Journal of Vegetation Science 9: 881-890, 1998
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Composition, structure and diversity of cove forest stands in the Great Smoky Mountains: a patch dynamics perspective

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Abstract. Cove forests of the Great Smoky Mountains are North American examples of old-growth temperate forest. Ecological attributes of seven stands were studied using one 0.6 - 1.0 ha plot per stand. Stand basal area (39 - 55 m^2/ha) and biomass (326 - 471 Mg/ha) were high for temperate deciduous forest. Density ranged from 577 to 1075 stems/ha. All stands had a mixture of deciduous canopy species. Only rarely did a single species comprise more than half of the stand by density, basal area or biomass. Shade-intolerant species were present at low levels (1 - 5 % of total stand density). A wide range of stem diameters was characteristic of most species. However, some species lacked small stems, indicating discontinuous regeneration. Stands tended to have 10 - 20 tree species per ha and at least five species had biomass levels > 10 Mg/ha, indicating high evenness. Canopy gaps covered 10 % of the total area (2 - 21 % by stand). Gaps and conspecific patches of canopy trees > 0.05 ha in size were infrequent. Spatial analyses revealed a variety of patterns among species at inter-tree distances of 1 to 25 m. When all species were combined, juveniles showed aggregation, and adults were often hyperdispersed. Analyses for individual species confirmed that the mosaic of canopy species is influenced by non-random spatial processes. Adults of several species were aggregated at distances > 10 m. Juveniles of all major species exhibited aggregation. Several species exhibited regeneration near conspecific adults. This pattern suggested limited mobility for such species within the shifting mosaic. A diverse patchwork resulted despite the fact that many species did not exhibit segregation of adults and juveniles. Further understanding of patch dynamics and the potential for compositional steady state in cove forests requires long-term study with spatial data.

Keywords: Canopy gap dynamics; Forest structure; Old-growth forest; Patch size; Spatial pattern; Species diversity; Temperate deciduous forest.

Nomenclature: Radford et al. (1968).

Introduction

The northeastern Great Smoky Mountains harbor some of the best examples of old-growth temperate forest in eastern North America. Sheltered from major disturbance and receiving abundant precipitation throughout the year, mountain coves have well-developed mesic forests. Cove forests are noted for their plant species richness (Cain 1943; Braun 1950; Whittaker 1956, 1965, 1975; Glenn-Lewin 1977; Golden 1981), but data on patterns of tree species composition, diversity and equitability for areas greater than 0.1 ha are scarce. Some ecologists contend that, unlike many temperate forests, composition and structure of these old cove forests are near equilibrium (Whittaker 1956; Peterken 1996; Runkle 1996). Certain mechanisms and patterns of cove forest dynamics, disturbance and species coexistence have been studied. It is widely held that small-scale disturbances and canopy gap processes are of great importance in canopy turnover and the maintenance of species diversity (Barden 1979, 1980, 1981; Runkle 1981, 1982; Runkle & Yetter 1987; Clebsch & Busing 1989). However, species patch dynamics, the establishment and disappearance of localized populations of species (Glenn-Lewin & van der Maarel 1992), have not been characterized.

The objective of this paper is to examine tree species composition, species diversity, and structure of seven old-growth forest stands using a plot size large enough to characterize the patch structure of tree species. I have published several studies based on subsets of these data, including assessments of: (1) compositional change through time (Busing 1989, 1993); (2) the implications of area effects on the equilibrium of forest attributes (Busing et al. 1993; Busing & White 1993); (3) canopy cover and tree regeneration (Busing 1994); (4) simulation models of forest dynamics (Busing 1991, 1995); and (5) the role of canopy gaps in the maintenance of species richness (Busing & White 1997). By contrast, this paper has three goals: (1) to characterize variation in species composition and diversity among these old growth stands using estimates of tree biomass in addition to tree basal area and stem density; (2) to characterize variation in species size-class structure among stands; and (3) to answer several questions about the spatial structure of stands, with regard to patchiness, population structure, species diversity, and stand dynamics (e.g. Pickett & White 1985; van der Maarel 1996). These questions include: 1. What is the size of species patches in stands of old-growth cove forest?

2. How does this compare to canopy gap size? 3. Are adult trees, taken by dominant species or all species combined, randomly distributed in horizontal space? 4. Are juveniles, taken by species or all species combined, randomly distributed in horizontal space? 5. Are juveniles randomly distributed with respect to conspecific adults? 6. Given these data what inferences can be made about patch dynamics and the shifting-mosaic steady state (*sensu* Bormann & Likens 1979) in cove forests?

Methods

Data collection

I selected seven old-growth stands at four locations on the north slope of the eastern Great Smoky Mountains (35° 40' N, 83° 23' W) (Table 1). The stands at Long Branch, Porters Creek and Dunn Creek were chosen because forest data had been collected and documented in previous studies within these stands. Locations of the previous plot boundaries at Long Branch could not be determined, but the new plots lie within the same 10-ha area of each stand (Busing 1989). The Long Branch, Porters Creek and Dunn Creek stands were predominantly mixed deciduous. By contrast, the three stands at Roaring Fork were chosen to represent *Tsuga*-mixed-deciduous old growth.

At each site a plot (0.6 - 1.0 ha in area) was established on a gentle north-facing slope (< 35°). Plot dimensions were often constrained by local topography. Slopes > 35° were avoided because of the potential for damage to understory vegetation during sampling. The length of each plot was at least 100 m and the width was at least 50 m. Low cover of the shrub species *Rhododendron maximum* was an additional criterion for plot placement except at Dunn Creek. Shrub cover was negligible within six of the plots. A seventh plot, at Dunn Creek, had moderate cover (50 - 70 %) of *Rhododendron.*

I divided each plot into contiguous 10 m × 10 m subplots. Within each subplot I recorded the species and DBH (diameter 1.37 m above-ground) of live trees > 2 cm DBH. The location of each live tree >2 cm was mapped. I tallied all live individuals of the small sapling stratum (>1.37 m tall to 2 cm DBH) by species. Edges of canopy openings >25 m^2 visible from the ground were drawn. In these forests, gap saplings must be at least 10-20 m tall to obstruct visibility of gap edges (Runkle 1992). Thus, in this study, gaps are canopy openings >25 m^2 lacking substantial ingrowth >10 m tall.

