MULTIPLE BASINS OF ATTRACTION IN A TROPICAL FOREST: EVIDENCE FOR NONEQUILIBRIUM COMMUNITY STRUCTURE

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Abstract. We analyzed a data set accumulated over a 12-year period subsequent to the catastrophic disturbance of a rain forest by a hurricane. We analyzed the data to determine whether observed trajectories correspond to expectations from an equilibrium or nonequilibrium model of community structure. The equilibrium case, implying a single basin of attraction, suggests that trajectories should become ever more similar over time. The nonequilibrium case, implying multiple basins of attraction, suggests the opposite. The data from this particular forest, located on the eastern seaboard of Nicaragua, strongly support the multiple basin hypothesis, and thus the nonequilibrium model.

Key words: basins of attraction; equilibrium; hurricanes; Nicaragua; tropical forests.

INTRODUCTION

Recent attempts at understanding tree species diversity of tropical rain forests have elucidated complicated patterns that may emerge from nonequilibrium approaches (Hubbell and Foster 1986, Denslow 1987, Hubbell 2001). While it seems to be universally acknowledged that some complex combination of equilibrium and nonequilibrium forces are ultimately at work (Zagt and Werger 1998, Vandermeer et al. 2001), data are repeatedly mined in the search for characteristic signals of transient vs. equilibrium dominance in explanatory schema (Terborg et al. 1996, Wills 1996, Wills et al. 1997, Chazdon et al. 1999, Hubbell et al. 1999, Vandermeer et al. 2000).

One consequence of the nonequilibrium approach is the implied existence of multiple equilibria and associated basins of attraction. If, as the extreme form of the nonequilibrium approach suggests, the theoretically ultimate state of the forest is dominance of a single species of tree (Hubbell and Foster 1986), yet interspecific competitive effects are equal, it is equally likely that any one of the hundreds of species in the species pool could be that dominant species. Each of those potentially dominating species represents a possible

equilibrium point, each of which must exist in a separate basin of attraction. Of course, over the long term, some force must intervene to stop one of the equilibrium states from being reached, the essence of the nonequilibrium model. (We note in passing that nonequilibrium in this sense is commonly used in the literature on nonlinear dynamics and has become common in the tropical forest ecology literature, implying that there exists an unstable point, or repellor, and multiple alternative attractors; the classical Lotka Volterra case of a saddle point is thus a nonequilibrium case according to this terminology.) This problem has been normally approached as a stochastic one in which a random disturbance of some sort repeatedly shifts the trajectories from basin to basin (Chesson and Warner 1981, Hubbell and Foster 1986, Durrett and Levin 2001). While this stochastic focus is a centerpiece of the nonequilibrium theory over the long term, its underlying deterministic form requires multiple basins of attraction. Evidence for multiple basins in the short term thus would be a signal in support of the nonequilibrium theory.

The possibility of alternate basins of attraction in ecological communities has been well known for some time in the theoretical literature (Noy-Meir 1975, May 1977, Vandermeer and Yodzis 1999), yet few workers have sought evidence of such alternative basins in the natural world. If nonequilibrium ideas of rain forest structure are even close to reality, it could be that the tropical rain forest is indeed an example of multiple
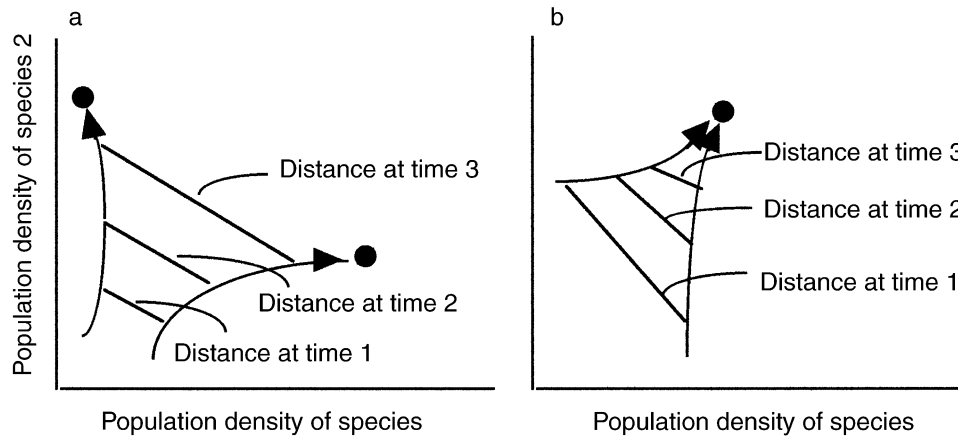
FIG. 1. Diagrammatic representation of the distance between two trajectories in population density space. Solid circles represent stable equilibria, and curves with arrowheads represent alternate trajectories (a) when there are alternative basins of attraction and (b) when there is a single basin of attraction. If trajectories are in different basins (a) they are expected to increase in their deviation from one another over time. If trajectories are in the same basin (b) they are expected to decrease their deviation from one another over time.

