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SHORT COMMUNICATION

Three years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua: evidence in support of the direct regeneration hypothesis

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Catastrophic perturbation is a vital part of ecosystem dynamics (Pickett & White 1985, Sousa 1984) leading to particular forms of ecological succession. The particular form of succession has long been a subject for discussion and analysis (Clements 1916, Connell & Slatyer 1977, Drury & Nisbet 1973, Egler 1954). A persistent component of this discussion and analysis has been the observation of Egler (1954) that two distinct processes may be involved, 'relay floristics' versus 'initial floristic composition'. In the context of a tropical rainforest, relay floristics implies a post-disturbance pattern of pioneer trees followed by a succession of secondary species, eventually reaching the so-called primary forest or a forest closely resembling that before the disturbance. Initial floristic composition suggests that the same species pool that existed immediately after the catastrophic event is the source of the regeneration that will directly form the new forest.

Many tropical rainforest areas are subjected to regular hurricanes (Boucher 1989, 1992), yet the pattern of post-hurricane succession has been documented

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largely for island floras (Lugo *et al.* 1983, Sauer 1962, Wadsworth & Englerth 1959, Walker 1991, Weaver 1986, 1989). Through Nicaragua's Center for Research and Documentation of the Atlantic Coast (CIDCA), a monitoring programme was established following the particularly severe Hurricane Joan which struck the Caribbean coast of Nicargua in October 1988. Initial observations revealed extreme damage (80% of trees toppled or snapped off), yet suggested regenerative processes already under way only four months after the hurricane, and led to the formation of the 'direct regeneration hypothesis' (Vandermeer *et al.* 1990, Yih *et al.* 1991), which implies that initial floristic composition would dominate over relay floristics. Rather than expecting the post-hurricane forest to become dominated by pioneer tree species, followed by a more-or-less regular sequence of more shade-tolerant species, the direct regeneration hypothesis proposes that the (same) species pool existing immediately prior to the hurricane is the source of the regeneration that will directly form the new forest.

Part of the direct regeneration hypothesis was the suggestion that a large amount of the initial floristic composition would come from the resprouting of damaged trees. If relay floristics dominates the process, the ingrowth following the hurricane would be mainly from individuals arriving subsequent to the damaging event. If a large fraction of the ingrowth is from resprouting, the hypothesis of relay floristics can be rejected. This component of the hypothesis is examined in this note.

In February 1989, four months after the hurricane, two 100 × 4 m transects were established (a third was established in February 1990) near the centre of the area damaged by Hurricane Joan (11° 53′ N, 83° 58′ W, approximately 10 km upstream from the mouth of the Kukra river in the southern part of Bluefields Bay, Regiȯn Autonoma del Atlantico Sur, Nicaragua). In February of 1990, all trees greater than 10 cm in breast height circumference were located and permanently marked in each of the three transects. In February/March of each of the two subsequent years, 1991 and 1992, all new trees with a circumference greater or equal to 10 cm were located and permanently marked. Thus the trees located and marked in 1991 and 1992 exclude any that were already in the 10 cm and above category before the hurricane (since they exclude all those in that category in 1990), and are defined as post-hurricane 'ingrowth'.

In March 1992 the three transects were censused with respect to the regeneration condition of all ingrowth originating during 1990–1991 and 1991–1992. All trees entering the census in 1991 or 1992 were evaluated as to their point of origin: sprouting from a fallen log, sprouting from a snapped trunk, sprouting from an exposed root mass or emerging directly from the ground. About 60 m of one of the transects burned in the dry season of 1991, and thus all trees were lost. Regeneration in this part of the transect was excluded from the present study, and therefore for purposes of this paper this transect is only 40 m long.

There are two main inherent inaccuracies in these data. First, any tree judged as emanating directly from the ground could very well have been a sprout from a small trunk which had completely decayed in the three years since the hurricane. The data thus represent a minimal estimate of resprouting. Second, for several individuals it was somewhat ambiguous whether they were emerging from a trunk or directly from the ground. These were categorized separately, and the analysis done both including and excluding them.

The results of this survey are presented in Table 1. In all three transects the basic pattern is the same: the majority of ingrowth results from resprouting. From a lowest value of 46% (transect 1 excluding questionables) to a high value of 69% (transect 3, including questionables), there can be little doubt that a significant part of the regeneration is coming from sprouts, all of which are of primary forest species.

The data set includes four species that are clearly pioneers (*Cecropia obtusifolia*, *Croton killipianus*, *Ochroma pyramidalis*, *Solanum rugosum*). All individuals of these species (a total of 24 of the 206 individuals encountered) originated from the ground, and if excluded from the analysis change the figures only slightly, as presented in the final column of Table 1.

