

# Recovery of the rain forest tree *Vochysia ferruginea* over 5 years following Hurricane Joan in Nicaragua: a preliminary population projection matrix

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Accepted 15 July 1996

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## Abstract

Initial observations of the effects of Hurricane Joan on southeastern Nicaraguan rain forest in 1988 indicated that, although damage to the forest was heavy, only one common tree species, *Vochysia ferruginea*, appeared to have declined so much as to be in danger of local extinction. We followed the population dynamics of this species over the next 5 years and developed a mathematical model of its recovery, using a stage-projection (Lefkovitch) matrix. The finite rate of natural increase,  $\lambda$ , for the population was 1.156, indicating rapid growth. Projection of the 1994 population gives a forecast of over ten-fold growth in the next 5 years, with a rapid approach to the stable stage distribution. Elasticities for survival, growth and fertility were respectively 64%, 28% and 7%.

Applying Cochran and Ellner's (1992) methods, we found that most individuals in the population are under 10 years old, transitions between stages take only a few years, and mean age at first reproduction is just 7 years. Within-stage stable age distributions show decreasing peaks, decreasing skewness and decreasing kurtosis with increasing stage class. Forecasts of abundance after a few decades of growth at present rates result in impossibly high values, suggesting strongly that competition will reduce survival, growth and/or fertility rates in this species in the near future. © 1997 Elsevier Science B.V.

**Keywords:** Model; Competition; Stage; Stable age distribution

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“Studies of stage-classified populations often have to rely on a mixture of methods to get estimates—any estimates—of needed parameters. The resulting coefficients may be derived from different experiments, with different sample sizes, conducted at different times. It is hard to justify this

approach on formal statistical grounds, but harder to justify the loss of potentially valuable insight by not at least trying.” (Caswell, 1989)

## 1. Introduction

In this article we present a preliminary population projection matrix model of post-disturbance growth

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in *Vochysia ferruginea*, a common tree of the rain forest of southeastern Nicaragua. This region was strongly affected by Hurricane Joan, which struck the Nicaraguan coast on 22 October 1988 with winds of up to 250 km h<sup>-1</sup> (Boucher, 1989; Vandermeer et al., 1990; Boucher et al., 1994). About 500 000 ha of tropical rain forest were heavily damaged; the first evaluations showed 80% of trees snapped off or completely felled (Yih et al., 1991). While several other hurricanes have had major impacts on temperate and tropical forests in recent years (Lugo et al., 1983; Walker, 1991; Whigham et al., 1991; Frangi and Lugo, 1991; Bellingham et al., 1992; Boose et al., 1994; Elmquist et al., 1994; Loope et al., 1994; Smith et al., 1994), these levels of damage seem to make Hurricane Joan the most massive and extensive natural disturbance to a tropical forest in many years (Brokaw and Walker, 1991; Yih et al., 1991).

The initial study of the regeneration of the rain forest after Hurricane Joan found that, contrary to our expectations, the creation of this 'super-gap' in primary rain forest did not lead to a successional process starting with the typical pioneer genera of the area, such as *Cecropia* and *Ochroma*. Rather, the forest continued mostly to be dominated by the same species that had been prevalent before the storm. This phenomenon, which we called 'direct regeneration', was chiefly the result of high rates of sprouting by most species of primary forest trees (Boucher, 1990; Vandermeer et al., 1990, 1995, 1996; Yih et al., 1991).

*Vochysia ferruginea* was an apparent exception to this general trend. *Vochysia* had been relatively abundant before the hurricane (density of 85 ha<sup>-1</sup> for trees of 5+ cm DBH, relative density 4.5%, fourth most abundant dicot tree found), but it suffered 100% mortality of its adult trees during the storm (Yih et al., 1991). Thus, in the first year after the disturbance *Vochysia ferruginea* appeared to be on the brink of local extinction.

However, rapid growth of its abundant seedlings (94 500 ha<sup>-1</sup> in 1989, making up 75% of the seedling layer) quickly began to restore the tree's population density. Moreover, it also colonized sites where it had not previously been found (Boucher et al., 1994).

