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Oikos, Vol. 78, No. 3. (Apr., 1997), pp. 562-568.

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Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts

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Busing, R. T. and White, P. S. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. – *Oikos* 78: 562–568.

The importance of spatial partitioning of gap resources in the maintenance of tree species diversity was studied in an Appalachian old-growth forest. We established three 1-ha plots, subdivided into contiguous 10 × 10 m subplots, in a mesic cove forest with a disturbance regime characterized by small canopy gaps (<0.1 ha). For tests of partitioning along the gradient from gap interior to the shaded understory, canopy cover of each subplot was classified as gap, gap border, or non-gap. For tests of gap-size partitioning, gap and gap border subplots were classed by gap size. Species-accumulation curves for the regeneration stratum (stems >1.37 m tall and ≤ 10 cm DBH) based on: (1) species per unit area, and (2) species per individual were plotted for each of the canopy cover classes and for all subplots combined. The species-area curve for gaps was steeper than the all-subplots curve that represented the entire gradient from gap centers to the shaded understory. By contrast, all of the species-individuals curves were similar. Sorrenson's indices showed that only gap subplots, particularly those associated with large gaps, had highly self-similar species composition. Furthermore, the relative abundance of most species was similar between gaps and the shaded understory. However, intolerant species often had higher relative abundance in gaps, especially in gaps ≥ 0.04 ha in size. We concluded that gap partitioning hypotheses applied to some intolerants, but not to tolerants. The density hypothesis, a null model attributing species richness levels to stem density levels, largely explained the richness patterns in our study forest.

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Relationships between local diversity (i.e., diversity at the 0.1 to 10-ha scale) and disturbance have been recognized in many studies of vegetation (Loucks 1970, Connell 1978, Sousa 1984, van der Maarel 1988). It has been theorized that small-scale disturbance at moderate frequencies enhances plant species diversity (Connell 1979, Huston 1979, Denslow 1985). This holds true in forests of temperate and tropical regions where disturbances created by the fall of dominant trees stimulate plant regeneration (Prentice and Leemans 1990). In temperate and tropical forests, small-scale disturbances created by tree falls are known to promote regeneration

of a diverse array of species (Runkle 1982, Brokaw and Scheiner 1989), but the cause and effect relationship is not fully understood.

Several hypotheses have been proposed to explain how small-scale disturbances enhance diversity in forests. In its original form, the gap partitioning hypothesis holds that an array of regeneration niches occurs along the gradient from the center of a disturbance patch (or canopy gap) to the shaded understory of undisturbed forest (Ricklefs 1977, Denslow 1980). Ricklefs suggests that this gradient is particularly broad in tropical forests because the contrast in conditions

Accepted 31 July 1996

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ISSN 0030-1299

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Table 1. Characteristics of old-growth forest study plots in Roaring Fork watershed.

Plot	Elevation (m)	Slope (deg.)	Aspect	Basal area (m ² ha ⁻¹)	Density ^a (stems ha ⁻¹)	Dominants ^b
RF1	995	10	N	48	897	<i>Tsuga, Halesia, Fagus, Acer</i>
RF2	960	10	N	55	972	<i>Tsuga, Halesia, Acer, Fagus</i>
RF3	1140	20	N	40	763	<i>Tsuga, Halesia, Aesculus</i>

^a Live stems ≥ 2.0 cm DBH.

^b Species with basal area >4 m² ha⁻¹.

between gaps and the shaded understory is so great. Although some empirical evidence for resource partitioning along such a gradient exists (Sipe and Bazzaz 1994), its significance in the development and maintenance of species diversity has not been demonstrated convincingly (Denslow 1995). Since its origin, the gap partitioning hypothesis has evolved to embrace gap size as a central issue (Hartshorn 1978, Whitmore 1978, 1982, 1988, 1989, Denslow 1980, Pickett 1983). Under this hypothesis, hereafter referred to as gap-size partitioning, species exhibit niche differentiation along a gap-size gradient. Evidence for this simple but powerful hypothesis is unclear (Barton 1984, Brokaw 1985, Brown and Whitmore 1992, Kennedy and Swaine 1992, Lertzman 1992). It does appear that certain shade-intolerant tree species are more successful in large gaps (Runkle 1982, Runkle and Yetter 1987, Brokaw and Scheiner 1989), but gap-size partitioning among shade-tolerant species has not been demonstrated as a widespread phenomenon.