Data analysis

Species composition, structure and diversity

I summarized species composition, population structure and species diversity by stand. Composition was evaluated from species density (live stems >2 cm DBH), live basal area, and live above-ground biomass. I estimated above-ground biomass of live trees >2 cm DBH with allometric equations for species in the Great Smoky Mountains and eastern Tennessee (Busing et al. 1993). Densities of small saplings were summarized by species. Population structure was described using stem densities by DBH class for all live stems >5 cm DBH divided into 10-cm DBH classes. I evaluated species diversity with dominance-diversity curves based on species biomass and with species-accumulation curves. Two types of species-accumulation curves were plotted for stems >1.37 m tall: (1) species-area curves and (2) species-individual curves. Both were based on species counts from series of nested plots (0.01, 0.04, 0.16, and 0.6-1.0 ha) within each stand. A mean richness value was calculated for each plot 0.01 to 0.16 ha in size ($n = 3$). Mean stem density values for each plot size were used in the species-individual curves (Condit et al. 1996).

Canopy patch structure and species dispersion

I constructed a mosaic diagram showing canopy species patches and canopy gaps in each stand. After outlining gaps, I drew unweighted Dirichlet tessellation diagrams (Kenkel 1990) having discrete tiles for all live trees >30 cm DBH by stand. I proceeded to estimate the size frequency of conspecific patches. Single- and multiple-tree patches were included. Multiple-tree patches

Table 1. Characteristics of study stands in cove forests of the northern Great Smoky Mountains.

Site	Plot code	Plot size (ha)	Elevation (m)	Slope (°)	Aspect	Sampling history
Roaring Fork	RF1	1.0	960	10	N	1990
Roaring Fork	RF2	1.0	990	10	N	1990
Roaring Fork	RF3	1.0	1140	20	N	1990
Long Branch	LB1	0.6	920	10	N	1936[1]/1988
Long Branch	LB2	0.6	950	15	N	1936[1]/1988
Porters Creek	PC	0.6	720	20	N	1959[2]/1989
Dunn Creek	DC	0.6	970	5	N	1962[3]/1992

[1]S.A. Cain sampled this stand in the 1930s; [2]R.H. Whittaker sampled 0.1 ha in this stand; [3]E.E.C. Clebsch sampled 0.4 ha in this stand.

had conspecific individuals joined on at least one tile edge. Patch size distributions were summarized across all stands.

I used multivariate Mantel correlograms (Legendre & Fortin 1989) to further characterize patch size. Multi-species spatial pattern was assessed by computing Bray-Curtis similarity indices (Ludwig & Reynolds 1988) of species composition for all possible pairs of subplots in each stand. The resulting matrices were generated using absolute biomass of species by subplot in the calculation of similarities. Also, a matrix of physical distances between all subplot pairs was constructed. In this matrix, the elements were integers representing 10 m distances classes (e.g. class 1 = 10 m, class 2 = 20 m). A normalized Mantel statistic (*r*) was calculated for each of the eight distance classes. Distances greater than 80 m were excluded because of small sample size. I used Mantel's normal approximation to evaluate significance of the *r*-statistic (Legendre & Fortin 1989).

I explored tree dispersion patterns using *K*-function analyses (Ripley 1977) of stem maps. Live individuals were classified as juveniles (2 - 12.5 cm DBH) or adults (> 12.5 cm DBH) for analyses of spatial structure. Several questions were addressed: 1. Does the spatial pattern of adults, taken by species or all species combined, deviate from random patterns? 2. Does the spatial pattern of juveniles, taken by species or all species combined, deviate from random patterns? 3. Do the spatial associations between adults and juveniles, taken by species or all species combined, deviate from those with random associations? These analyses were completed for all cases with more than five stems per class. Functions were calculated for inter-tree distances from 1 to 25 m at 1-m intervals. The first two questions were addressed with the univariate *K*-function algorithm, while the third question was addressed with the bivariate-algorithm (Duncan 1991; Haase 1995). 99 simulations of random pattern were used in all cases.

Results and Discussion

Species composition

Only rarely did any single species comprise more than half of a stand's density, basal area or biomass (Table 2). Shade-tolerant species, those species classified as a least intermediate in tolerance, dominated all stands, but shade-intolerants occurred in the canopy of every stand. The shade-intolerants: *Betula lenta*, *Carya cordiformis*, *Fraxinus americana*, *Liriodendron tulipifera*, *Prunus pensylvanica* and *Prunus serotina* comprised 1 - 5 % of the density (mean = 2 %), 1 - 17 % of the basal area (mean = 7 %), and 1 - 18 % of the stand biomass (mean = 8 %).

Table 2. Species composition and dimensions of old-growth stands in coves of the northern Great Smoky Mountains.

