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Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest

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Abstract

We compared five-year old forests developing after agriculture to those recovering from Hurricane Joan (1988) and to the pre-hurricane forest, at two sites in tropical rain forest in southeastern Nicaragua. We used non-parametric cluster analysis to group transects by their species compositions, and compared their species richness, estimated total species richness, dominance, density and basal area. Post-agriculture transects showed distinctive species compositions and lower diversity than post-hurricane transects, which were in turn more similar to the pre-hurricane forest. These results are similar to those found by other researchers in the Amazon and in Puerto Rico. Land use history was more important than proximity in the landscape in determining the composition and structure of post-disturbance forests in this region.

Introduction

Succession occurs after both natural and human-caused disturbances, and both kinds have been studied for many decades. The classic “old-field” successions begin with the abandonment of agricultural fields or pastures (Budowski 1965; Ewel 1980; Gomez-Pompa et al. 1972; Golley 1977; 1985; Uhl 1987; Aide et al. 1995; Zimmerman et al. 1995), while natural disturbances which initiate regeneration processes include tornadoes (Peterson and Carson 1996), river meanderings (Salo et al. 1986; Terborgh et al. 1996), volcanoes (Thornton 1984; Vitousek et al. 1992), earthquakes (Garwood et al. 1979; Myster and Fernandez 1995), storm downbursts (Nelson et al. 1994), and hurricanes (Bellingham et al. 1994; Boose et al. 1994; Brokaw and Walker 1991; Foster and Boose 1995; Lugo et al. 1983; Pascarella 1997; Vandermeer et al. 1995; Whigham et al. 1991). Many of these kinds of disturbances can be followed by fires, which can occur even in tropical rain forests, both naturally (Goldammer 1992) and from human causes (Sanford et al. 1985; Uhl 1998; Cochrane and Schulze 1999).

In recent years various authors have pointed out similarities and differences in the composition and structure of successional vegetation after natural versus human disturbances (Goldammer 1992; Janzen 1990; Riera 1992; Walschburger and von Hildebrand 1991). Several ecologists have also emphasized that tropical successional forests can in some situations both be very productive and maintain high levels of biodiversity (Brown and Lugo 1990; Ewel 1980; Finegan 1992; Lugo 1995).

We have been studying the regeneration of the tropical rain forest of southeastern Nicaragua since it was heavily damaged by hurricane Joan in October, 1988. Our original expectation was that the initial phases of post-hurricane regeneration would be dominated by the pioneer genera typical of post-agricultural succession in this region (e.g. *Cecropia*, *Ochroma*, *Piper*, *Heliconia*, *Calathea*). However this is not the case; rather, nearly all of the species found in primary forest before the hurricane regenerated directly, both by resprouting and from seedlings and saplings already present (Boucher 1990; Boucher et al. 1994; Ferguson et al. 1995; Vandermeer et al. 1990, 1995; Yih et al. 1991). Thus, regeneration after the hurricane has not been "succession" in the sense of species replacement; rather a substantial part of it has been the regrowth of individual plants which survived the hurricane.

This unexpected trend made it particularly interesting to compare the course of post-hurricane succession with succession after agricultural land use in the same area. Here we present such a comparison based on censuses done in 1993, five years after the hurricane.

Methods

Our comparisons are based on data from annual censuses of 10 by 100m (0.1ha) transects in rain forest at two different sites in the hurricane-damaged region (see maps in Vandermeer et al. (1990); Yih et al. (1991)). The forests in these areas are high-diversity, dicot-and-palm-dominated lowland neotropical rain forest. Detailed descriptions of the sites and their vegetation have been given elsewhere (Vandermeer et al. 1990; Yih et al. 1991; Granzow-de la Cerda et al. 1997).

The initial detailed evaluation of forest damage from Hurricane Joan, done in February 1989 about four months after the storm, included two sites: La Bodega (11°52′ N., 83°58′ W., elevation 10–20m.) and Las Delicias (12°18′ N., 83°52′ W., elevation 30–60m.). A third site, Fonseca (12°16′ N., 83°58′ W., elevation 20–40m.), was added in February 1990. We were unable to locate suitable post-agricultural secondary forest near the Las Delicias site, since this is an area of active settlement and what had been either pasture or agriculture at the time of the hurricane was still pasture and agriculture in 1993. Thus the present article is concerned only with the Bodega and Fonseca sites.

Two transects were established at Bodega in February 1989, four months after the hurricane, and all woody plants of 5cm DBH and up, whether living or dead, were identified and their heights, diameters and coordinates within the transect were recorded. The combined data set of all plants censused, both living and dead, was used as the estimate of the composition of the forest at the time of the hurricane, in October 1988 (Vandermeer et al. 1990; Yih et al. 1991). In February and March of 1990 four more transects were added: one additional one at Bodega and three at Fonseca. None of the transects were in areas which had burned after the hurricane. Diameters and coordinates were recorded for all live trees of 3.2cm DBH or more. The censuses have been repeated annually in February–March.