An alternative hypothesis, devoid of niche partitioning arguments, is based on the reasoning that gap interiors are important sources of diversity simply because they are the primary sites of regeneration. Gaps may allow abundant and diverse regeneration thereby promoting diversity. Denslow (1995) presents the hypothesis that high stem densities in gaps are the primary reason for high diversity in gaps. The density hypothesis serves as a null model for the effects of gaps on diversity.

Tree regeneration patterns at one point in time may be sufficient to support or refute gap partitioning hypotheses. Under the original gap partitioning hypothesis we would expect that: (1) species accumulate rapidly as one progresses along the gradient from gap center to the shaded understory; and (2) the relative abundance of species in gaps differs from that in the shaded understory. Under the gap-size partitioning hypothesis we would expect relative abundances to differ across gaps of various sizes. By examining species diversity of the regeneration stratum within and among portions of the gap-understory gradient (gap, gap border, and nongap) and the gap size gradient (small gap to large gap) we search for evidence of spatial partitioning of resources. If species richness and diversity across such gradients exceed that of portions of the gradient, then gap partitioning concepts may apply. Alternatively, tree

species richness may largely depend on stem density. If gaps do nothing more than increase the availability of common resources, then the density hypothesis is applicable. However, if gaps also provide rare resources or conditions that stimulate the regeneration of specialized species, diversity should be greater than predicted solely by density effects (Denslow 1995).

Methods

Data collection

We studied a *Tsuga*-mixed deciduous forest within Roaring Fork watershed of the Great Smoky Mountains (35°40' N, 83°23' W). Three mesic cove stands having gentle slopes and sparse shrub cover were selected within the extensive old-growth forest. Data on composition, structure and diversity of the tree stratum were collected in a 1.0-ha plot at each site (Table 1). Each of the three plots was divided into contiguous subplots with dimensions of 10 × 10 m, yielding a total of 300 subplots. Species and DBH (diameter at 1.37 m above ground) were recorded for all live trees >1.37 m tall in each subplot. Species richness of trees >1.37 m tall was enumerated by subplot. Richness of the tree regeneration stratum, defined as the number of species having stems in the >1.37 m tall to 10 cm DBH size range, was enumerated by subplot as well.

We characterized overstory disturbance for each subplot by noting the presence of overlying or adjacent openings ≥ 25 m² in size. Subplots directly beneath openings were classified as gap sites. Subplots lacking gaps, but lying within 10 m of openings to the south, east or west were classified as gap border because of their intermediate light regimes (Canham et al. 1990). The remaining subplots were classified as non-gap. In addition to these basic cover classes, an index of gap size was calculated for all but the non-gap subplots. The index was calculated as the number of neighboring subplots to the south, east and west with a canopy gap (>25 m²). The central subplot was included in the tally and an integer value from one to six resulted. This index value indicated a gap or a series of gaps spread across an area of 0.01 to 0.06 ha, respectively.

We calculated the relative density of saplings (>1.37 m tall to 10 cm DBH) by canopy cover class for each

Table 2. Species richness and density measures per 0.01 ha for the tree regeneration stratum.

Parameter	Non-gap	Gap border	Gap	Gap area index (ha)		
				0.01– <0.02	0.02– <0.04	≥0.04
Tree species richness	3.4 ± 1.9 ^a	3.5 ± 1.9	5.3 ± 2.1	3.6 ± 2.0	5.2 ± 2.1	6.1 ± 1.8
Number of stems	14.0 ± 11.9	14.7 ± 12.6	25.6 ± 15.0	14.7 ± 13.2	21.2 ± 15.0	27.1 ± 12.0
Richness per stem	0.37 ± 0.23	0.38 ± 0.26	0.27 ± 0.16	0.40 ± 0.27	0.32 ± 0.17	0.26 ± 0.12

^a Mean and standard deviation.

species. Sapling tallies from three 0.6-ha plots in an adjacent old-growth watershed supplemented the Roaring Fork data. The additional stands were similar to those at Roaring Fork, except that *Tsuga* was not the primary dominant (Busing 1994).

To explore the role of disturbance to the forest floor on regeneration processes we noted the substrate (undisturbed forest floor, exposed mineral soil, rock or log) directly beneath each ramet >1.37 m tall to 2 cm DBH at Roaring Fork. The percentage of individuals growing on each type of substrate was calculated for each species.