		Density (stems >2 cm DBH/ha)							Basal area (m^2/ha)							Biomass (Mg/ha)[1]						
Species	Tolerance[2]	RF1[3]	RF2	RF3	LB1	LB2	PC	DC	RF1	RF2	RF3	LB1	LB2	PC	DC	RF1	RF2	RF3	LB1	LB2	PC	DC
Acer pensylvanicum	VT	62 (7[4])	15 (2)	144 (19)	7 (1)	10 (1)	0	0	0.2 (<1)	0.2 (<1)	0.7 (1)	<0.1 (<1)	<0.1(<1)	0	0	1 (<1)	1 (<1)	3 (1)	<0.1 (<1)	<1 (<1)	0	0
Acer rubrum	T	4 (<1)	34 (3)	6 (1)	0	0	0	48 (8)	0.3 (1)	7.7 (14)	3.7 (7)	0	0	0	12.7 (24)	2 (<1)	54 (12)	30 (6)	0	0	0	99 (24)
Acer saccharum	VT	144 (16)	23 (2)	132 (17)	77 (13)	142 (20)	208 (19)	27 (4)	4.5 (9)	2.0 (4)	3.3 (6)	22.2 (49)	10.2 (26)	7.1 (18)	0.5 (1)	45 (11)	19 (4)	32 (7)	226 (57)	100 (30)	72 (22)	1 (<1)
Aesculus octandra	T	35 (4)	0	66 (9)	22 (4)	133 (18)	420 (39)	3 (<1)	2.3 (5)	0	7.1 (13)	1.3 (3)	6.0 (15)	10.4 (26)	<0.1 (<1)	18 (4)	0	51 (11)	8 (2)	45 (14)	76 (23)	<1 (<1)
Betula lenta	I	2 (<1)	7 (1)	1 (<1)	3 (1)	0	0	7 (1)	<0.1 (<1)	1.2 (2)	0.1 (<1)	0.7 (2)	0	0	0.5 (1)	<1 (<1)	28 (6)	2 (<1)	17 (4)	0	0	6 (1)
Betula lutea	M	3 (<1)	1 (<1)	19 (2)	0	12 (2)	33 (3)	47 (8)	0.1 (<1)	<0.1 (<1)	1.5 (3)	0	0.5 (1)	1.6 (4)	4.5 (9)	1 (<1)	<0.1 (<1)	8 (2)	0	3 (1)	8 (2)	27 (7)
Fagus grandifolia	VT	147 (16)	184 (19)	10 (1)	7 (1)	67 (9)	47 (4)	22 (4)	4.8 (10)	7.2 (13)	0.3 (1)	<0.1 (<1)	1.9 (5)	0.5 (1)	2.0 (4)	32 (8)	53 (12)	2 (<1)	<0.1 (<1)	12 (4)	3 (1)	18 (4)
Fraxinus americana	I	2 (<1)	1 (<1)	9 (1)	5 (1)	5 (1)	5 (<1)	5 (1)	0.5 (1)	<0.1 (<1)	1.3 (2)	<0.1 (<1)	1.6 (4)	1.8 (5)	1.4 (3)	3 (1)	<0.1 (<1)	9 (2)	<1 (<1)	11 (3)	12 (4)	9 (2)
Halesia carolina	T	148 (16)	137 (14)	156 (20)	235 (41)	163 (22)	242 (23)	115 (19)	13.8 (29)	7.9 (14)	11.9 (22)	6.6 (15)	10.5 (27)	10.6 (27)	8.9 (17)	145 (35)	82 (19)	120 (25)	58 (15)	103 (31)	91 (28)	96 (23)
Liriodendron tulipifera	I	1 (<1)	6 (1)	1(<1)	5 (1)	0	2 (<1)	15 (2)	<0.1 (<1)	2.9 (5)	0.2 (<1)	1.4 (3)	0	1.7 (4)	6.2 (12)	<0.1 (<1)	22 (5)	1 (<1)	10 (3)	0	14 (4)	35 (9)
Magnolia fraseri	M	8 (1)	14 (1)	4 (1)	0	0	0	20 (3)	0.3 (1)	0.3 (1)	0.2 (<1)	0	0	0	0.4 (1)	2 (<1)	3 (1)	1 (<1)	0	0	0	2 (<1)
Prunus serotina	I	1 (<1)	5 (1)	5 (1)	0	0	0	2 (<1)	<0.1 (<1)	0.6 (1)	0.7 (1)	0	0	0	0.8 (2)	<0.1 (<1)	6 (1)	6 (1)	0	0	0	7 (2)
Tilia heterophylla	T	15 (2)	25 (3)	33 (4)	28 (5)	23 (3)	32 (3)	10 (2)	1.0 (2)	2.1 (4)	2.3 (4)	2.5 (6)	0.8 (2)	1.3 (3)	0.8 (2)	8 (2)	14 (3)	14 (3)	16 (4)	5 (2)	9 (3)	4 (1)
Tsuga canadensis	VT	321 (36)	504 (52)	150 (20)	178 (31)	172 (24)	55 (5)	282 (47)	20.1 (42)	23.0 (42)	20.9 (39)	10.0 (22)	7.3 (19)	1.5 (4)	14.1 (27)	160 (38)	157 (36)	193 (41)	59 (15)	51 (16)	9 (3)	106 (26)
Other species[5]		5 (1)	16 (2)	27 (4)	8 (1)	0	32 (3)	1 (<1)	<0.1 (<1)	0.3 (1)	<0.1 (<1)	<0.1 (<1)	0	3.4 (9)	<0.1 (<1)	<0.1 (<1)	2 (<1)	<1 (<1)	<0.1 (<1)	0	33 (10)	<0.1 (<1)
Total		898	972	763	577	727	1075	603	47.8	55.3	54.2	44.9	38.8	39.8	52.7	416	441	471	394	329	326	410

[1] Biomass is the sum of above-ground compartments for leaves, branches and boles.

[2] Shade tolerance classification: VT=very tolerant; T=tolerant; M=intermediate; I=intolerant; and VI=very intolerant (Burns & Honkala 1990).

[3] See Table 1 for stand codes.

[4] Relative values expressed as percent of the total are provided in parentheses.

[5] Other species with stems > 2 cm DBH include *Acer spicatum* (in stand RF3), *Amelanchier arborea* (RF2, RF3), *Carya cordiformis* (PC), *Cornus alternifolia* (RF3), *C. florida* (RF1, PC), *Hamamelis virginiana* (LB1, PC), *Ilex opaca* (RF2, DC), *Magnolia acuminata* (RF2, LB1,PC), *Ostrya virginiana* (LB1), and *Prunus pensylvanica* (RF3).