In February of 1993, working with local farmers, we identified areas of secondary forest at Bodega and Fonseca which had been abandoned from agriculture in 1988, the year of the hurricane. At each site a 10m by 130m transect was established in this secondary forest and all live trees of 3.2cm DBH or more were censused. Thirty meters' length of each transect was later dropped from the analysis, both to avoid edge effects and to make the areas censused comparable to those for the transects in post-hurricane forest.

At Fonseca, the post-agriculture transect was located on the land of Mr Ildefonso Torres, about 2km from each of the three post-hurricane transects. According to Mr Torres, this land had been in maize before abandonment, and had also contained a substantial amount of weedy grasses. It had not been burned between the time of abandonment and our census in 1993. At Bodega the post-agriculture transect was on former crop land belonging to Mr Antonio Reyes, about 1km from each of the post-hurricane transects. Based on conversations with Mr Reyes and the appearance of the area, it apparently had not been burned since abandonment, but we do not know for certain which crops had been planted on this land previously.

The data set thus consists of ten transects: two pre-hurricane (BodPre1 and BodPre2), six post-hurricane (BodHur1, BodHur2, BodHur3, FonHur1, FonHur2 and FonHur3), and two post-agriculture (BodAgr and FonAgr). In each case the first three letters indicate the site (Bodega or Fonseca), the next three letters the treatment (Pre = pre-hurricane, Hur = post-hurricane, Agr=post-agriculture) and the number indicates the replicate.

For each of these transects we calculated tree density, the number of tree species present, the total basal area and the number of individuals of each species present. Dominance was measured by the relative density of the 10 most abundant species in each transect; using the 5 most abundant or 20 most abundant species gave the same results.

Non-parametric measures of association (Spearman's ρ) and analyses of variance (Kruskal-Wallis) were used for statistical analysis because of the non-normality, heteroscedasticity and unbalanced design of the data. Similarity of species composition, measured using Spearman's ρ, was used to group the transects by cluster analysis using unweighted pair-group averages (as with a similar data set by Terborgh et al. (1996)). Non-metric multidimensional scaling, using SPSS procedure ALSCAL with Euclidean distance as the proximity measure, was used to illustrate the difference in composition among the transects.

We used the S_1* estimator of Chao (1984) to estimate the total number of species in each assemblage, using the data on the number of species actually found in each transect and the number of species for which only one or only two individuals were found. This estimator, calculated by:

$$S_1^* = S_{obs} + F_1^2/2F_2,$$

where S_{obs} is the observed number of species, F_1 is the number of species found exactly once (singletons), and F_2 is the number of species found exactly twice (doubletons), has been found to perform well with real data from similar taxa in a region close to our study areas (Colwell and Coddington 1994; Chazdon et al. 1998) and does not depend on assumptions about the form of the species accumulation curve. Among its advantages over other estimators are that it is relatively insensitive to small numbers of quadrats and to moderate patchiness of spatial distributions (Chazdon et al. 1998).

Voucher specimens were collected for each unknown species, and have been deposited in the herbaria of the Universidad Centroamericana in Managua, Nicaragua, the Instituto Nacional de Biodiversidad in Santo Domingo de Heredia, Costa Rica, and the University of Michigan, Ann Arbor, USA.

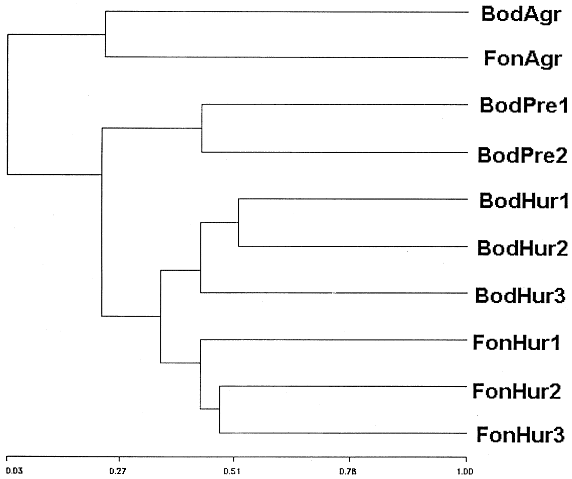

Figure 1. Cluster analysis of ten rain forest transects in southeastern Nicaragua, using unweighted pair group averages with Spearman's non-parametric coefficient of association (ρ) as the measure of similarity. Transects are labeled by site and transect name; final letters of label indicate whether the transect census is pre-hurricane (Pre), post-hurricane (Hur), or post-agriculture (Agr), and numbers indicate replicates. X-axis shows value of ρ at which clusters are linked.