Since *Vochysia ferruginea* had been one of the most abundant species in the forest before the disturbance, attaining large sizes (its mean pre-storm DBH

was 22 cm), it cannot be considered a pioneer species such as *Cecropia obtusifolia* or *Ochroma pyramidale*. But neither was it similar in response to the majority of the primary forest species, which maintained themselves in the forest through their resistance to storm damage and/or their ability to resprout afterwards (Putz et al., 1983; Putz and Brokaw, 1989; Vandermeer et al., 1996).

In the first 5 years after the hurricane, *Vochysia ferruginea* has taken advantage of high-light conditions and its abundance of seedlings to recolonize, spread to new sites and grow rapidly (mean DBH growth averaging over 1.4 cm per year, with two trees reaching over 10 cm DBH in 4 years). Indeed, population growth appears to be so rapid that *Vochysia* could become quite dominant in this area, as has been observed by Finegan (1992) in older secondary forests in Costa Rica. Such dominance by one or a few species has been thought to be rare in tropical rain forests (Hart et al., 1989). Here, its occurrence would be as a result of a natural disturbance—one whose frequency has been estimated at once every 100 years (Boucher, 1992).

The species is also of interest because of the similarities, suggested by Oldeman and Fundter (1986), between the Vochysiaceae and the dominant southeast Asian family Dipterocarpaceae. They point out that 'both families increase in importance after catastrophic events', and ask 'If Vochysiaceae need two centuries to become dominant, would an increased frequency of catastrophes, say from once every three centuries to once every two centuries, be enough to enhance a permanent increased frequency of trees from this family in the forest? May the high frequency of dipeterocarps be linked to a faster succession of catastrophes in Asia than in tropical America?'

For these reasons, we have used our available data on the growth, survivorship and fertility of *Vochysia ferruginea* to develop a preliminary projection matrix model of its population dynamics since Hurricane Joan. This has required making several untested assumptions and combining data taken in different years for different purposes. The differing census periods over which mortality rates were estimated for different stages (1–4 years) also introduces the problem, pointed out by Scheil and May (1996), that rate estimates will tend to be biased

downwards with increasing census period. Despite these limitations, however, the results are useful both in forecasting developments expected in the next decade, and as a baseline against which to compare future changes in survival, growth and fertility.

## 2. Methods

We modeled the population of *Vochysia ferruginea* using a stage-classified projection matrix model of the type originally proposed by Lefkovitch (1965) and developed by Caswell (1989). This kind of model has proven useful for studies of tropical plants in both disturbed (e.g. Pinard, 1993; Olmsted and Alvarez-Buylla, 1995) and undisturbed (e.g. Piñero et al., 1984, Horvitz and Schemske, 1995) environments. In our case, the exact form of the model was determined by the availability of the data, which had originally been gathered for community-level studies of the regeneration of the entire forest rather than for modeling of population dynamics.

### 2.1. Data sources and matrix parameter estimates

The initial detailed evaluation of forest damage from Hurricane Joan, done in February 1989 about 4 months after the storm, used two rain forest sites: Las Delicias (12°18' N, 83°52' W, elevation 30–60 m) and La Bodega (11°52' N, 83°58' W, elevation 10–20 m). The forests at these areas are high-diversity, dicot-and-palm-dominated lowland neotropical rain forest, as is our third site, Fonseca (12°16' N, 83°58' W, elevation 20–40 m), added in February 1990. Detailed descriptions of the sites and their vegetation are given elsewhere (Vandermeer et al., 1990, 1995, 1996; Yih et al., 1991; Mallona, 1992).

In February 1989, we censused all trees of 5 cm DBH or greater, both living and dead, in four 10 m × 100 m transects, two at Las Delicias and two at La Bodega. In 1990, we added two more transects at Las Delicias, one more at La Bodega and three at the new site, Fonseca. Additionally, we lowered the minimum DBH for censusing to 3.2 cm in 1990. The Las Delicias transects had to be abandoned due to burning damage from nearby agriculture in 1992–1993. We have continued to record, tag and measure all trees of 3.2 cm DBH or more at the other two sites from 1990 through 1994.