Analyses of species diversity

Grain size considerations

The use of 0.01-ha subplots across the study area allows the study of diversity at contrasting spatial scales. A 0.01-ha grain size corresponds roughly to the area occupied by a single dominant organism of the system, which is often important in the study of phenomena related to natural disturbance patches (White and Pickett 1985). Richness at this scale can be related to canopy cover (gap, gap border, or non-gap). By contrast, richness across aggregations of 0.01-ha subplots can be related to environmental gradients at larger scales. In particular, species richness across the entire breadth of the gap-to-shaded-understory gradient or the gap-size gradient can be assessed when subplots are aggregated across all of the aforementioned cover classes. Richness of subplot aggregations within gap, gap border or non-gap classes can also be assessed for comparison. In this study, aggregations were made across 1-ha plots; so the results pertain to the study forest in general.

Species-accumulation curves

We plotted two types of species-accumulation curves: (1) number of species vs area sampled, and (2) number of species vs number of ramets sampled. Although the species-area curve is used commonly in plant diversity studies, it does not reveal density effects directly. By contrast, the species-individuals curve, where number of species is plotted against number of stems, is ideal for the study of density effects (Denslow 1995). In this study, for example, if the species-individuals curve for

gap subplots is similar to that of other subplot pools, then high diversity in gaps is largely a consequence of high stem density.

Similarity indices

We investigated compositional similarity between certain pairs of subplots using Sorrenson's index (Magurran 1988). Both the qualitative (species presence) and quantitative (species abundance) measures were calculated for the tree regeneration stratum. These two measures provided information on compositional change at different analytical levels as the abundance-based measures are more sensitive indicators of change (Rahel 1990). We paired subplots by random drawings without replacement from specified pools of subplots. Four pools were used in analyses of diversity along the gap to shaded understory gradient: (1) all subplots, (2) gap subplots, (3) gap border subplots, and (4) shaded understory subplots. Three pools were used in analyses of diversity along the gap size gradient: (1) gap and gap border subplots, (2) small gap and gap border subplots, and (3) large gap subplots.

Results

Canopy cover and species richness

Thirty-nine subplots (13%) were designated as gap, 78 as gap border (26%), and 183 as shaded understory (61%). Most gaps were <0.01 to 0.03 ha in size and occupied one to three subplots. Only nine subplots (3%) were in gaps of 0.04 ha or more.

Richness of all arborescent individuals >1.37 m tall fell within the range of 10 to 15 species per hectare. Richness of canopy trees (>25 cm DBH) was on the order of 10 tree species per hectare.

At the scale of 0.01 ha, species richness of the tree regeneration stratum was high in gaps, particularly in large gaps (Table 2). Density of the tree regeneration stratum was almost twice as high in gaps as in the shaded understory and it increased with gap size. As a result, the species per stem ratio was low in the larger gaps.

At spatial scales spanning all three plot sites at Roaring Fork, the tree regeneration stratum in gaps was species rich (Fig. 1a, b). The number of species

accumulated per unit area in gap subplots was greater than that of 99 random series of subplots spanning the gap to shaded understory gradient (Fig. 1a). However, on a per stem basis, species accumulation in gaps was not as extreme (Fig. 1b).

Clearly, disturbances to the canopy increased the regeneration of most tree species at Roaring Fork. Disturbances to the forest floor were less important in promoting regeneration and richness. Ninety-seven percent of small saplings grew on the undisturbed forest floor (Table 3). Most species had less than 20% of small saplings on other substrates. However, *Betula lutea* and *B. lenta* often occurred on logs, and *Acer spicatum*

often occurred on bare rock surfaces. Mineral soil was exposed by a few uprooted canopy trees, but only two small saplings of *Betula lutea* occurred on this substrate.

Species relative abundance in the tree regeneration stratum

Despite the high richness in gaps, species composition (0.01 ha grain size) was self-similar in gaps (Table 4). The abundance-based measures of similarity in the gap subplot pool were significantly higher than in the entire subplot pool. Similarity was most pronounced in subplots of the larger gaps (Table 5).

Few species had narrow distributions of regeneration along the gap-to-shaded-understory gradient or along the gap-size gradient (Table 6). The relative density of some shade tolerant species showed weak trends across one or both gradients, but *Liriodendron tulipifera*, an intolerant, was one of the few species to show a strong trend. It occurred almost exclusively in large gaps.