potential equilibria with multiple basins of attraction. Proposed nonequilibrium (transient) dynamics then represent the continual shuffling among various basins as disturbance events repeatedly affect the forest and deter any particular basin from capturing the trajectory permanently.

Casting the equilibrium/transient dichotomy as alternative hypotheses, it makes sense to search for signals that would distinguish between the two. From the point of view of alternative basins of attraction, such a signal could be simply the dynamic behavior of the multidimensional distance between two trajectories. This idea is illustrated in Fig. 1. Of course, the illustrations in Fig. 1 are in only two dimensions, while any real test would consider the multidimensional case.

In 1988, Hurricane Joan struck the eastern coast of Nicaragua near Bluefields, doing considerable damage to the lowland rain forests of the region (Vandermeer et al. 1990, 2001, Yih et al. 1991). Since the physical damage was almost complete, yet many of the individual trees resprouted, this represents a case in which, effectively, the community was initiated at a low population density of all species of concern at the time of the hurricane. (While many trees resprouted, the population densities in general were significantly reduced through a mortality rate of almost 70%; see Yih et al. [1991].) Following the trajectories of different but nearby plots over time thus enables us to ask whether there is a signal that could distinguish between the equilibrium and nonequilibrium case. In particular, if the community is organized along the nonequilibrium lines, we expect multiple basins of attraction and thus a continual increase in the multidimensional distance between any two trajectories moving towards distinct

equilibrium points (Fig. 1). Alternatively, if the community is organized according to the equilibrium hypothesis, we expect a single basin of attraction and thus a continual decrease in the multidimensional distance between any two trajectories. So the test for nonequilibrium structure is whether any comparison between two distinct trajectories gives the signal of increasing multidimensional distance (i.e., some trajectories may give the opposite signal even if the community is in nonequilibrium simply because the two trajectories happen to be in the same basin of attraction).

METHODS

Hurricane Joan was a large storm (category 4) and caused extreme physical damage to rain forests when it struck the Caribbean coast of Nicaragua in October 1988. Our studies of post-hurricane succession were initiated in February of 1990. Since that time we have monitored six plots (100 × 10 m) located at two sites (three plots at each site), one site in the center of the damaged area and one near the edge of the damaged area. All trees >3.2 cm DBH (10 cm girth; DBH measured at 1.3 m above the ground surface) in all plots were located, identified, measured, and permanently marked. Identifications were made initially in the field, verified later in the herbarium, and voucher specimens for all species were deposited in herbaria (INB, HNMN, and MICH). Trees have been relocated and remeasured with new recruits marked and measured annually (February/March) for the past 12 yr (data available online).[8]

[8] URL: ⟨http://www.biology.lsa.umich.edu/research/hurricane/hurricanewebpage.html⟩

Comparing all pairs of plots within each of the two sites provides us with six comparisons in the search for increasing multidimensional distance, the signal for a nonequilibrium community and multiple basins.