Table 3. Small sapling densities (stems/ha) and tolerance (Tol) of woody species old-growth stands in coves of the northern Great Smoky Mountains.

Species	Tol[1]	RF1[2]	RF2	RF3	LB1	LB2	PC	DC
Acer pensylvanicum	VT	134	63	120	18	12	0	0
Acer rubrum	T	1	15	0	0	0	0	0
Acer saccharum	VT	716	153	188	10	48	205	7
Acer spicatum	-	0	0	37	0	0	0	0
Aesculus octandra	T	51	0	38	3	73	537	0
Amelanchier arborea	-	4	7	4	0	0	0	0
Betula lenta	I	0	4	1	2	2	0	0
Betula lutea	M	18	35	34	7	3	3	20
Carya cordiformis	I	1	0	0	3	0	10	0
Castanea dentata	M	1	0	0	0	0	0	0
Cornus alternifolia	-	0	0	6	0	0	3	0
Fagus grandifolia	VT	273	372	8	2	85	22	18
Fraxinus americana	I	11	40	2	3	0	0	0
Halesia carolina	T	130	208	118	278	283	282	68
Hamamelis viginiana	-	0	0	0	12	0	2	0
Ilex ambigua	-	0	0	0	2	0	0	0
Ilex opaca	VT	0	2	0	0	0	0	0
Liriodendron tulipifera	I	1	5	0	87	0	0	0
Magnolia acuminata	M	2	0	0	0	0	0	0
Magnolia fraseri	M	26	59	0	5	0	0	12
Ostrya virginiana	T	0	0	0	2	0	0	0
Prunus serotina	I	8	9	1	0	0	0	2
Quercus rubra	M	3	0	0	0	0	0	0
Tilia heterophylla	T	19	26	13	27	8	33	0
Tsuga canadensis	VT	91	203	23	28	37	8	10
Total		1490	1202	593	488	553	1105	137

[1] Shade tolerance classification: VT = very tolerant; T = tolerant; M = intermediate; I = intolerant; VI = very intolerant; - not known (Burns & Honkala 1990).

[2] See Table 1 for stand codes.

The small-sapling stratum was rich in species, most of which were shade-tolerant (Table 3). Species regenerating by vegetative means were among the most abundant (e.g. *Fagus grandifolia, Halesia carolina, Magnolia fraseri* and *Tilia heterophylla*). Intolerants comprised 1 - 19 % of the sapling stratum density (mean = 4%). It is likely that the intolerant species entered by gap-phase regeneration (Runkle 1981, 1985; Busing 1994).

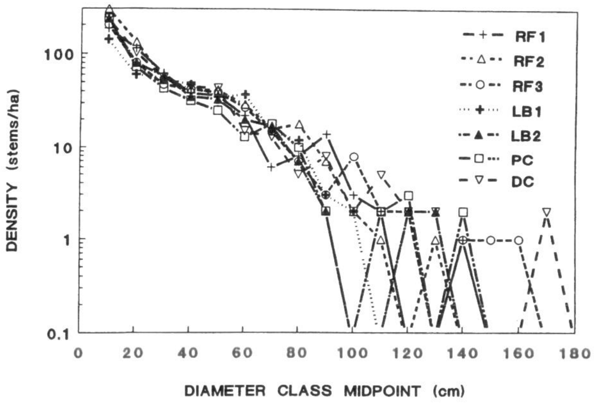

Fig. 1. Size-class curves for all live trees ≥ 5 cm DBH plotted by stand.

Biomass, basal area and density

Total above-ground biomass estimates of 326 to 471 Mg/ha (Table 2) were at or above values for other eastern deciduous forests (Whittaker 1975). Similarly, basal area values of 38 to 55 m^2/ha tended to exceed average values, even those for other old-growth forests (Keddy & Drummond 1996). Stands with a substantial component of *Tsuga* had the highest basal area and biomass values (cf. Woods & Cogbill 1994).

Density of live stems > 1.37 m tall ranged from 737 to 2387/ha (mean = 1597; Tables 2 and 3). These old-growth densities tended to be lower than young cove forest densities, which ranged from about 1000 to > 7000 stems/ha (Della-Bianca 1983; Clebsch & Busing 1989). Presumably, the development of large trees with high shading potential (e.g. high leaf mass; Clebsch & Busing 1989) reduced stem density in old cove forests.

Species diversity

Dominance-diversity curves showed that, in each stand (0.6 - 1.0 ha), several species had high biomass (Fig. 1). All stands had at least five species with more than 10 Mg/ha. The curves dropped precipitously in the 7 to 14 species range. Species ranked beyond this range contributed very little to total stand biomass.

Species-area curves showed that mean levels of accumulation were in the range of 10 to 20 species per ha (Fig. 2). At the scale of 0.1 ha, mean levels ranged from 6 to 12 species. For 0.01 ha they ranged from 2 to 6 species.

Species-individual curves revealed that when tallying species in contiguous quadrats, more than 100 stems (almost 500 or more in some cases) must be encountered to obtain more than 10 species (Fig. 3). The number of stems in a stand did not serve to estimate its relative richness at the 0.6 to 1.0 ha scale. For example, stands LB1 and DC had the lowest densities at this scale, but they had high richness. Evidently, density effects (*sensu* Denslow 1995) were not so strong or consistent among stands that they alone explained differences in richness.

