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Have we forgotten the forest because of the trees?

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KEYWORDS

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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 trees^{2, 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 vines^{2, 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 forest^{2, 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 dependent^{5, 6}. The role of gaps in the maintenance of shrubs is less clear, although there is some evidence that gaps promote shrub growth and reproduction^{7, 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 worldwide^{4, 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.			

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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 density^{2, 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.

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