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Diversity and ecosystem functioning in managed tropical communities

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The high productivity, nutrient retention, and stability (resistance and resilience in response to pests, pathogens, and invasive weeds) observed in natural systems are frequently attributed to their high diversity (Tilman, 2000). High productivity, nutrient retention, and stability are also associated with ecosystem sustainability. In much of the temperate world – as also in parts of the tropics – these aspects of ecosystem functioning have been achieved in highly simplified human-managed systems through subsidies in the form of fertilizers and pesticides. Over much of the tropical world, however, such fossil-energy-based subsidies continue to be an economically unviable option. Understanding the ecological underpinnings of the diversity–functioning relationship, therefore, is crucial to the design of sustainable human-managed tropical systems.

There is some evidence for increased productivity associated with high diversity (the so called 'intercropping advantage'; Willey, 1985). The mechanism proposed to explain this phenomenon is akin to the idea of niche partitioning in animal communities (Vandermeer, 1981), that a diverse

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species mixture can more completely capture and use available resources than can a single species on its own. There is both empirical and theoretical support for resource partitioning by diverse plant communities as demonstrated by: a) the spatial partitioning of resources by leaves (Trenbath, 1986) and roots (Jackson *et al.*, 1995), (b) the temporal partitioning of resources by species of varying phenologies (Felker, 1978) or lifespans (Rao, 1986), (c) the use of different forms of the same resource, as in mixtures of legumes and non-legumes (Binkley *et al.*, 1992), and d) the use of resources in different proportions (as demonstrated theoretically by Trenbath (1976) and Tilman (1988).

Just as there is evidence in support of the proposed diversity–functioning relationship in human-managed systems, there are also exceptions. An example comes from an experiment (by Ewel and co-workers) in which monocultures were compared with successional vegetation and with high-diversity mimics of successional vegetation. The monocultures, it turned out, were as productive (Ewel, 1999), and as effective at resource capture (Berish and Ewel, 1988) as the more diverse systems. The diverse systems, on the other hand, demonstrated greater responsiveness to herbivory damage (Brown and Ewel, 1987), and greater nutrient retention (Ewel *et al.*, 1991). These findings suggest that greater diversity may be more crucial for risk aversion and ecosystem resilience (in the face of unforeseen perturbations, or nutrient losses) than for augmenting productivity (Ewel, 1986).

The idea of resource partitioning by plant communities also has certain conceptual and practical limitations. First, all plants rely on the same basic suite of resources, so greater diversity need not inevitably lead to resource partitioning unless there are inherent differences among species in their architecture, habit, or physiology of resource use. Thus, apparent spatial separation of resource acquisition by species occurring together may actually be an effect of competition, rather than a cause of resource partitioning. Second, augmentation of species numbers in experimental systems is often confounded with increased density of planting. Thus, increased resource capture or use by an increased number of species may in fact only be an artefact of incomplete resource use in the original community.

To assess the possible role of species diversity in ecosystem functioning, monocultures dominated by three different tree species were compared with polycultures in which each of those tree species was co-planted with two large, perennial monocots, which are important components of tropical forests. One monocot was a palm (thus had an apical meristem, therefore indeterminate height growth) and the other a heliconia (having a basal meristem, thus biomechanically constrained height growth). The idea of combining different lifeforms was that if there are differences in species' modes of accessing and using resources, these differences are most likely to be manifest in species that differ in their allocation to resource capture and use. Ecosystem nutrient use efficiency – a measure of ecological functioning that integrates productivity and nutrient retention – was one of many response variables assessed in an effort to investigate the relationships between diversity and ecosystem functioning.

The presence of the additional lifeforms increased nutrient use efficiency in two of the three experimental systems, in two of four years. These results indicate that it is not a greater diversity of lifeforms, per se, but the mix of species and lifeforms that determines efficiency at the ecosystem level. Furthermore, the impact of lifeform diversity on ecosystem functioning is not a static phenomenon; instead, it varies with the growth (thus nutrient uptake) of the community's components, rising when growth is vigorous and declining when growth slows. In addition, although productivity and nutrient uptake varied over time, total nutrient accrual (a measure of ecosystem nutrient retention) remained high in the more diverse systems in all four years, despite the large-scale die-back of one of the lifeforms early in the experiment, with nutrient accrual by the other lifeforms compensating. Although lifeform diversity significantly affected ecosystem functioning across all systems and years, ecosystem nutrient use efficiency was better related to soil nutrient supply than to species' resource-use characteristics.

Just as there are notable exceptions to the diversity–functioning relationship in natural systems (as attested to by the existence of some very successful low-diversity natural systems: the monodominant *Gilbertiodendron* forests of Africa, mangroves on tropical coasts, and the *Shorea* swamp forests of SE Asia), so also there are exceptions in managed systems. The role of diversity may be most critical in ensuring ecosystem resilience in the long term, rather than high productivity in the short term. Ecosystem functioning results from the interaction of both bottom-up and top-down factors, the former related to traits of individual species as well as the mix of species or lifeforms composing the community, and the latter related to external factors such as soil nutrient supply.

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