	3.732	ns
All	99	30	69	42.3	56.7	6.452	<0.05

Note: See Table 1 for site abbreviations. FAGR, *Fagus grandifolia*; TSCA, *Tsuga canadensis*; ACSA, *Acer saccharum*; PIRU, *Picea rubens*; BEAL, *Betula alleghaniensis*. ns, not significant.

Interactions between old-growth riparian forest structure and low-order streams

Although we observed an association between riparian landforms and gap fraction, we did not detect a direct relationship between distance from stream and gap size as predicted. Gap frequency did increase with decreasing distance from the nearest stream at two sites, suggesting greater canopy disturbance. Additionally, the mean gap area observed at our sites was larger than reported in studies focused primarily on upland forests (Runkle 1982; Dahir and Lorimer 1996; Ziegler 2000). Our plots extended 150 m to both sides of stream bank-full width and, thus, included a mosaic of landforms within an extended riparian corridor (Gregory et al. 1991).

Our prediction that gap fraction is higher on convergent landforms when compared with divergent landforms was supported by our results. However, we also expected increased soil moisture in concave areas (O'Loughlin 1986; Dietrich et al. 1993) to increase uprooting likelihood. This prediction was not supported because the percentage of uprooted gapmakers was greater on divergent landforms, suggesting that these sites also can have high susceptibility to windthrow even if overall gap fraction is less. That soil moisture also can be important for windthrow was supported by data from DB, where more uproots occurred on concave landforms and our field observations indicated a higher density of forested seeps in those areas. These landform associations may differ among species, reflecting their distributions and susceptibility to windthrow (Foster and Boose 1992; Canham et al. 2001; Woods 2004). There was a greater tendency for conifers to uproot on divergent landforms; hardwood species showed the opposite association.

Our results suggest that even low-order streams, when dominated by structurally complex, late-successional forests, are consistent with the view of riverine corridors as mosaics of patches (Thorp et al. 2006; Gooderham et al. 2007). This is interesting because recent research has shown that greater spatial variability in the light environment along old-growth forest streams influences the distribution of autotrophic versus heterotrophic production (Stovall et al. 2009). Because of the abundance of large canopy gaps, old-growth riparian forests are not strictly closed canopied as envisioned in the river continuum concept proposed by Vannote et al. (1980).

Conclusions and management implications

Disturbance-based forest management is gaining interest in northeastern North America as an approach that more closely emulates stand dynamics associated with natural disturbance regimes (North and Keeton 2008). Such management involves emulation of the horizontal structural complexity associated with fine-scale disturbances and gap dynamics (Franklin and Van Pelt 2004). This has not been previously described for old-growth riparian hemlock – northern hardwood forests. Thus, our results are relevant to considerations of harvesting scale and frequency (see Franklin et al. 2007; North and Keeton 2008) in gap-based management systems, such as group selection. Systems that provide a wide range of gap sizes and spatial distributions, including