Discussion

The pattern of higher tree species richness in canopy gaps, particularly within the larger gaps of our study forest, is typical of temperate and tropical forests (Runkle 1982, Denslow 1987). Possible explanations for elevated richness in gaps include: 1) increased regeneration of all species in the local pool of propagules, and 2) regeneration of gap specialists. Under gap partitioning hypotheses, specialization causes differences in composition along gradients created by gaps. However, we find few gap specialists and no strong differences in composition along gap gradients. No evidence of gap partitioning by shade-tolerant species is apparent. Regeneration of most species occurs along the entire breadth of gap gradients, but it is elevated in or near gaps. This increase in regeneration is the main reason why gaps have higher species richness. Thus, the density hypothesis is by far the strongest explanation for elevated species richness in gaps of our study forest. In the following discussion we elaborate our findings and consider further implications of the density effect on species diversity.

The use of species-individuals curves in addition to species-area curves provides insight into small-scale disturbance and tree species diversity. Similarity of species-individuals curves from different portions of the gap-to-shaded-understory gradient is evidence that density effects largely determine species richness. Regeneration richness is high in gaps simply because regeneration density is high. However, the somewhat steeper species-individuals curve in gaps (Fig. 1b) suggests that density effects may not be the sole reason for high richness.

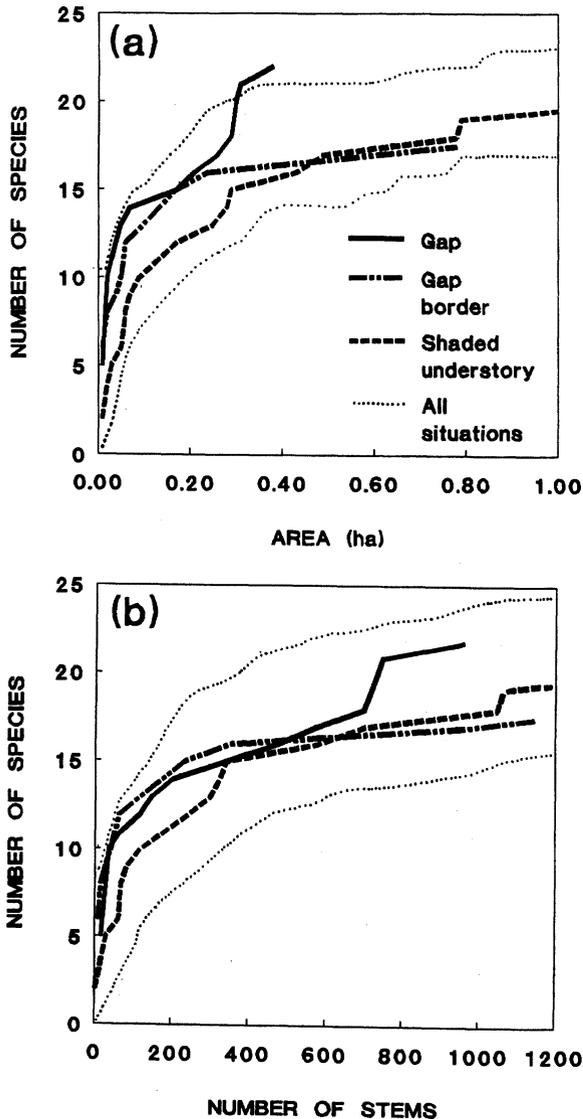


Fig. 1. Species-accumulation within the tree regeneration stratum: (a) species-area curves, and (b) species-individuals curves. Curves were created from a random series of subplots within each canopy cover class. For comparison, the envelope of 99 random series of subplots drawn from the entire pool of subplots is indicated with dotted lines.

Table 3. Substrates of live saplings (>1.37 m tall and <2 cm DBH).