The censuses at these three sites provided the data for the three largest size classes in the matrix: 3.2–4.9 cm DBH, 5.0–9.9 cm DBH, and 10 cm DBH and up. Since only one of the 176 trees in the three largest size classes was observed to die over the period 1990–1994, the mortality rates for these three classes were assumed to be the same and were calculated by pooling the data for all three.

Additionally, we have estimates of densities for seedlings (up to 1.5 m high) for 1989, 1991 and 1992, and for saplings (1.5 m high, under 3.2 cm DBH) for 1991 and 1992 (Mallona, 1992). These estimates come from ten subplots spaced systematically within each of the tree transects (5 m × 5 m for saplings and 2 m × 2 m for seedlings). The *Vochysia* plants in these censuses were counted and measured but most were not marked. This has made it necessary to estimate matrix parameters involving seedlings and saplings (growth and survival for these two categories, and fertility expressed as seedlings per tree per year) indirectly, using the subplot densities, as follows: since all the adult trees of *Vochysia ferruginea* recorded in 1989 were dead, and no seed dormancy is known in this species (Chudnoff, 1984; Morales Vargas et al., 1988), we assumed that no new seedlings were produced in 1990 or 1991. This made it possible to calculate annual seedling mortality from seedling densities in 1989 and 1991. 'Out-growth' of saplings into the 3.2–5 cm tree category was known from the transect censuses.

Using the above estimates for the matrix parameters  $a_{11}$  and  $a_{23}$ , the remaining two parameters for seedlings and saplings (sapling survival in the same size category,  $a_{22}$ , and seedling growth into the sapling category,  $a_{12}$ ) could be estimated by linear regression. If we assume that 'de-growth' of saplings did not occur (i.e. that  $a_{21} = 0$ ), then sapling density in 1992 can be written as:

$$\begin{aligned} \text{Sapling density}(1992) \\ = [a_{22} - a_{23}][\text{Sapling density}(1991)] \\ + a_{12}[\text{Seedling density}(1991)] \end{aligned}$$

Since  $a_{23}$  was already known, the  $a_{23}[\text{Sapling}(1991)]$  term could be subtracted out, leaving  $a_{22}$  and  $a_{12}$  as the coefficients of Sapling(1991) and Seedling(1991), respectively, in the linear regression through the origin using Sapling(1992) as the dependent variable.

To estimate fertility, we used a polynomial regression of the 1989 seedling densities against the DBH of the nearest trees to the seedling subplots in 1989. This assumes that seedlings are most likely to be the offspring of the pre-hurricane trees to which they had been closest. This estimate of total seedling production per tree was converted to annual seedling production per tree by discounting survival of seedlings from years previous to 1988 using the mortality rate estimated from 1989 and 1991 densities, as discussed above. Applying this method assumes there is no seed dormancy. The polynomial regression gave a negative estimate for the fertility of the 3.2–4.9 cm tree category. Since this is biologically meaningless, the parameter  $a_{31}$  was set to zero. In fact, we have observed no fruiting or flowering by trees of this size since the hurricane.

## 2.2. Analysis

Following standard projection matrix modeling methods, we calculated the eigenvalues and eigenvectors of the projection matrix to determine the finite rate of increase ( $\lambda$ ), the damping ratio, and the vectors of the stable stage distribution and reproductive value, which were normalized to sum to 100% (Caswell, 1989). Pre-multiplication of initial stage distribution vectors by the projection matrix was used to project the development of the population forward over the next few decades starting from 1994. Since the population is growing rapidly and environmental conditions are changing as the forest regenerates (Boucher et al., 1994; Vandermeer et al., 1996; see also Section 3, Results), we only have confidence in the validity of such projections for periods of a decade or less.

Elasticity and sensitivity matrices (Piñero et al., 1984; deKroon et al., 1986; Caswell, 1989; Silvertown et al., 1993) were calculated as indications of the relative influence of different matrix entries on  $\lambda$ . The elasticities, which must sum to 100%, were decomposed by size class, and were also summed to give totals for survival (diagonal elements), growth (subdiagonal elements), and fertility (first row non-diagonal elements) (Enright and Watson, 1991; deKroon et al., 1986; Caswell, 1989; Silvertown et al., 1993).