Size-class distributions

Although each stand tended toward a log-linear size-class distribution when all species were combined (Fig. 4), individual species exhibited a variety of size distributions (Fig. 5). Most canopy species in these old-growth stands had abundant regeneration. However, some species were deficient in small stems at certain sites (e.g. *Acer rubrum* at RF3, *Liriodendron* at DC and *Acer saccharum* at LB1). Presumably, these bell-shaped distributions deviating from log-linearity

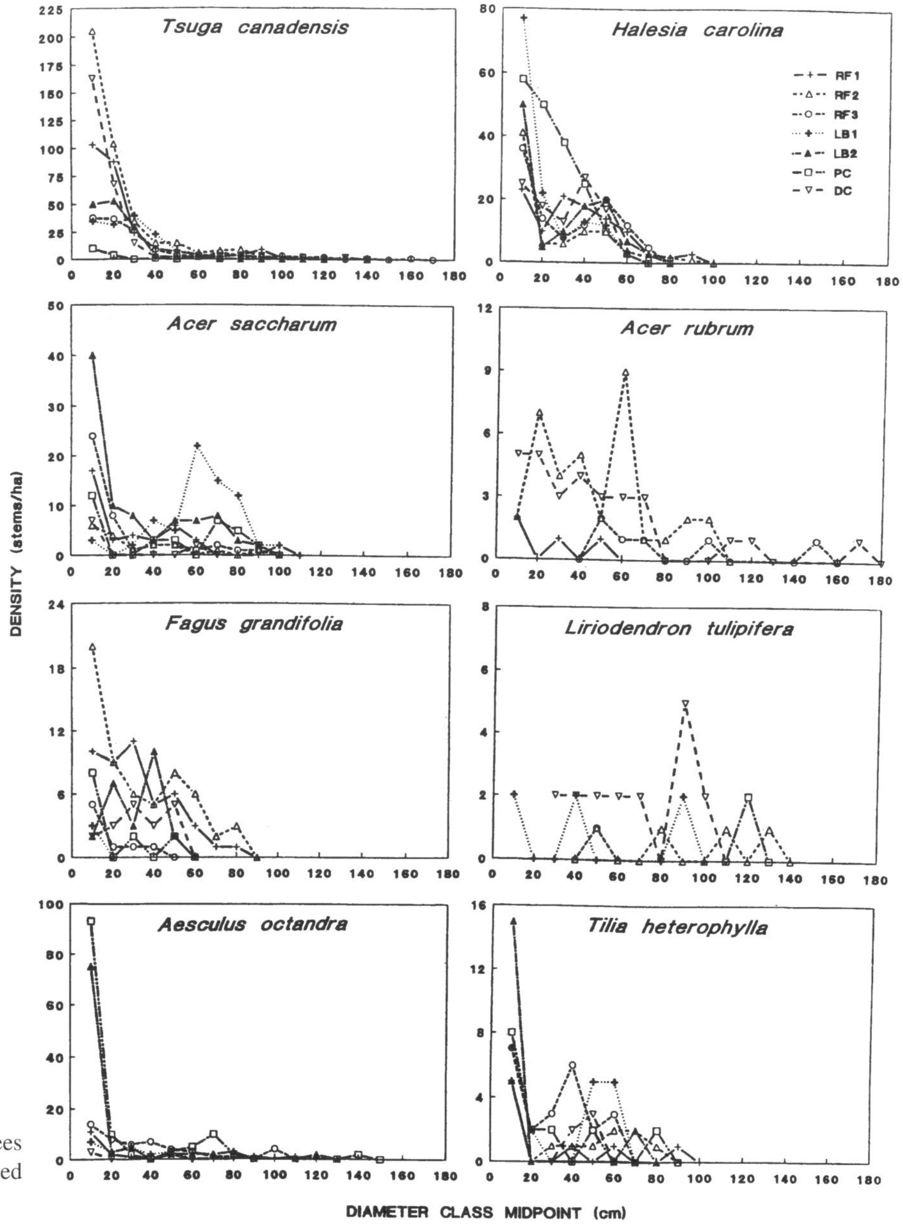

Fig. 2. Size-class curves for live trees ≥ 5 cm DBH of major species plotted by stand.

reflected episodic regeneration. Such distributions were known to be common among shade-intolerant species (Nakashizuka et al. 1992), but some shade-tolerant species deviated from the log-linear structure as well (e.g. *Acer saccharum* at LB1 and *Fagus* at LB2). Apparently, the regeneration success of some shade-tolerant species can fluctuate substantially, at least at a spatial scale of ca. 1 ha.

Canopy patch structure and species dispersion

Canopy gaps covered 10% of the total area studied. Stand-level percentages ranged from 2 to 21. These values agreed well with Runkle's (1982) transect-based estimates for mesic old-growth stands of the eastern United States.

Analyses of tesselation diagrams revealed conspecific aggregation of canopy trees in several cases. Size-class distributions of canopy gaps and conspecific patches of canopy trees showed that patches > 0.05 ha were infrequent (Fig. 6). Patches < 0.01 ha predominated for gaps and species patches, but the latter typically outnumbered gaps in size classes > 0.01 ha. The median and third quartile for gaps were both 0.005 ha. The median and third quartile for species patches were 0.005 and 0.015 ha, respectively. In general, the area of a conspecific canopy patch ranged from one to several times the area of a small canopy gap.

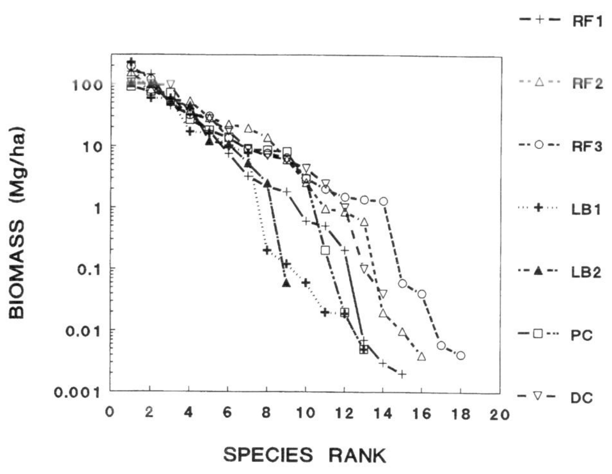

Fig. 3. Dominance-diversity curves plotted by stand. Live stems > 2 cm DBH are considered.