Results

The cluster analysis of the ten transects (Figure 1) shows clearly that the history of land use rather than location is the important determinant of species composition. All six of the post-hurricane transects cluster together, as do the two pre-hurricane transects. The post-agriculture transects cluster separately, and only link to the pre- and post-hurricane transects at the same sites at the final step (ρ = .027).

Thus the cluster analysis results perfectly match the history of use of the transects, and only *within* land-use-history groups do they match the pattern of geographic proximity. While post-hurricane forests first cluster with each other, at a second level (ρ = .230) they most closely resemble the pre-hurricane forests, rather than post-agricultural successional forests of the same age.

Both the actual number of species and the estimated total number of species were significantly higher, and dominance significantly lower, in post-hurricane transects compared to post-agriculture transects (Kruskal-Wallis non-parametric ANOVA using the ranks of the data in Table 1; P = .0455 in each case). Density and basal area, on the other hand, did not differ significantly between these two land-use-histories (P = 1.00 and P = .1824, respectively). None

Table 1. Observed species richness, total species richness (estimated by S_1*; Chao (1984)), dominance as measured by the relative density of the 10 most abundant species, density (ha^{-1}) and basal area of trees 5.0cm DBH or more (m^2/ha), for ten rain forest transects in southeastern Nicaragua

Use History	Post-Agr	Post-Agr	Pre-Hur	Pre-Hur	Post-Hur	Post-Hur	Post-Hur	Post-Hur	Post-Hur	Post-Hur
Site	Bodega	Fonseca	Bodega	Bodega	Bodega	Bodega	Bodega	Fonseca	Fonseca	Fonseca
Transect Name/Number	Ag	Ag	1	2	1	2	3	1	2	3
Variable										
Actual number of species	30	27	42	40	73	82	74	57	65	55
Estimated total species (S_1*)	42.0	37.0	52.2	52.8	89.9	150.1	99.9	83.5	97.1	83.6
Dominance (%)	93	85	54	57	51	45	52	60	69	57
Density (ha^{-1})	4650	1880	1220	1120	2570	3230	2330	2550	3420	2550
Basal Area (m^2/ha)	11.55	2.88	20.95	27.30	7.95	23.04	24.16	7.75	23.44	12.59

of the variables in Table 1 differed significantly between the Bodega and Fonseca sites.

The dominant species in post-agriculture succession fall into three groups. Some are also important in post-hurricane succession, at least in some of the transects (e.g. *Croton smithianus*, *Goethalsia meiantha*, *Cecropia obtusifolia* and *Isertia hankeana*). Others are important in both the pre-hurricane and post-hurricane transects (e.g. *Byrsonima crassifolia*, *Miconia elata*, *Dendropanax arboreus*). A third group are specific to post-agricultural succession, and were not found in either pre- or post-hurricane transects (*Miconia argentea*, *Tabernaemontana chrysocarpa*). There is one potential combination which was totally absent: no species were found in both post-agriculture and pre-hurricane transects, which were not also found in the post-hurricane transects.

Most of the important species in post-hurricane succession are *not* found in post-agriculture succession (e.g. *Vochysia ferruginea*, *Cupania glabra*, *Rinorea squamata*, *Miconia prasina*, *Pseudolmedia spuria*, *Inga thibaudiana*), while all of these *were* common in the pre-hurricane forest also. Thus the pattern shown by the cluster analysis (Figure 1) is due to post-agriculture transects sharing only a few species with the other transects, while pre-hurricane and post-hurricane transects both have more species, and have more of them in common.

Discussion

Land use history, rather than geography, is clearly the predominant factor in determining the composition of five-year old successional forests in this area. The clustering of the transects (Figure 1) corresponds exactly to their history of previous use rather than to their geographic location – despite the fact that the Bodega and Fonseca sites are about 65km apart, and the transects within each site are at most 2km apart. Pre- and post-hurricane forests are relatively similar in composition, while post-agriculture successional forests are quite distinctive (Figure 2). Post-agriculture forests are also notable in having fewer species and greater dominance by a few species. Thus both components of diversity – richness and evenness – are lower in early successional post-agriculture forests (Table 1).

