9-1-2000

Have we forgotten the forest because of the trees?

Stefan A. Schnitzer
Marquette University, stefan.schnitzer@marquette.edu

Walter P. Carson
University of Pittsburgh

Accepted version. *Trends in Ecology & Evolution*, Vol. 15, No. 9 (9/1/2000): 375-376 DOI.
Stefan Schnitzer was affiliated with the University of Pittsburgh at the time of publication.

Trends in Ecology & Evolution, Vol. 15, No. 9 (9/1/2000): 375-376 DOI.

Have we forgotten the forest because of the trees?

Stefan A. Schnitzer

University of Pittsburgh

Walter P. Carson

University of Pittsburgh

KEYWORDS

Ecology

Keywords

Niche partitioning; Forest gaps; Gap dynamics; Density effect; Diversity

In their recent TREE Review, Brokaw and Busing argued that there is limited evidence for niche partitioning of tree species within forest gaps1. Consequently, gaps appear to play a relatively minor role in the maintenance of

tree species diversity in forests via traditional resource partitioning. This conclusion is strongly supported by the existing empirical evidence, particularly for shade-tolerant tree species. However, most studies of gaps have failed to take into account plant groups other than trees2, 3, 4. Gaps might be a necessary habitat for the persistence of a large proportion of vascular plant species other than shade-tolerant trees – specifically, pioneer trees, lianas, herbs, shrubs and herbaceous vines2, 3, 4, 5, 6, 7, 8. For example, in a study on Barro Colorado Island (BCI), Panama, gaps had higher liana and pioneer tree diversity compared with the surrounding forest2, 3, on both a per area and a per stem basis (thus removing the effect of density). These two plant groups alone account for approximately 43% of the woody species in this tropical forest2. There is also evidence that many forest herbs are gap dependent5, 6. The role of gaps in the maintenance of shrubs is less clear, although there is some evidence that gaps promote shrub growth and reproduction7, 8. Overall, when the major vascular plant groups are considered, as much as 65% of the flora of BCI might be gap dependent (Table 1). The specific mechanism that leads to the higher diversity of these groups in gaps remains unknown. Nonetheless, because these vascular plant groups represent most of the plant species in tropical forests worldwide4, 9, gaps might often play a strong role in the maintenance of species diversity.

Table 1. The number and percentage of species in different vascular plant groups on Barro Colorado Island, Panama[a]

Plant group	No. of species	% of species	% of woody species
Shade tolerant trees	267	34	43
Pioneer trees	89	11	14
Lianas (woody vines)	171	22	28
Shrubs	93	12	15
Forest herbs	75	10	–
Herbaceous vines	83	11	–
[a]Data taken from Ref. 9.			

a Data taken from Ref. 9.

Brokaw and Busing also argued that gaps might maintain diversity via the density effect10; specifically, that gaps will have a higher diversity of trees solely because they have a higher density of trees compared with the surrounding forest. However, tree density in gaps declines (thins) with age and thus the density effect could maintain diversity in the mature forest primarily in two ways. First, if individuals in gaps reach reproductive age before thinning, then they could potentially colonize new gaps; however, data are lacking on whether trees reach reproductive age sooner (i.e. smaller size or age class) in gaps than in non-gap sites. Second, there must be niche partitioning. Without niche partitioning, thinning of individuals occurs randomly and the initial increase in diversity would be merely a transitory result of the short-term increase in plant density2, 11. Consequently, given the scanty evidence for niche partitioning and accelerated reproduction in gaps, the evidence for the density effect as a viable mechanism to explain the maintenance of diversity in forests is equivocal at best.

We argue that papers sounding the death knell for the role of gaps in the maintenance of forest diversity11 might be premature. The focus of previous research on the ability of tree species to partition resources in gaps might have caused us to overlook the importance of gaps for many other groups of vascular plants (Table 1). Future research is necessary to quantify further the proportion of species in these groups (and others, such as epiphytes) that require gaps for persistence in the community.

References

N. Brokaw, R.T. Busing. Niche versus chance and tree diversity in forest gaps, Trends Ecol. Evol., 15 (2000), pp. 183-188

Schnitzer, S.A. and Carson, W.P. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* (in press)

S.A. Schnitzer, *et al.* The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration, J. Ecol., 88 (2000), pp. 655-666

A.H. Gentry, C. Dodson. Contribution of nontrees to species richness of a tropical rain forest, Biotropica, 19 (1987), pp. 149-156

R. Dirzo, *et al.* The effects of gap size and age on the understorey herb community of a tropical Mexican rain forest, J. Ecol., 80 (1992), pp. 809-822

D. Goldblum. The effects of treefall gaps on understory vegetation in New York State. J. Veg. Sci., 8 (1997), pp. 125-132

D.J. Levey. Tropical wet forest treefall gaps and distributions of understory birds and plants, Ecology, 69 (1988), pp. 1076-1089

J.S. Denslow, *et al.* Growth responses of tropical shrubs to treefall gap environments, Ecology, 71 (1990), pp. 165-179

T.B. Croat. The Flora of Barro Colorado Island, Stanford University Press (1978)

J.S. Denslow. Disturbance and diversity in tropical rain forests: the density effect, Ecol. Appl., 5 (1995), pp. 962-968

S.P. Hubbell, *et al.* Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest, Science, 283 (1999), pp. 554-557