The basic idea of the multidimensional distance is illustrated in Fig. 1 for two dimensions. Its extension into multidimensional Euclidean space is evident. Consider the space defined by X_k, the population density of the kth species in the community. If X_{ki} is the population density of the kth species in the ith plot, the Euclidian distance between plot i and plot j at time t is

$$\Delta_{ij}(t) = \left[\sum_k (X_{ki} - X_{kj})^2\right]^{1/2}$$

Since the summation is taken over all k, the expectation will be biased by the number of species in the sample, necessitating some point of comparison to eliminate that bias. To generate a null distribution of Δ for statistical comparison and for adjusting the observed value of Δ, we defined the pool of individual trees as all individuals occurring at some point during the interval 1990–2001 (or 1990–1998 for those comparisons lacking data for 1999–2001). Knowing that there are a total of N_i individual trees in plot i, and N_j individual trees in plot j in the actual data from a particular year, we randomly sampled N_i trees from the pool and N_j from the pool (the pool, of course, contains $N_i + N_j$ individuals). From these random samples we counted the number of individuals in each species and called that number Y_{ki} (the randomly sampled number of individuals of species k in sample i). The expected distance then was calculated as

$$E[\Delta_{ij}(t)] = \left[\sum_k (Y_{ki} - Y_{kj})^2\right]^{1/2}$$

This randomization procedure was repeated 1000 times and the number of times $E[\Delta_{ij}(t)]$ was greater than the observed $\Delta_{ij}(t)$ counted. That number, relative to 1000, is the probability that the value of $\Delta_{ij}(t)$ was generated by chance. In addition, the mean value of $E[\Delta_{ij}(t)]$ for the 1000 samples was taken as the value of $E[\Delta_{ij}(t)]$ to make the calculations for Eq. 1.

We computed the relative multidimensional distance, Δ_{ij}^*, as

$$\Delta_{ij}^*(t) = \frac{\Delta_{ij}(t)E[\Delta_{ij}(0)]}{\Delta_{ij}(0)E[\Delta_{ij}(t)]} \quad (1)$$

where $\Delta_{ij}(t)$ is the multidimensional distance between trajectories i and j (in the space of population densities—the multidimensional extension of Fig. 1) at time t, $E[\Delta_{ij}(t)]$ is the value of the multidimensional distance expected under a random hypothesis, and $\Delta_{ij}(0)$ is the

multidimensional distance calculated at time zero (in this case, in the year 1990). If both samples are identical the distance is zero, and if the multidimensional distance is the same as it was at time zero (i.e., 1990) $\Delta_{ij}^* = 1.0$. The signal for a nonequilibrium community is $\Delta_{ij}^* > 1.0$ for at least one comparison of two trajectories, while the signal for an equilibrium community is $\Delta_{ij}^* < 1.0$ for all possible pairwise comparisons of trajectories.

Since Δ_{ij}, the actual multidimensional distance, is statistically biased, we used a resampling technique to estimate the probability of obtaining a value equal to or greater than Δ_{ij} by chance alone. Of a total of 57 comparisons, 51 were significant at the 0.001 level, three at the 0.01 level, one at the 0.05 level, and two were nonsignificant. The two nonsignificant comparisons were in 1990, which is to say, at time zero. Given the results obtained, our resampling procedure was conservative, in that ignoring the statistical bias would have created even larger values of Δ_{ij}^*.

RESULTS AND DISCUSSION

The results of this analysis are presented in Fig. 2. It is clear that for four of the six comparisons the multidimensional distances tend to be greater than 1.0 near the latter portion of the study with a general increase over time. Simple linear regressions indicated that three of these four cases had significant increases (the one nonsignificant increase had a P value of 0.058, marginally significant) and one of the cases of decrease was significant at the 0.05 level (see Table 1).

These results strongly suggest that there are multiple basins of attraction for this rain forest and thus provide support for the nonequilibrium interpretation of rain forest dynamics. While one of the comparisons showed a significantly negative regression coefficient (case JM in Table 1), that decrease in distance was ecologically small, as can be seen in Fig. 2, even though it was statistically significant. It would appear that these two plots are both approaching the same equilibrium point and the fact that they began so near to one another leads to the small changes over time in the multidimensional distance between them. On the other hand, the four cases of positive regression coefficients seem to be ecologically large (see Fig. 2). These plot pairs are deviating rapidly from one another, suggesting that the hurricane left them in different basins of attraction and confirming the hypothesis of multiple basins of attraction.