Fig. 6. Variation of species composition of live, dominant perimeter trees and of the gapmaker class between landform types. See Fig. 4 for site abbreviations. FAGR, *Fagus grandifolia*; TSCA, *Tsuga canadensis*; ACSA, *Acer saccharum*; ACRU, *Acer rubrum*; PIRU, *Picea rubens*; BEAL, *Betula alleghaniensis*.
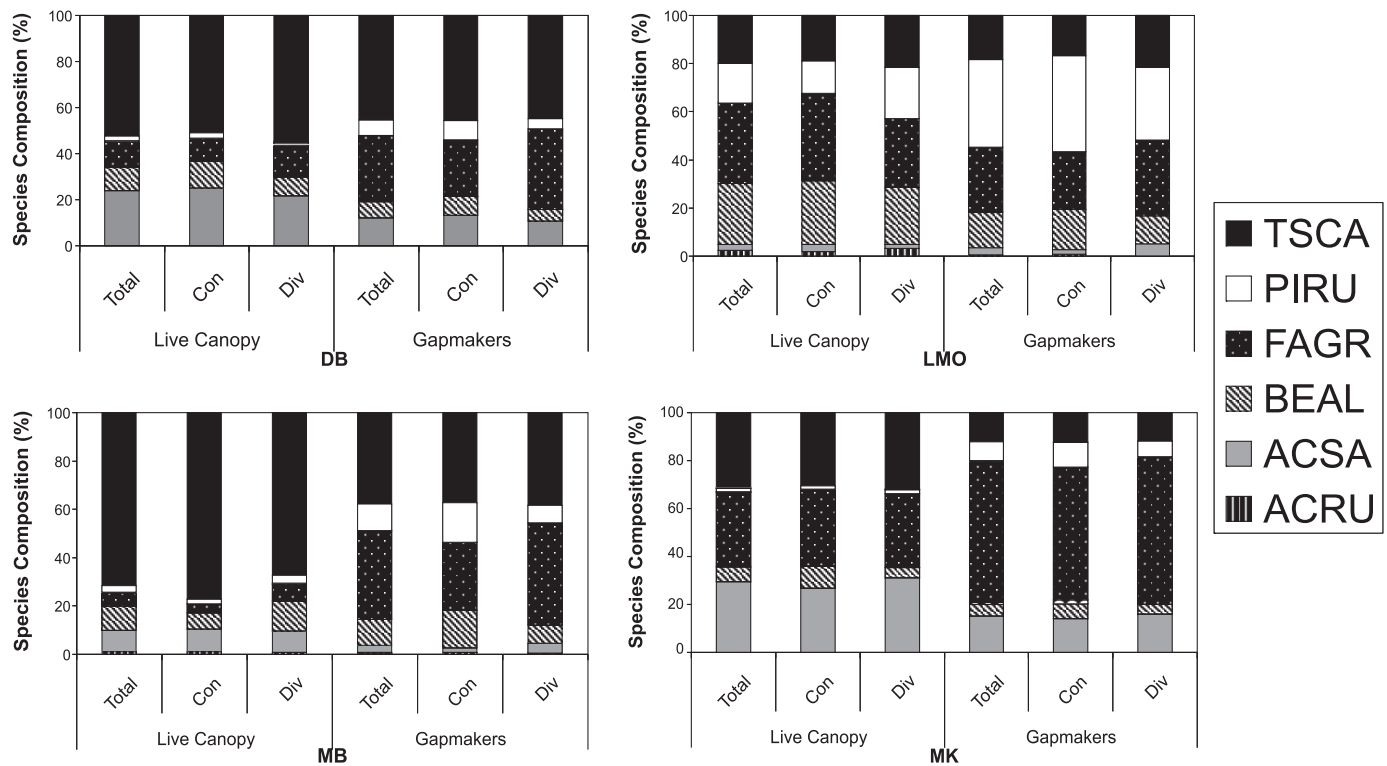
clustered larger gaps, and residual trees (biological legacies) within gaps would most closely approximate patterns associated with wind disturbances in riparian areas.

Intermediate disturbance is increasingly viewed as an important component of the natural disturbance regime in northern hardwood – conifer systems (North and Keeton 2008); however, with a few exceptions (e.g., Woods 2004; Hanson and Lorimer 2007), few empirical data are available (Seymour et al. 2002). Larger, wind-related gaps may have related effects on the light environment over streams and may play a role in pulse recruitment of large woody debris into streams (Keeton et al. 2007; W.S. Keeton, unpublished data). Our results suggest that intermediate disturbance can have important influences on function and structure in hemlock–hardwood forests. Disturbance-based forest management practices (North and Keeton 2008) that include moderate-intensity harvesting (e.g., partial harvests) and multiaged management (Hanson and Lorimer 2007) in mature stands could produce structural conditions analogous to the conditions encountered at our sites in some cases. Use and appropriateness of these practices along stream reaches would have to be evaluated carefully to avoid deleterious impacts associated with canopy removals and harvest entries in riparian areas (Gregory 1997; Stuart and Edwards 2006). Protected riparian buffers in which late-successional forest characteristics develop and interact with disturbance processes provide another alternative.

In conclusion, riparian landforms influence spatial patterning in old-growth forests prone to periodic wind disturbances, particularly with respect to species distribution, types of tree damage, gap fraction, and the distribution of canopy gaps. This could have important implications for riparian functions related to stand structural complexity, such as the spatial dynamics of large woody debris recruitment into streams (Harmon et al. 1986; Keeton et al. 2007), erosion processes relating to wind disturbed sites along streams (Naiman et al. 2005), and the distribution of light availability and in-stream primary production (Stovall et al. 2009).

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