Species	n	Percentage of saplings on substrate			
		Undisturbed forest floor	Mineral soil	Rock	Log
<i>Acer sacharum</i>	1057	100	0	<1	0
<i>Fagus grandifolia</i>	653	100	0	0	0
<i>Halesia carolina</i>	456	100	0	<1	0
<i>Tsuga canadensis</i>	317	94	0	1	4
<i>Acer pensylvanicum</i>	317	96	0	2	2
<i>Aesculus octandra</i>	89	98	0	2	0
<i>Betula lutea</i>	87	54	2	10	36
<i>Magnolia fraseri</i>	85	100	0	0	0
<i>Tilia heterophylla</i>	58	100	0	0	0
<i>Fraxinus americana</i>	53	100	0	0	0
<i>Acer spicatum</i>	37	49	0	51	0
<i>Prunus serotina</i>	18	94	0	6	0
<i>Acer rubrum</i>	16	88	0	0	12
<i>Amelanchier arborea</i>	15	100	0	0	0
Eight other species	27	93	0	0	7
All species	3285	97	<1	1	2

Table 4. Sorrenson's index means for subplot pairs drawn from one of four pools representing the shade to gap gradient.

Index	All situations (n = 149)	Shade (n = 92)	Gap border (n = 36)	Gap (n = 19)
Qualitative	0.401	0.362	0.454	0.484
Quantitative	0.280	0.238	0.301	0.402*

* Significantly different from all situations pool ($P < 0.05$; Mann-Whitney U-test).

Table 5. Sorrenson's index means for subplot pairs drawn from one of three pools representing the gap size gradient.

Index	All gaps ^a (n = 42)	Small gaps (n = 33)	Large gaps (n = 9) ^b
Qualitative	0.402	0.445	0.549
Quantitative	0.301	0.326	0.516*

^a Gap border subplots are included in this pool.

^b Each large gap covers at least 0.02 ha.

* Significantly different from all gaps pool ($P < 0.05$; Mann-Whitney U-test).

Whether gap specialization or other forms of niche partitioning related to disturbance also apply is discussed below.

Evidence for partitioning of spatial gradients created by gap disturbances is weak. Within the tree regeneration stratum, shade-tolerant species span the full width of the gap-to-shaded-understory and small-to-large-gap gradients. Only *Liriodendron tulipifera*, a shade-intolerant species that tends to be restricted to large gaps, has narrow distributions along these gradients. The presence of *Liriodendron* in larger gaps is one reason why gaps have distinctive, self-similar composition as indicated by the abundance-based index of similarity. Because gap subplots often occur in clusters, spatial autocorrelation must also be considered as a source of similarity. Index values for other divisions of the spatial gradients in question did not differ significantly from the understory as a whole. So, these gradients cannot be the overriding source of diversity within the regeneration stratum.

Contrasting results between analyses based on species presence-absence (species richness and Sorrenson's qualitative index) and those based on species abundance (Sorrenson's quantitative index) are not unexpected. The abundance-based measures are much more sensitive to compositional differences (Rahel 1990). Yet, even the most sensitive analyses, based on species abundance, show significantly high self-similarity in just one portion of each gradient tested (gap subplots). If partitioning is strong, then each portion of the gradient in question would be more self-similar than the entire gradient. The mixed results depending on analytical approach, and the failure of the most sensitive analysis to reveal compositional trends in regeneration across the entire breadth of each gradient support the argument that spatial partitioning of gap gradients is not a key source of niche differentiation.

Attempts to explain coexistence of many plant species solely as a consequence of niche partitioning are often unsuccessful (Silvertown and Law 1987). Species

Table 6. Relative abundance of species within the tree regeneration stratum.

Species	Tolerance ^a	Non-gap	Gap border	Gap	Gap area index (ha)		
					0.01 – <0.02	0.02 – <0.04	≥0.04
<i>Acer pensylvanicum</i>	VT	8 ^b	8	9	8	11	10
<i>Acer saccharum</i>	VT	22	26	30	24	26	30
<i>Aesculus octandra</i>	T	10	15	7	17	15	3
<i>Betula lutea</i>	M	2	1	2	1	3	3
<i>Fagus grandifolia</i>	VT	14	15	15	13	4	10
<i>Halesia carolina</i>	T	21	16	15	20	22	18
<i>Liriodendron tulipifera</i>	I	<1	0	5	2	1	9
<i>Magnolia fraseri</i>	M	2	2	1	2	2	<1
<i>Tilia heterophylla</i>	T	3	2	2	2	4	3
<i>Tsuga canadensis</i>	VT	13	10	10	8	9	7

^a VT = very shade tolerant, T = tolerant, M = intermediate, and I = intolerant (Burns and Honkala 1990).