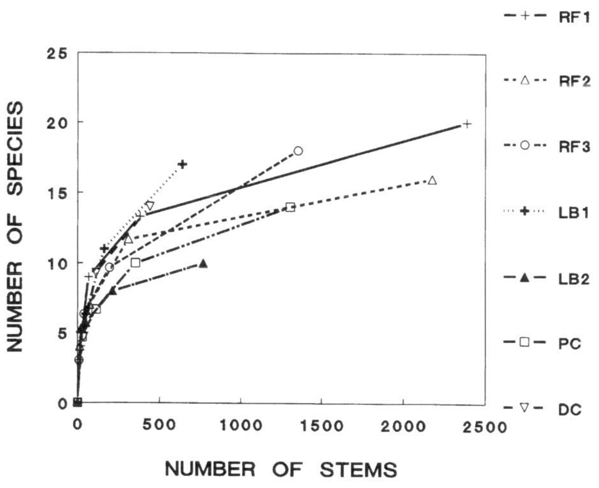

Fig. 5. Species-individual curves plotted by stand. Live stems > 1.37 m are considered.

Patch size was reflected in the multispecies Mantel correlograms (Fig. 7). Five of the seven stands had significantly high compositional similarity between subplots that were 10 m apart. Four stands continued to show significant similarity at a spacing of 20 m. Of these stands, one continued to exhibit significant similarity at 30 m. By contrast, at a spacing of 70 m, three stands showed significant dissimilarity in subplot composition. The Mantel tests revealed that homogeneous conspecific patches tended to be no more than 20 to 30 m in width. Assuming a circular patch shape, patches greater than 0.03 to 0.07 ha in size were infrequent.

Spatial patterns of all juveniles and adults reflected processes influencing patch structure. Many instances of deviation from a random (or null) spatial pattern were evident (Table 4). Hyperdispersion of adults was evident in five of the seven stands. All five exhibited hyperdispersion at distances < 10 m. Only two stands exhibited hyperdispersion at distances >10 m. Aggregation of adults was evident in one stand at distances > 4 m. By contrast, aggregation of juveniles occurred in all stands. Hyperdispersion of juveniles occurred in only one stand (distances > 21 m). The pattern of hyperdispersion of adults and aggregation of juveniles at distances < 10 m was consistent with processes of resource competition among adults and of regeneration in patches. Where regeneration patches were in canopy gaps, segregation of juveniles and adults was expected. Segregation of this type occurred in three of the stands, whereas aggregation occurred in two stands. There was considerable variation among stands. Not all stands conformed to the pattern expected under resource competition among adults and regeneration in canopy gaps.

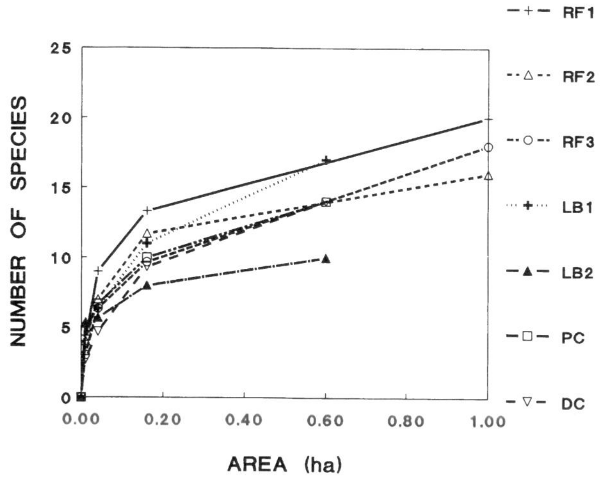

Fig. 4. Species-area curves plotted by stand. Live stems > 1.37 m are considered.

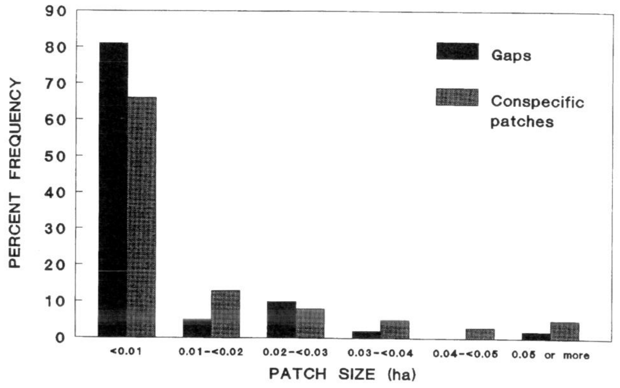

Fig. 6. Size distributions of canopy patches across all stands.

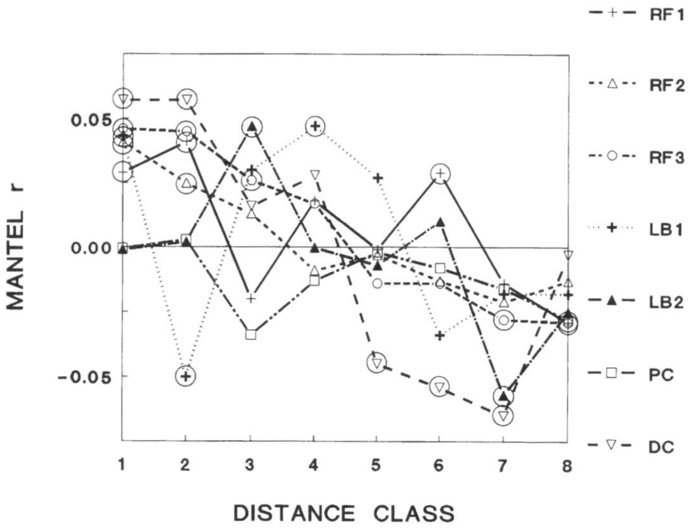

Fig. 7. Mantel correlograms of multispecies pattern by stand. Distance classes are in 10 m units. Positive values of the standardized Mantel statistic (r) indicate compositional similarity. Circled values are significant ($p \leq 0.05$).