A significant number of individuals from non-pioneer species had their trunks emanating from the ground (86 of the 206 non-pioneer individuals sampled). These individuals were either saplings or seedlings at the time of the hurricane, or emerged as seedlings subsequent to the hurricane. It seems very unlikely that many of these individuals, considering the generally slow growth of most primary forest trees, could have germinated and reached a 10 cm circumference size within a mere three years. It seems much more likely that these individuals were already in the forest, either as saplings or seedlings, although we cannot be certain.

Comparing species (Table 2), we find a range of patterns, from the pioneers, none of which were represented as sprouts, to several species that were almost entirely represented by sprouts (e.g. *Casearia arborea*, *Qualea panamensis*, *Cupania glabra*, *Terminalia amazonia*). *Cupania glabra* was the most common non-pioneer in our sample and was frequently encountered, both within these samples and in observations outside of the sampling area, with a line of sprouts along a trunk that had been felled by the hurricane. Only rarely did an individual of

Table 1. Number of trees in each sampled category and percentage trunks originating from sprouts, from the survey of 1992. Numbers in parentheses result from excluding those trunks that were questionably sprouts (see Methods).

Plot	Sprout from fallen trunk	Sprout from broken trunk	Sprout from roots	Originate from ground	Percent sprouts (including pioneers)	Percent sprouts (excluding) pioneers)
1	24 (21)	15 (13)	1	42	49 (46)	62 (59)
2	23 (19)	33 (31)	2	34	63 (61)	66 (63)
3	8 (5)	14 (14	0	10	69 (66)	71 (68)
Total	55 (45)	62 (58)	3	86	58 (55)	66 (63)

Table 2. Species represented by five or more individuals in the three transects (the only pioneer species entered in this table is *Croton killipianus*).

Species	Number of individuals	Sprout from fallen trunk	Sprout from broken trunk	Originate from ground	Percent sprouts
Croton killipianus	18	0	0	18	0
Cupania glabra	16	9	5	2	88
Miconia aff. *appendiculata*	14	1	8	5	64
Vochysia ferruginea	13	2	5	6	54
Casearia arborea	8	4	4	0	100
Nectandra salicifolia	8	3	3	2	75
Terminalia amazonia	7	5	1	1	86
Inga cocleensis	6	2	2	2	67
Lacistema agregatum	6	3	2	1	83
Qualea panamensis	5	0	5	0	100
Rinorea sp.	5	2	1	2	60

C. glabra die due to the hurricane. Rather, several 'individuals' now stand where one individual fell earlier.

Another interesting case is that of *Vochysia ferruginea.* In our original censuses at this and two other sites four months after the hurricane, we failed to find any sprouting individuals of this species, although large numbers of seedlings were encountered (Boucher *et al.*, 1994, Vandermeer *et al.* 1990, Yih *et al.* 1991). Yet the data reported here count 7 of 13 individuals as sprouts. Such sprouts in this case likely arise either from felled trunks of small individuals (such that they did not enter our original survey data), or from trunks which sprouted after the four-month post-hurricane period that preceded our first expedition to the area.

Of a total of 206 saplings sampled in these three transects from a site near the centre of the damage caused by Hurricane Joan, more than half were resprouts of trees that had been damaged by the hurricane. Fully two-thirds of the individuals representative of primary forest trees came from such resprouting. Thus we can clearly reject the hypothesis of relay floristics dominating the successional pattern. The massive resprouting observed four months subsequent to the hurricane (Vandermeer *et al.* 1990, Yih *et al.* 1991) in fact did contribute significantly to the next two years' ingrowth, countering what had been an obvious alternative to the direct regeneration hypothesis that the resprouting represented a last growth spurt before death.

These data are very similar to the data of Putz & Brokaw (1989) who catalogued a great deal of damage to rainforest trees in Panama. While their data gave no firm estimate on proportions of ingrowth to be comparable to the present study, their observations are certainly consistent with those reported herein (also see Putz *et al.* 1983).

In two other localities in the damaged forest in Nicaragua (Vandermeer *et al.* 1990, Yih *et al.* 1991) we do not have quantitative data on fraction of ingrowth deriving from sprouts, but casual observation indicates a similar phenomenon. The only complicating factor is that in two of four transects at one of those sites a significant number of pioneer trees (especially *Cecropia obtusifolia* and *Croton killipianus*) arrived the first year after the hurricane (Vandermeer & Perfecto, 1991), and the fraction of new ingrowth in the past two years is more significantly represented by them than in the data reported here. On the other hand, the individuals of these two pioneer species are now, four years after the hurricane, rapidly expiring in the two (of ten) sites in which they were common.