^b Abundance values are percentages of total stem density (>1.37 m tall to 10 cm dbh) across six plot sites. Species with less than 60 stems are excluded.

comprising temperate forests cannot be expected to be highly coevolved because their ranges have shifted in an individualistic fashion under the dynamic climate regime (Davis 1981). Biogeographic history is probably of greater importance than species interactions in determining the richness of local species pools (Whittaker 1956, Schluter and Ricklefs 1993). Small-scale disturbance appears to affect tree species diversity at a site primarily by altering the density of trees. Niche partitioning along spatial gradients produced by small-scale canopy openings is not the major source of regeneration diversity in our study forest. Gap-size partitioning plays a role in the regeneration of at least one intolerant species, but not so much for tolerant species. Whereas *Liriodendron*, an intolerant, tends to have a minimum gap size requirement, shade tolerants, comprising more than 80% of the species pool, do not. Evidently, the density hypothesis largely explains the richness patterns in our study because there are few specialized species with regard to gap disturbances. How well this hypothesis applies to forests with other disturbance regimes and compositions is unclear. In forests with a higher proportion of intolerants, species richness in gaps may not be a consequence of density effects alone.

The possibility that other attributes of gap disturbances provide a basis for niche partitioning must not be overlooked. For example, in our study forest, species of *Betula* occur on logs and exposed mineral soil in

addition to the undisturbed forest floor, where most species occur. In other temperate forests, soil microsites or coarse woody debris within or near gaps are known to promote the regeneration of certain species (Beatty and Stone 1986, Harmon and Franklin 1989, Peterson et al. 1990). If species are heavily dependent on such conditions for regeneration, then species richness may depend, in part, on the availability of substrates.

Our observations at one point in time provide evidence that spatial partitioning of gap resources applies only to a small subset of tree species and that species richness is largely a function of stem density in our study forest. However, forests are not static and richness can change as gaps age (Dirzo et al. 1992, Clinton et al. 1994). Repeated observations of changes within gaps should lead to a better understanding of small-scale disturbances and diversity. Long-term studies may address: (1) the effects of gap regeneration on diversity of the canopy; and (2) the role of temporal gradients resulting from small-scale disturbances. We have demonstrated that niche partitioning is weak along certain spatial gradients, but we have not considered the possibility of temporal niche partitioning. Is there a succession of regeneration or dominance by different species following gap creation? Could there be temporal aspects of the disturbance regime that influence regeneration success and foster niche partitioning? In this regard, Canham (1989) suggests that differences among shade-tolerant species in their ability to survive periods

of suppression are critical. Clearly, temporal patterns of small-scale disturbance and their consequences for regeneration success require further study. Whether the density hypothesis also applies to temporal patterns of species richness during recovery processes remains to be seen.

Acknowledgements – We thank Patty Aune, Fred Huber, Mark Drew, and Bill Patterson for assistance in the field. Bengt Jonsson provided valuable comments on an earlier draft of the manuscript. Data collection was supported by National Park Service funding to the Univ. of North Carolina.