Table 4. Results of *K*-function analyses of juvenile (juv) and adult (ad) spatial patterns.

Analysis / Stand[1]	RF1	RF2	RF3	LB1	LB2	PC	DC
All species							
Univariate, ad	S[2] 4, 6 (n = 332)	S 2; A[3] 5-25 (n = 393)	Null[4] (n = 282)	S 3, 6-8 (n = 165)	S 4, 7, 11, 12 (n = 169)	S 2-4, 6, 7, 14, 16-19 (n = 150)	Null (n = 165)
Univariate, juv	A 1-25 (n = 504)	A 1-25 (n = 552)	A 1-25 (n = 311)	A 1, 3-12, 16, 18 (n = 150)	A 1-25 (n = 268)	A 4-25 (n = 496)	A 1-6; S 22-25 (n = 130)
Bivariate, ad/juv	S 3-6, 9-12	S 6; A 11, 12	A 1	S 6, 7	Null	Null	Null
Acer rubrum							
Univariate, ad	( )[5]	A 2-25 (n = 34)	A 10-17 (n = 6)	( )	( )	( )	A 2-25 (n = 19)
Acer saccharum							
Univariate, ad	Null (n = 23)	Null (n = 12)	A 3, 11, 15-23 (n = 21)	S 8 (n = 39)	S 10-17 (n = 33)	Null (n = 12)	( )
Univariate, juv	A 1-25 (n = 121)	A 1-25 (n = 11)	A 1-25 (n = 111)	A 4-5, 8-22 (n = 7)	A 3-25 (n = 52)	A 3-25 (n = 113)	A 2-3, 5-9 (n = 12)
Bivariate, ad/juv	Null	Null	Null	Null	Null	S 9-11, 13, 14	( )
Aesculus octandra							
Univariate, ad	A 20-21 (n = 7)	( )	A 10-25 (n = 34)	A 12-18, 20, 22-24 (n = 9)	Null (n = 15)	Null (n = 24)	( )
Univariate, juv	A 2-25 (n = 28)	( )	A 5-20 (n = 32)	( )	A 4-25 (n = 65)	A 1-25 (n = 229)	( )
Bivariate, ad/juv	A 9, 15, 16, 18-20	( )	Null	( )	Null	S 2	( )
Betula lutea							
Univariate, ad	( )	( )	Null (n = 9)	( )	( )	( )	Null (n = 6)
Univariate, juv	( )	( )	A 1-25 (n = 10)	( )	( )	A 2-4 (n = 16)	A 2-13 (n = 10)
Bivariate, ad/juv	( )	( )	A 17	( )	( )	( )	Null
Fagus grandifolia							
Univariate, ad	A 5, 7-25 (n = 39)	Null (n = 41)	A 3-25 (n = 6)	( )	Null (n = 14)	( )	A 5-21, 23 (n = 10)
Univariate, juv	A 1-25 (n = 108)	A 1-25 (n = 143)	( )	( )	A 2-25 (n = 26)	A 1-25 (n = 26)	( )
Bivariate, ad/juv	A 3-5	A 1-11	( )	( )	A 1, 3	( )	( )
Halesia carolina							
Univariate, ad	A 10-25 (n = 81)	Null (n = 44)	Null (n = 74)	S 4; A 14-25 (n = 41)	Null (n = 40)	S 2, 3 (n = 84)	A 5, 6 (n = 47)
Univariate, juv	A 1-25 (n = 67)	A 1-25 (n = 93)	A 1-25 (n = 82)	A 1, 4-25 (n = 86)	A 1-10, 14-16 (n = 58)	A 9-19, 21-24 (n = 61)	Null (n = 17)
Bivariate, ad/juv	A 1	S 15-25	A 1, 2, 4	A 1-10, 12, 14, 15, 17-20, 22, 24, 25	Null	Null	A 1
Liriodendron tulipifera							
Univariate, ad	( )	( )	( )	( )	( )	( )	Null (n = 6)
Magnolia fraseri							
Univariate, juv	( )	A 1-7 (n = 12)	( )	( )	( )	( )	A 1-25 (n = 11)
Tilia heterophylla							
Univariate, ad	( )	A 1, 24, 25 (n = 8)	A 1-8, 22 (n = 18)	A 1-16 (n = 7)	( )	( )	( )
Univariate, juv	A 1-8 (n = 12)	A 1-25 (n = 17)	A 1-10 (n = 15)	A 1-16 (n = 6)	A 2-15, 21-25 (n = 12)	A 1-7 (n = 15)	( )
Bivariate, ad/juv	( )	A 1	A 1-7, 10-12	A 2-7	( )	( )	( )
Tsuga canadensis							
Univariate, ad	A 11, 16-18, 21-25 (n = 171)	S 2-4, A 11-25 (n = 240)	S 3; A 8-25 (n = 103)	A 23, 25 (n = 71)	Null (n = 59)	Null (n = 14)	Null (n = 63)
Univariate, juv	A 1-22 (n = 149)	A 2-25 (n = 264)	A 2-4, 15-25 (n = 47)	A 1-5, 9-14, 18 (n = 32)	A 1-5, 8-11 (n = 44)	A 3, 10-23 (n = 19)	A 3-18 (n = 75)
Bivariate, ad/juv	Null	Null	A 8-11	Null	Null	A 4, 6, 7, 9	A 4-15, 17, 20-22

[1] Stand codes are explained in Table 1; [2] S indicates hyperdispersion or segregation of individuals at the specified distances (m);
[3] A indicates aggregation or attraction; [4] Null indicates no deviation from 99 simulations of random pattern; [5] ( ) indicates no analysis available.