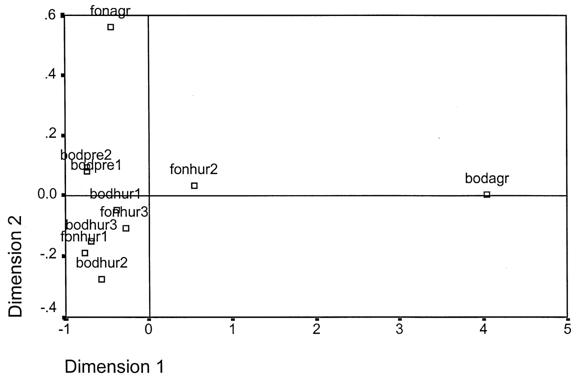

Figure 2. Configuration in two dimensions of non-metric multidimensional scaling, using SPSS procedure ALSCAL with Euclidean distance as measure of proximity, for ten rain forest transects in southeastern Nicaragua. Transect labels as in Figure 1.

Diversity did not differ significantly by site in successional forests, nor did density or basal area. The cluster and NMDS results also suggest that between-site similarity for post-hurricane transects is greater than for post-agriculture transects (ρ values of .358 vs. .237, respectively). Geographic proximity is only a useful predictor of structure or composition for successional forests which have the same history of previous land use (Figure 1).

Walschburger and von Hildebrand (1991) found patterns quite similar to ours in comparing natural gaps, post-agriculture sites (*rastrojos*) and mature rain forest of various ages in the Colombian Amazon. During the early years of succession the *rastrojos* were strongly dominated by a few species of *Cecropia*, *Vismia* and *Miconia* (e.g. 8 species in these three genera made up 87% of relative density in 3-year-old stands). Most of these dominants of *rastrojos* were rare or absent in both natural gaps of the same age and mature forest. Natural gaps had different species as dominants (e.g. *Clathrotropis macrocarpa* and *Macrolobium* sp.), and these species made up much smaller proportions of total density.

Comparing 60-year-old forest, abandoned coffee plantations and abandoned pastures in Puerto Rico, Zimmerman et al. (1995) found no significant differences in species richness, evenness, density or basal area according to previous land use. They did, however, show strong effects of land use history on species composition, with former coffee plantations being dominated by *Guarea guidonia* and abandoned pastures by *Tabebuia heterophylla*, *Myrcia deflexa* and *Palicourea riparia*. As in our study, the major species in areas damaged by Hurricane Hugo (e.g. *Cecropia schreberiana*, *Psychotria berteriana*) were different from the dominants of post-agricultural succession.

In another study in Puerto Rico, Aide et al. (1995) similarly found that the course of post-pasture succession, dominated by herbaceous plants and then by shrubs of the families Rubiaceae, Melastomataceae and Myrtaceae, is quite different from that of recovery after natural disturbances, in which pioneer species such as *Cecropia schreberiana*, *Ochroma pyramidale* and *Schefflera morototoni* predominate. They found that the rate of recovery after abandonment of long-used pastures is much slower than after other kinds of disturbance, a difference explained by the lack of seedlings, sprouts and buried seeds as potential propagules. All of these sources of regeneration are available after hurricanes, on the other hand, allowing more rapid recovery.

The predominant life history characteristics of the major post-hurricane species, which we have discussed previously (Vandermeer et al. 1997; Boucher et al. 1994), are useful in understanding the selection imposed by the hurricane and by conditions immediately afterwards. Based on pre-hurricane densities and diameters, post-hurricane densities and growth rates, and modes of regeneration after disturbance (e.g. sprouting, seedlings, seeds), there appear to be three major groups of species which do well in post-hurricane forest. By far the largest number of these species were resprouters, characterized by vegetative regeneration from individuals which survived the hurricane and slow diameter growth afterwards. A second group of previously rare "pioneer" and "heliophyte" species colonized from seed (e.g. *Cecropia*, *Croton*, *Trema*, *Isertia*) and initially increased rapidly in abundance, showing high rates of diameter growth. After about 5 years, however, their densities leveled off or declined and their diameter growth rates fell to close to zero. Finally *Vochysia ferruginea*, a common species before the hurricane, was unusual in that while practically all the adults died immediately after the storm, its high seedling density and rapid height and diameter growth rates allowed it to recover quickly. It differs from the pioneer/heliophyte group in its continuing high density and diameter growth rate, a decade after the hurricane, as well as by the fact that it is abundant in all size classes in pre-disturbance forest (Boucher et al. 1994).

Agricultural land use generally seems to select strongly among the species present in rain forest, so that relatively few species dominate the early years of post-agricultural succession (Riera 1992; Fujisaka et al. 1998). The traits on the basis of which this selection has operated include fire resistance, drought resistance, fast growth rates in full sunlight and the ability to resprout repeatedly when burned or cut with a machete (Budowski 1965; Gomez-Pompa et al. 1972; Ewel 1980; Uhl 1987; Janzen 1990; Walschburger and von Hildebrand 1991; Goldammer 1992; Nepstad et al. 1996). Many of the characteristics favored by hurricane disturbance thus differ substantially from those favored by agricultural disturbance, leading to quite different communities.

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