Our original observations of massive resprouting have been noted elsewhere in several island floras. In particular the observations of Lugo *et al.* (1983) on the island of Dominica and more recently of Walker (1991) on Puerto Rico are notable. Walker (1991) reports that 9% of the trees were uprooted and 11% snapped from the effects of Hurricane Hugo, but that the effects were quite patchy. In particular, one site had only 56% defoliation while another had 'nearly 100%'. We cannot emphasize strongly enough the difference between these studies and the Nicaraguan study in the initial effects of the hurricane. Hurricane Joan was far more severe than other Caribbean hurricanes studied. Damage was not particularly patchy (Vandermeer *et al.* 1990) and included 27% of the trees uprooted, and 53% with trunks snapped (Yih *et al.* 1991). All trees, without exception, were defoliated. Both the strengths of the hurricane and the absence of significant relief in the area of landfall contributed to such intense damage. Despite this difference between the Nicaraguan site and the other Caribbean sites, observations of resprouting are quite similar. In all cases almost all species seem to exhibit resprouting, even in the most severely damaged forest, as reported here. Furthermore, resprouting seems to be a major contributor to the subsequent several years of ingrowth, and is thus likely to be a major contributor to the forest structure. We expect that if such an observation can be made in the severely damaged forest of the Nicaraguan coast, similar observations will certainly yield the same result in the less damaged forests elsewhere in the Caribbean.

From a practical perspective it is worth noting that because of the importance of resprouting, post-hurricane fires could be more disastrous than the damage event itself. Such was the case in the large regions of *Raphia* palm swamp forests scattered throughout the area of the present study, where peculiarities of the ecosystem invited severe post-hurricane fires (Vandermeer & Perfecto 1991) that destroyed whatever sprouting had already begun. To date, the sections of the forest that burned after the hurricane remain treeless, with only scattered seedlings visible in the dense herbaceous vegetation. The same phenomenon was reported by Unwin *et al.* (1988) for rainforest regions of north-east Australia.

Finally, it is worth noting that planners in the region tended to concentrate their attention on the problem of removing and selling as many of the felled trunks as possible subsequent to the hurricane. This activity may be counterproductive in the long run, in that the economic gain from sale of the downed trunks must be calculated against the future economic losses resulting from damage that may be done to the potentially important resprouting. More generally, while hurricane damage may be superficially similar to a commerical clear-cut, such appearance may be illusory, depending on the nature of the logging. If a significant fraction of the saplings and damaged trees are taken out through secondary activities such as skidding and road building, the recuperative power of the forest may be damaged.

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Book Review

PEARCE, D. & MORAN, D. 1994. The economic value of biodiversity. Earthscan, London, UK. 172 pages. ISBN 1-85383-195-6. Price £12.95 (paperback).

Professor David Pearce has been one of the leading lights in the popularisation of environmental economics in Europe for a number of years, dating from his joint work with Markandya and Barbier "Blueprint for a Green Economy", published in 1989. As an explainer of simple concepts in environmental economics to the non-economist, he has few rivals. However, this most recent book, co-written with a colleague from University College (Dominic Moran) is a little disappointing. Environmental economists will learn little new from the book, whilst non-economists may be mis-led into believing that estimating the economic value of biodiversity is a simple matter.

For economists, biodiversity has economic value if it either (i) contributes to the support of ecosystems from which we derive marketable benefits (such as food or medicines); and/or (ii) is a source of direct "utility" to individuals. Clearly in this latter case separating the amenity value of plants or animals is from the value of biodiversity *per se* is difficult. Other recent texts on the economics of biodiversity (e.g. Barbier *et el.* (1994)) do a rather better job of explaining the causes of biodiversity loss, the role that biodiversity plays in stabilising ecosystems, and the limitations of conventional economic analysis applied to biodiversity protection decisions. Pearce and Moran do a particularly poor job in this last regard, assuming perfect information on the costs and benefits of biodiversity protection which are currently unavailable.

Chapter 1 addresses the meaning and measurement of biodiversity. Chapter 2 then sets out the major reasons why too little biodiversity is preserved from an economic efficiency criterion. This criterion is that the level of diversity which maximises the net benefits of preservation should be chosen. Setting aside that such a calculation is practically impossible, the authors identify these reasons as (i) market failure, whereby not all of the benefits of preservation accrue to landowners and tenants whose actions impact on diversity; (ii) policy failure, whereby government intervention actually speeds up the rate of loss; and (iii) the global public good nature of biodiversity. This global public good aspect is best explained by pointing out that countries in the West benefit from biodiversity preservation in developing countries, yet all of the costs of such preservation (e.g. foregone logging revenues) fall on the developing countries. these arguments are well-known in the literature. Chapter 4 addresses these issues in more detail.

The book then turns to a description of methods available for valuing non-marketed aspects on biodiversity. This is a very familiar trudge through a now-well known list, and the authors fail to really show how biodiversity is distinct from, say, recreational fishing, as a valuation problem. A useful table of empirical results are presented, but these are really ecosystem values, rather than biodiversity values. The valuation of medicinal properties of plants, and of genetic resources for the development of new agricultural crop varieties are also addressed. Finally, the