For example, the dispersion of adults in two stands (DC and RF3) did not deviate strongly from a random pattern. Also strong segregation of adults and juveniles was not found in four stands (LB2, PC DC & RF3). The aggregation of adults and juveniles evident in two stands (RF2 & RF3) suggested effects of limited seed dispersal, vegetative regeneration or microhabitat restrictions.

Conspecific patch structure was influenced by nonrandom dispersion of conspecific canopy trees. With the exception of *Betula lutea* and *Liriodendron*, major canopy species showed strong deviation from random dispersion within the adult class (Table 4). Although patterns for adults of individual species were diverse, some common patterns emerged. For instance, adults of *Halesia*, *Fagus*, *Tsuga*, *Aesculus*, *Tilia* and *Acer rubrum* often showed aggregation at distances > 10 m. Apparently, many conspecific patches or clusters of patches formed by processes that promoted aggregation. One of these processes was regeneration. Juveniles of all major species showed strong aggregation in most stands analyzed. Often juveniles were aggregated near conspecific adults. This was most evident for species exhibiting prolific vegetative regeneration (*Halesia*, *Fagus* and *Tilia*). At least one seed regenerating species (*Tsuga*) showed this tendency as well.

Species having positive associations between juveniles and adults may maintain patches over several generations and spatial shifts may be slow. By contrast, species having random or segregated associations between adults and juveniles are more likely to shift each generation. Thus, species mobility (*sensu* van der Maarel 1996) and the turnover rate of species patches may vary greatly within a stand. Persistent patches are occupied by species that are self-replacing or very long-lived (e.g. *Halesia*, *Fagus*, *Tilia* and *Tsuga*). Patches of other species are likely to be more dynamic in space and time.

One hypothesis of species coexistence in diverse forests holds that spatial segregation of conspecific juveniles and adults promotes diversity (Hubbell 1979). The hypothesis is closely related to theories citing intraspecific density-dependence as a factor in the maintenance of diversity (e.g. Janzen 1970). While the logic of the spatial segregation argument appears reasonable, there is little evidence that such segregation occurs in diverse forests (Hubbell 1979; Grubb 1996). The same is true for old cove forests. Strong segregation of juveniles and adults is uncommon for dominant species. None of the major species showed this type of segregation in more than one stand (Table 4). The results thus suggest that the spatial segregation hypothesis is not a strong explanation of coexistence in cove forests. Theories based solely on niche differentiation are also inadequate (Busing & White 1997). Alternative theories and models accounting for the patch dynamics and mobility of species may be helpful in understanding the maintenance of diversity within stands (van der Maarel & Sykes 1993, 1997; Bakker et al. 1996). In the case of old cove forests, models considering species dynamics within a shifting mosaic driven by tree-fall gaps may be particularly useful. Also, the use of long-term observations on the recruitment, growth and death of individuals with regard to interactions among neighboring trees is a necessary approach to the study of diversity (e.g. Wills et al. 1997). Observations on mapped individuals through time not only allow the study of interactions among individuals, but they also serve as a basis for characterizing species patch dynamics and mobility which may improve our understanding of diversity.

Previous studies by Barden (1979, 1981) and Runkle (1981) suggest that old cove forests exemplify the steady-state phase of forest development (Peet & Christensen 1987). Small canopy gaps are the predominant form of natural disturbance in these forests (Runkle 1982), and diversity of the canopy mosaic is maintained, in part, by gap dynamics. Presumably, a shifting mosaic steady state (Bormann & Likens 1979) accounts for the dynamic behavior of patches within stands. How small-scale disturbances influence patch dynamics and species mobility within stands is only beginning to be understood. Several inferences can be made from plot data for seven stands. For example, as one would expect if patch formation is influenced by gap dynamics, conspecfic-patch-size distributions do not differ greatly from gap-size distributions. Species patch sizes tend to be one to three times the area of small canopy gaps (0.005 - 0.02 ha per gap). The larger patch sizes exhibited by some species are one reason why the land area required for compositional steady state may exceed the area required for steady state in other stand parameters (e.g. total basal area and biomass; Busing & White 1993). Spatial patterns of conspecific juveniles and adults suggest that substantial temporal variation in the persistence of species patches may exist. Some species occupy the same patch for extended periods of time, while others are mobile, shifting location each generation. Rates of patch turnover are influenced by species-specific traits (e.g. tree longevity and the capacity for self-replacement). It is unlikely that rates of canopy-tree turnover and species patch turnover are spatially uniform within these old, mixed-species stands. Full understanding of the effects of spatial structure and turnover processes on community composition, structure and diversity requires further study. Inferences on the steady-state mosaic, canopy turnover, and patch dynamics are best confirmed or refuted by long-term study of stands with spatial data.

Acknowledgements. I thank Patty Aune, Mark Drew, Fred Huber, Ben Hafer, Alex Sloan and Bill Patterson for assistance in the field. My research on cove forests was inspired by Ed Clebsch's succession study at Long Branch. He and Peter White helped to acquire funding from the University of Tennessee, the National Park Service, and the Great Smoky Mountains Conservation Association. Steve Acker provided helpful suggestions and comments on the analyses of spatial pattern. Richard Duncan wrote the computer programs used in *K*-function analyses. Pierre Legendre and Alain Vaudor wrote the computer programs used to produce tesselation diagrams and Mantel correlograms. The field work was completed during postdoctoral appointments at the University of Tennessee and at the University of North Carolina.

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Received 26 February 1997;
Revision received 14 November 1997;
Final revision received 30 June 1998;
Accepted 13 August 1998.