References

- Barton, A. M. 1984. Neotropical pioneer and shade-tolerant tree species: do they really partition treefall gaps? – *Trop. Ecol.* 25: 196–202.
- Beatty, S. W. and Stone, E. L. 1986. The variety of soil microsites created by tree falls. – *Can. J. For. Res.* 16: 539–548.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. – *Ecology* 66: 682–687.
- and Scheiner, S. M. 1989. Species composition in gaps and structure of a tropical forest. – *Ecology* 70: 538–541.
- Brown, N. D. and Whitmore, T. C. 1992. Do dipterocarp seedlings really partition tropical rainforest gaps? – *Philos. Trans. R. Soc. Lond. B* 335: 369–378.
- Burns, R. M. and Honkala, B. H. 1990. *Silvics of North America*. Vol. 2, Hardwoods. – USDA, Washington.
- Busing, R. T. 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. – *Vegetatio* 115: 19–27.
- Canham, C. D. 1989. Different responses to gaps among shade-tolerant tree species. – *Ecology* 70: 548–550.
- , Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A. and White, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. – *Can. J. For. Res.* 20: 620–631.
- Clinton, B. D., Boring, L. R. and Swank, W. T. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influences of topographic position and evergreen understorey. – *Am. Midl. Nat.* 132: 308–319.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – *Science* 199: 1302–1310.
- 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. – In: Anderson, R. M., Turner, B. D. and Taylor, L. R. (eds), *Population dynamics*. Blackwell, Oxford, pp. 141–163.
- Davis, M. B. 1981. Quaternary history and the stability of deciduous forests. – In: West, D. C., Shugart, H. H. and Botkin, D. B. (eds), *Forest succession: concepts and application*. Springer-Verlag, New York, pp. 132–177.
- Denslow, J. S. 1980. Gap partitioning among tropical rain forest trees. – *Biotropica* 12: 47–55.
- 1985. Disturbance-mediated coexistence of species. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, pp. 307–323.
- 1987. Tropical rainforest gaps and tree species diversity. – *Annu. Rev. Ecol. Syst.* 18: 431–451.
- 1995. Disturbance and diversity in tropical rain forests: the density effect. – *Ecol. Appl.* 5: 962–968.
- Dirzo, R., Horvitz, C. C., Quevedo, H. and Lopez, M. A. 1992. The effects of gap size and age on the understorey herb community of a tropical Mexican rain forest. – *J. Ecol.* 80: 809–822.
- Harmon, M. E. and Franklin, J. F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. – *Ecology* 70: 48–59.
- Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. – In: Tomlinson, P. B. and Zimmerman, M. H. (eds), *Tropical trees as living systems*. Cambridge Univ. Press, Cambridge, pp. 617–638.
- Huston, M. 1979. A general hypothesis of species diversity. – *Am. Nat.* 113: 81–101.
- Kennedy, D. N. and Swaine, M. D. 1992. Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. – *Philos. Trans. R. Soc. Lond. B* 335: 357.
- Lertzman, K. P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. – *Ecology* 73: 657–669.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. – *Am. Zool.* 10: 17–25.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. – Princeton Univ. Press, Princeton, NJ.
- Peterson, C. J., Carson, W. P., McCarthy, B. C. and Pickett, S. T. A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. – *Oikos* 58: 39–46.
- Pickett, S. T. A. 1983. Differential adaptation of tropical tree species to canopy gaps and its role in community dynamics. – *Trop. Ecol.* 24: 68–84.
- Prentice, I. C. and Leemans, R. 1990. Pattern and process and the dynamics of forest structure: a simulation approach. – *J. Ecol.* 78: 340–355.
- Rahel, F. J. 1990. The hierarchical nature of community persistence: a problem of scale. – *Am. Nat.* 136: 328–344.
- Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. – *Am. Nat.* 111: 376–381.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests in eastern North America. – *Ecology* 63: 1533–1546.
- and Yetter, T. C. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. – *Ecology* 68: 417–424.
- Schluter, D. and Ricklefs, R. E. 1993. Species diversity: an introduction to the problem. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities*. Univ. of Chicago Press, Chicago, pp. 1–10.
- Silvertown, J. and Law, R. 1987. Do plants need niches? Some recent developments in plant community ecology. – *Trends Ecol. Evol.* 2: 24–26.
- Sipe, T. W. and Bazzaz, F. A. 1994. Gap partitioning among maples (*Acer*) in central New England: shoot architecture and photosynthesis. – *Ecology* 75: 2318–2332.
- Sousa, W. P. 1984. The role of disturbance in natural communities. – *Annu. Rev. Ecol. Syst.* 13: 353–391.
- van der Maarel, E. 1988. Species diversity in plant communities in relation to structure and dynamics. – In: During, H. J., Werger, M. J. A. and Willems, H. J. (eds), *Diversity and pattern in plant communities*. SPB Acad. Publ., The Hague, pp. 1–14.
- White, P. S. and Pickett, S. T. A. 1985. Natural disturbance and patch dynamics: an introduction. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, pp. 3–13.
- Whitmore, T. C. 1978. Gaps in the forest canopy. – In: Tomlinson, P. B. and Zimmerman, M. H. (eds), *Tropical trees as living systems*. Cambridge Univ. Press, Cambridge, pp. 639–655.
- 1982. On pattern and process in forests. – In: Newman, E. I. (ed.), *The plant community as a working mechanism*. Blackwell, Oxford, pp. 45–59.
- 1988. The influence of tree population dynamics on forest species composition. – In: Davy, A. J., Hutchings, M. J. and Watkinson, A. R. (eds), *Plant population ecology*. Blackwell, Boston, pp. 271–291.
- 1989. Canopy gaps and the two major groups of forest trees. – *Ecology* 70: 536–538.
- Whittaker, R. H. 1956. *Vegetation of the Great Smoky Mountains*. – *Ecol. Monogr.* 26: 1–80.