The methods of Cochran and Ellner (1992) were used to calculate age-based life history parameters, such as the life table ( $l_x$ ), fertility table ( $m_x$ ), various definitions of generation time, net reproductive rate ( $R_0$ ), stable age distribution, age-specific reproductive values, and age distribution and expected remaining life span for each stage. Calculations were done using the FORTRAN program STAGECOACH 2.3, created and released into the public domain by Margaret E. Cochran (ESA Supplementary Publication Service Document No. 9202, Ecological Society of America, 328 East State Street, Ithaca, NY 14850-4318), and MathCAD 4.0 for Windows (MathSoft Inc., Cambridge, MA).

## 3. Results

### 3.1. Growth

The finite rate of natural increase ( $\lambda_1$ , the dominant eigenvalue of the projection matrix), was 1.156, which represents over 15% growth per year. This corresponds to a population growth rate  $r$  ( $\ln \lambda_1$ ) of 0.145. The damping ratio,  $\lambda_1/|\lambda_2|$ , was 1.58, indicating that the population will quickly approach a stable stage distribution.

Projection of the 1994 initial population structure (averaged over four sites; Boucher et al., 1994) demonstrates how rapid this growth would be at the present parameter values (Table 1). While the degree of increase varies substantially among the five size categories, all of them show impressive increases. In the case of the seedlings and the largest trees (10 cm DBH and above), the projected density increases are over ten-fold in just 5 years.

Table 1

Densities for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan, forecast five and ten years in the future (to 1999 and 2004), starting from the actual February 1994 density (averaged over four sites). All figures are number of individuals/ha

	Seedling	Sapling	3.2 to 5	5 to 10	10 cm +
94 Actual	1304	282	78	83	15
99 Forecast	16450	290	62	123	164
04 Forecast	33450	688	155	201	348

**Table 2**  
Stable stage distribution (left eigenvector) and reproductive values (right eigenvector) for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan. Both vectors are normalized to sum to 100%

Stage	Stable stage distribution	Reproductive value
Seedling	96.00	0.09
Sapling	1.96	7.96
3.2 to 5	0.45	23.58
5 to 10	0.60	30.72
10 cm +	0.99	37.66

**Table 3**  
1994 actual and 1999 and 2004 forecast densities as percentages, and comparison with stable stage distribution, for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan

	Seedling	Sapling	3.2 to 5	5 to 10	10 cm +
94 Actual	74.0	16.0	4.4	4.7	0.9
99 Forecast	96.3	1.7	0.4	0.7	1.0
04 Forecast	96.0	2.0	0.4	0.6	1.0
Stable	96.0	2.0	0.4	0.6	1.0

The left and right eigenvectors corresponding to the dominant eigenvalue are shown in Table 2. The left eigenvector, which gives the stable stage distribution, is heavily concentrated in the seedling stage;

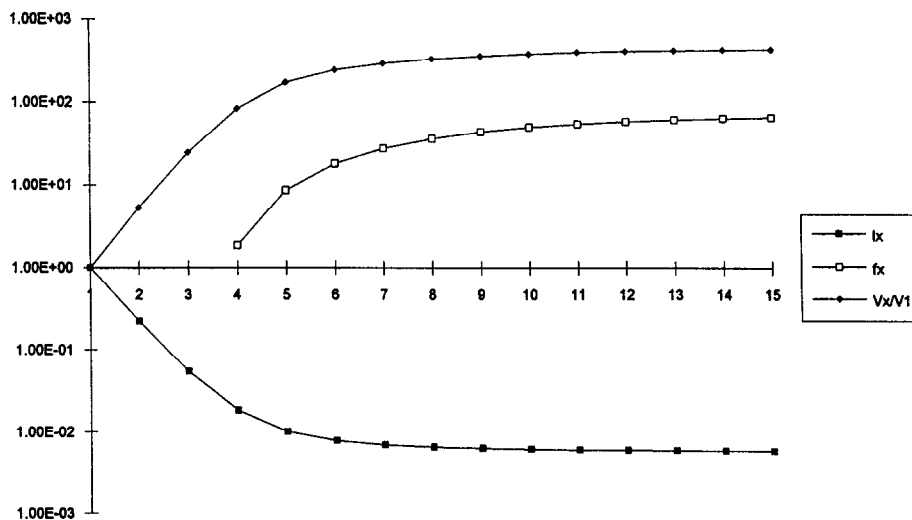
**Table 4**  
Sensitivity matrix ( $s_{ij}$ ) for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan

	Seedling	Sapling	3.2 to 5	5 to 10	10 cm +
Seedling	0.09	0.00	0.00	0.00	0.00
Sapling	8.47	0.17	0.04	0.05	0.09
3.2 to 5	25.11	0.51	0.12	0.16	0.26
5 to 10	32.72	0.67	0.15	0.20	0.34
10 cm +	40.12	0.82	0.19	0.25	0.42

**Table 5**  
Elasticity matrix ( $e_{ij}$ ) for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan

	Seedling	Sapling	3.2 to 5	5 to 10	10 cm +
Seedling	0.017	0	0	0.017	0.057
Sapling	0.075	0.098	0.0007	0	0
3.2 to 5	0	0.075	0.041	0	0
5 to 10	0	0	0.075	0.128	0
10 cm +	0	0	0	0.057	0.358

it is notable that it does not decrease monotonically with size class, but rather decreases to the 3.2–5 cm DBH class and then increases. The right eigenvector, which gives the relative reproductive values of the different stages, shows a steady increase with size; the reproductive value of seedlings is two orders of magnitude below those of the larger size classes.



**Fig. 1.** Survivorship function ( $l_x$ ), maternity function ( $f_x$ ) and relative reproductive value ( $V_x/V_1$ ) versus age for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan, semi-log scale.

Table 6

Mean age of residence ( $S_j$ ) for each stage and mean time for transition between stages (in years from row stage to column stage) for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan. Standard deviations in parentheses

	Mean age of residence	Transition time (row stage to column stage)			
		Sapling	3.2 to 5	5 to 10	10 cm +
Seedling	1.3 (0.6)	1.3 (0.6)	4.1 (2.4)	5.9 (2.7)	9.6 (4.2)
Sapling	4.2 (2.5)	–	2.9 (2.3)	4.6 (2.7)	8.4 (4.1)
3.2 to 5	5.9 (2.7)	–	–	1.8 (1.3)	5.5 (3.4)
5 to 10	9.6 (4.2)	–	–	–	3.7 (3.2)
10 cm +	342.9 (332.9)	–	–	–	–

While the 1994 stage distribution is rather different from the stable stage distribution, with a deficiency of seedlings and excesses of the next three stages, it is projected to approach the stable proportions quite rapidly (Table 3). In just 5 years, the percentages are projected to be within 0.3% of their stable values, and, in 10 years, within 0.1%.

### 3.2. Elasticities and sensitivities

Both the sensitivity matrix (Table 4; Caswell, 1978; Piñero et al., 1984; Caswell, 1989) and the

elasticity matrix. (Table 5: deKroon et al., 1986; Silvertown et al., 1993) indicate that the element of the transition matrix with most influence on the growth rate is the static-survival probability of the largest trees,  $a_{55}$ . The static-survival probabilities for medium trees and saplings,  $a_{44}$  and  $a_{22}$ , are next in importance, followed by growth probabilities,  $a_{12}$ ,  $a_{23}$ , and  $a_{34}$ . The influences of the fertilities and of the static-survival probability of seedlings,  $a_{11}$ , are small but not negligible.

Silvertown et al. (1993) have shown how the elements of the elasticity matrix can be summed to give elasticities indicating the relative importance of survival, growth and fertility. In the present matrix, these sums correspond, respectively, to the diagonal and above-diagonal elements ( $a_{11}$ – $a_{55}$  and  $a_{32}$ ), the subdiagonal elements ( $a_{21}$ – $a_{54}$ ), and the non-diagonal first-row elements ( $a_{14}$  and  $a_{15}$ ). Their values are 64.3% for survival, 28.2% for growth, and 7.4% for fertility.