It is of course conceivable that there are microhabitat differences among plots that account for the distinct attractors that apparently exist. We think this is unlikely. All pairwise comparisons have been made between plots that are quite close to one another (within 400 m), and each of the two sites have seemingly ho-
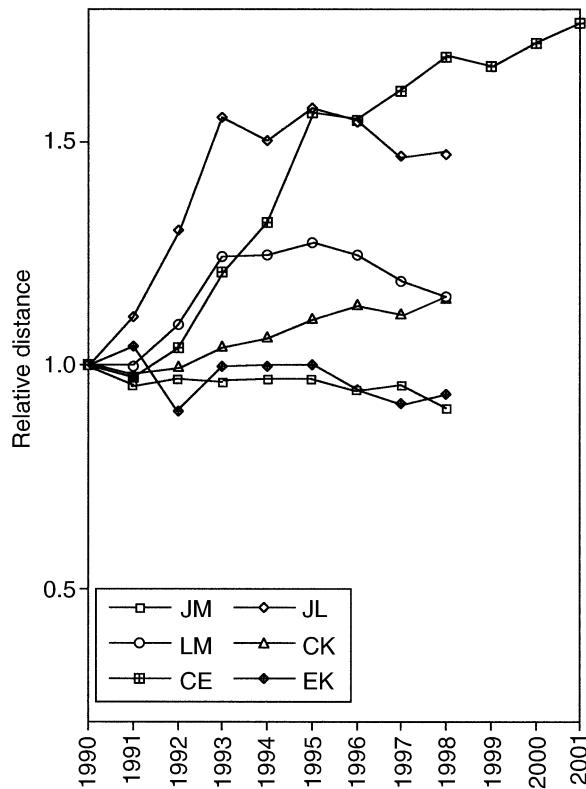
FIG. 2. Relative multidimensional distance as a function of time for six comparisons of plots in rain forest sites in eastern Nicaragua. Plots are labeled J, M, and L at one site and C, K, and E at the other site. Letter combinations indicate which plots are being compared. Only one comparison (C and E) is available for the years 1999–2001 because of extensive fire damage during the El Niño years of 1998–1999.

TABLE 1. Linear regression coefficients for all comparisons of plots in rain forest sites in eastern Nicaragua.

Comparison	Coefficient	Significance
JM	−0.014	0.018
JL	0.064	0.018
LM	0.045	0.058
CK	0.040	0.000
CE	0.115	0.000
EK	−0.014	0.160

Note: For an explanation of codes, see Fig. 2.

that any of the plots is going to accumulate before reaching some sort of equilibrium, the idea that we could be experiencing simply an aberration in the vector field is unlikely. The most likely explanation of these results is that of the six pairwise comparisons, four of them were indeed initiated in distinct basins of attraction, while two of them were initiated in the same basin. Thus the evidence for the existence of multiple basins (and thus the nonequilibrium interpretation) is strong.

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mogeneous background within. Furthermore, both localities are in areas with little relief and the hurricane was very strong, resulting in damage that was extreme and effectively uniform over an estimated 500 000 ha (Yih et al. 1991). Thus, it is quite reasonable to assume that any difference between two plots (within either of the two sites) is a consequence of either initial conditions or subsequent distinct successional pathways and not of possible microsite differences (such as, for example, differences in soil characteristics).

While the logic of multiple basins of attraction suggest that an increasing distance will be found for two trajectories whenever they are in the same basin, it is conceivable that such increases could also be observed, temporarily, within the same basin. Such would be the case if the initial dynamics were such that trajectories were very complex and the structure of the vector field extremely nonlinear. While we cannot completely rule out such a possibility, it is our feeling that after 12 yr and after accumulating probably almost all the species

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