### 3.3. Age-based measures

The survivorship function,  $l_x$  (Fig. 1) indicates that mortality is high in the first few years of life and then decreases to a low, fairly constant, rate. However, 1% of seedlings manage to survive to age 5

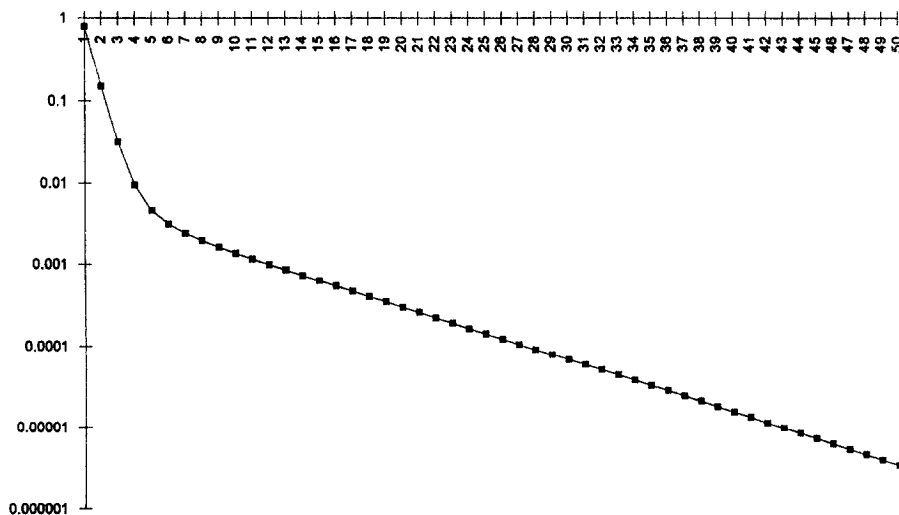


Fig. 2. Stable age distribution (frequency versus age) for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan, semi-log scale.

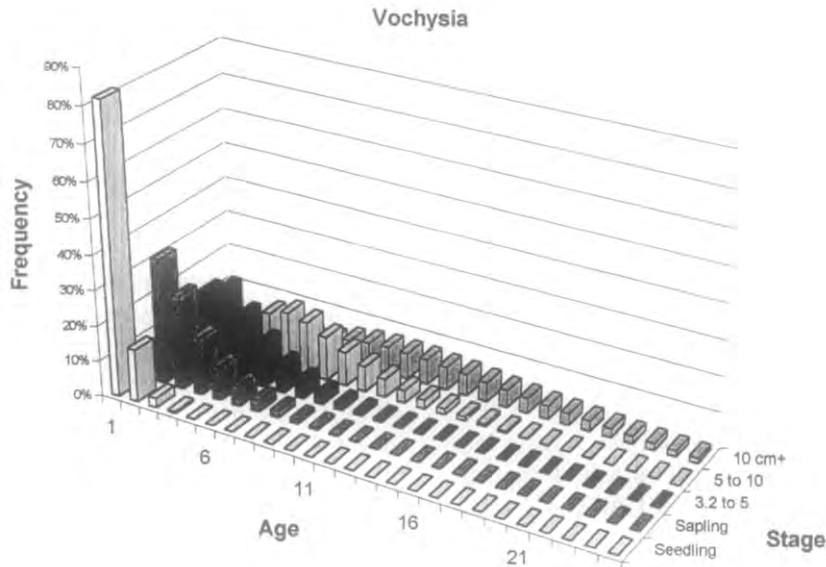


Fig. 3. Within-stage stable age distributions (frequency versus age) for each of the five stages, for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan. Each of the distributions is normalized to sum to 1.

years, and 0.6% to age 10 years. The maternity function  $f_x$  (Fig. 1) rises quickly starting at age 4 years and then approaches a plateau from about age 15 years onwards. The curve indicating relative reproductive value,  $V_x/V_1$ , has a similar form. The average age at which reproduction begins is quite young: just 6.9 years (SD 2.7 years). On the average, 0.6% of the seedlings survive to reproduce.

The average age for all size categories except the largest is less than 10 years, and movements between stages take only a few years (Table 6). The stable age distribution (Fig. 2) shows a rapid decrease in densities from the 1-year-old class (which makes up 78.6% of the population) until about age 6 years, and

a smooth, less rapid, decline thereafter. The stable age distributions within each stage are shown in Fig. 3. For seedlings, the distribution is highly skewed, with 82% of them being 1 year old. Saplings are concentrated in the 2-, 3- and 4-year-old classes. Larger sizes show lower, more symmetrical and less sharply peaked distributions, with the 10 + cm DBH size class being very broadly spread over several decades.

The 'mean time to first passage' out of a stage can be calculated simply as  $1/(1 - a_{ii})$ , i.e. the inverse of the probability of staying in the stage for a year (Cochran, 1992). This variable (Table 7) can be taken as a measure of the 'length', in years, of each stage; the relative shortness of the third stage is notable.

Table 7

Mean time to first passage out of each stage (years) for *Vochysia ferruginea* in rain forest in southeastern Nicaragua after Hurricane Joan

Stage	Time to 1st passage
Seedling	1.3
Sapling	2.9
3.2 to 5	1.7
5 to 10	3.7
10 cm +	333.3

#### 4. Discussion

The results of the preliminary model confirm that the population of *Vochysia ferruginea* in post-hurricane rain forest has been growing very rapidly (Boucher et al., 1994). The finite rate of increase (1.156) is considerably above the 1.00 level which indicates a stable population, and which has been closely approached by trees in mature forests in

Table 8

The transition matrix for *Vochysia ferruginea* during the first five years after Hurricane Joan in rain forest in southeastern Nicaragua

	Seedling	Sapling	3.2 to 5	5 to 10	10 cm +
Seedling	0.209	0	0	35.6	70.1
Sapling	0.010	0.653	0.020	0	0
3.2 to 5	0	0.170	0.407	0	0
5 to 10	0	0	0.570	0.731	0
10 cm +	0	0	0	0.266	0.997

many previous studies (Silvertown et al., 1993). Projection of the 1994 population just 5 years into the future indicates over ten-fold growth of the density of the largest trees (10 + cm DBH), as well as of the seedlings.

As is typical of rapidly growing populations, this is a young population, and is expected to become even more so in coming years (Table 3). Most individuals will continue to be under 10 years old as the population grows, and transitions between stages will take only a few years (Table 6). Survival of seedlings is relatively high (Fig. 1) and their growth is rapid.

Indeed, perhaps the most notable result of the model is the speed with which seedlings reach the size at which they can reproduce. Six in every thousand seedlings will reach reproductive maturity, and will do so in less than 7 years. The post-hurricane 'pulse' of seedlings should thus soon begin to generate 'echoes' of itself.

The within-stage stable age distributions (Fig. 3) show a reduction of maximum height and decreased skewness and kurtosis with increasing stage class; the distribution for seedlings has a sharp peak at age 1 year, while the largest trees have a broad, nearly flat distribution. The same trends were found for the orchid *Cypripedium acaule* by Cochran (Cochran and Ellner, 1992), and it appears to be quite a general pattern (Boucher, 1997).

One interesting result is the pattern of variation in the 'lengths' of the stages, measured by the time to first passage out of each stage (Table 7). The temporal shortness of the intermediate stages is a partial explanation of the shapes of the actual 1994, projected 1999 and 2004, and stable stage distributions (Table 3), which are not 'reverse-J' but rather U-

shaped. On the other hand, the long length of the final (10 + cm DBH) stage indicates that these stage distributions should not be directly proportional to densities; they will tend to overstate the density of the largest trees.

An adjusted stage distribution, corrected for differences in stage length, can be calculated by dividing the density in each stage by the stage's time to first passage. The adjusted distribution, with units of individuals  $\text{ha}^{-1}$  per year, provides little information that is not already given by the age-based measures in the present case. However, since it depends only on the  $a_{ii}$  values, not the entire matrix, such adjustment would be useful in cases in which only some of the parameters of the transition matrix can be estimated.

Caswell (1989) has made a useful distinction between 'forecasting' and 'projection' as differing interpretations of a model's output. Forecasting considers values for future times as actual estimates of the future state of the population, whereas projection sees them rather as a description of the population's present trajectory. The present preliminary model forecasts a rapid increase in dominance of the regenerating forest by *Vochysia ferruginea*—in fact, so rapid that it is very unlikely to occur. Using a conservative assumption concerning the average basal area of 10 + cm individuals (a constant mean value of 0.0225  $\text{m}^2$  per tree, corresponding to a 15 cm DBH), the basal area of 5 + cm trees of *Vochysia ferruginea* in 1999 is predicted to be 60% higher than it was in 1988 before the hurricane. By 2014, it is forecast to be almost as large as the total basal area of all woody species in the forest before the hurricane.

For comparison, Finegan (1992) records one site in Costa Rica at which *Vochysia ferruginea* was quite dominant, with a density of 133 trees  $\text{ha}^{-1}$  and a basal area of 11  $\text{m}^2 \text{ha}^{-1}$ . At another site (a 25-year-old secondary stand) nearly half of the 24  $\text{m}^2 \text{ha}^{-1}$  of basal area was composed of *Vochysia ferruginea*, with dominant trees having a DBH of 30–50 cm. Thus, if its present parameter values remain constant, *Vochysia ferruginea* would soon far exceed even the densities and basal areas attained at sites where it is very dominant. By 2029—just 40 years after the hurricane—*Vochysia ferruginea* would have more than one tree of 10 + cm DBH per



square meter, and a basal area  $\text{ha}^{-1}$  over 120 times its pre-hurricane value. Clearly, this is impossible.

This unreasonable forecast is due to the assumption of continued density-independent growth without any changes in the parameters of the transition matrix—i.e. an unchanging relationship between the population and its environment as forest regeneration proceeds. Its impossibility suggests that we should anticipate competitive decreases in growth, survival and/or fertility in some or all of the stages in the near future.

A crucial question, which cannot be answered with this model, is whether this slowing of the population's growth rate will be severe or only moderate. That is, will the growth of the population, particularly seedlings and saplings, drop off so much that the larger trees do not replace themselves, so total density will appear to overshoot a 'stable' level and then drop back?; or will growth slow down but continue to be positive, so that *Vochysia ferruginea* grows to become dominant in the regenerating forest?

The major limitation of the present model appears to be its density-independence, as discussed above. The differences between the 1994 and the stable stage distributions are apparently not a serious problem, since the damping ratio is moderately high and convergence to stability appears to take only a few years (Table 3).

Although the sensitivities (Table 4) are not corrected for the ranges of the  $a_{ij}$  as are the elasticities, they are useful in showing which of the entries that are estimated to be zero in the transition matrix (Table 8) would cause a major change in  $\lambda$  if they in fact were not zero. The probabilities of skipping stages ( $a_{13}$ – $a_{15}$  and  $a_{24}$ – $a_{25}$  especially) are most important in this sense. On the other hand, the relatively low value of the sensitivity for  $a_{13}$  (0.0004) suggests that knowing the stage at which reproduction begins is not critical.

Both sensitivities and elasticities, of course, are derived from and totally dependent on the estimates of the  $a_{ij}$ . Thus their use as an indication of the relative importance of errors in estimation of different  $a_{ij}$  suffers from circularity. However, they have value as order-of-magnitude indicators of the parameters for which it is most important to refine our estimates. In this light, it is heartening that the

fertilities ( $a_{1j}$ ), for which our estimates are the crudest, also have the lowest sensitivity and elasticity values (Tables 4 and 5).

## Acknowledgments

We thank the Center for Studies and Documentation of the Atlantic Coast (CIDCA) and the School of Ecology and Natural Resources (ECORENA), both of the Central American University (UCA), for their support of all our work; and John Vandermeer, Ivette Perfecto, Nelson Zamora, Marg Reeves, Iñigo Granzow de la Cerda, Linda Roth, Ernesto Lemus and all the students of the 1990–1994 UCA–University of Michigan Rainforest Dynamics courses for their hard work in the field. This study was supported by US National Science Foundation grants DSR-891768 and DEB-9524061 to John H. Vandermeer. This is Contribution No. 2786 from the Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies, University of Maryland.

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