Sapling Diversity in Canopy Gaps in an Ecuadorian Rain Forest

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ABSTRACT. In a “terra firme” rain forest (Amazonian Ecuador) we quantified the species abundance distribution, gap size, gap isolation, sapling diversity, and gap community similarity for 24 initial gap communities. The pooled community distributions showed a log-series distribution, mainly because 2-D space was partitioned during the forest cycle’s first stages, and randomness is accepted as influencing both species arrival and gap formation. Gap size interacted with species richness and evenness due to the low species abundances. The species composition in each gap was an almost unique set: on average, a gap shared <20% of its species with any other gap. A cluster analysis confirmed this observation: the first fusion occurred at a similarity level of 0.42, which related to <27% of common species. Despite this high intergap dissimilarity, association analysis showed that 33.7% of all pairwise gap comparisons represented a significant association, indicating that more species were in common than expected with random assumptions. A principal components analysis revealed three dimensions in the data; sapling diversity, community similarity, and gap size were found to be independent of gap isolation. The uniqueness of the communities in terms of sapling composition highlights the value of gaps for conservation. For. Sci. 49(6):909–917.

Key Words: Forest cycle, gap isolation, Gini evenness index, log-series model, Sørensen similarity index.

The overwhelming plant diversity in tropical rain forests is a phenomenon about which several divergent and/or complementary hypotheses have been proposed (e.g., Grubb 1977, Connell 1978, Denslow 1980, Fagerström 1988, Petraitis et al. 1989). Most hypotheses are based on the presence of “disturbance” during the life cycle of a plant species (Petraitis et al. 1989, Roberts and Gilliam 1995). Disturbance alters the biophysical environment (Raich and Christensen 1989, Clark 1990): it can lower an established dominance status (Canham and Marks 1985, Roberts and Gilliam 1995), and increase spatial and temporal heterogeneity (Denslow 1985). This creates opportunities for the emerging individuals in terms of new resources, and provides the basis for specialization and resource partitioning by which species coexistence can be explained (Grubb 1977, Denslow 1985). The highest diversity has been predicted at intermediate levels of scale, intensity, and frequency of disturbance (Connell 1978), although this has recently been questioned (Hubbell et al. 1999, Tilman 1999). Gap formation, defined here as the physical opening of the canopy by the fall of structural elements (Forman and Godron 1986, p. 324–326, Kellman and Tackaberry 1997, p. 134–172, Brokaw and Busing 2000), is considered an important natural disturbance affecting forest composition, structure, and tree population dynamics (Denslow 1985, 1987, Clark 1990, Feener and Schupp 1998). Consequently, gap formation plays an integral role in maintaining the high diversity observed in tropical rain forests.
role in the ecological and evolutionary dynamics of many tropical forests, affecting the spatio-temporal distribution of plants and the animals that interact with them (Feenner and Schupp 1998). In Ecuador, the forest area affected yearly by gap formation is only ~1% (Salvador-Van Eysenrode et al. 1999a), which contrasts with logging, fires, and other (anthropogenic) activities (Skole and Tucker 1993, Nepstad et al. 1999), accounting for thousands of hectares per year.

Plant responses to gaps involve growth strategies and reproductive characteristics (Gitay et al. 1999). Consequently, plant species have been grouped roughly as “pioneers” or “climax species” (Brokaw 1985, Swaine and Whitmore 1988, Condit et al. 1996, Kellman and Tackaberry 1997, p. 146–151, Barnes et al. 1998, p. 108–115, Gitay et al. 1999, Hubbell et al. 1999). Pioneer species seed into open areas following major disturbances; tree competition is small, and the environment is harsh; germination and growth are rapid (Barnes et al. 1998, p. 108–115). Pioneers are light-demanding and insensitive to moisture variation (Condit et al. 1996). Climax or shade/understory tolerant species are able to establish in the shaded understory and gradually penetrate the canopy (Barnes et al. 1998, p. 108–115). They form a more complex functional group, due to variation in moisture-demand, leaf lifetime, and deciduousness (Condit et al. 1996). Also species differences in branching architecture and allometry were observed for shade tolerant species (Kohyama 1987). Both groups represent extremes although intermediate types can be observed, such as generalist species; these are considered the largest group in tropical rain forests (Terborgh 1992, p. 89–95). With regard to gaps, two groups of plants can be distinguished independently of these characteristics: (1) plants which are already present at a gap location at the time of its formation, denoted as “advanced regeneration” (Raich and Christensen 1989, Brokaw and Busing 2000), and (2) plants arriving immediately upon, or soon after, the gap formation.

Because gaps promote seedling establishment and sapling density (Hubbell et al. 1999), the application of gap dynamics theory to outline tropical forest management and conservation is appealing. However, attempts to manage tropical forests based on these concepts are scarce (Hartshorn 1989). In this study, we focus on the sapling communities (woody plants) only at the time of, or soon after the gap formation. Together with the seedlings, the importance of these sapling communities for forest regeneration lies in their presence in the “units of forest regeneration” (i.e., the gaps), and hence at the beginning of the forest cycle. It is widely accepted that tropical forest gaps are “loci” for tree regeneration (e.g., Hartshorn 1989, Oldeman 1989, Raich and Christensen 1989, Barnes et al. 1998, p. 473–479; Brokaw and Busing 2000). The characteristics of these communities are expected to influence the succession during the gap construction phase, and hence forest diversity (Brokaw and Scheiner 1989, Brokaw and Busing 2000). We refer to this advanced regeneration community, together with the pioneer species arriving shortly after gap formation, as the “initial gap community.” In this study, we address the following questions: What are the characteristics of sapling species diversity at the time of gap formation or soon thereafter? Are there differences in species composition between the gaps? What is the role of gap size, and of isolation, with regard to the composition of the initial gap community?

**Study Site and Methods**

The study was performed from June 1996 until December 1998 at the Tiputini Biodiversity Station (TBS), owned by the Universidad San Francisco de Quito (USFQ), and Boston University (BU). TBS is located in the Orellana province (0°37′55″S, 76°10′19″W, altitude c. 300 m), and comprises a 650 ha tract of old-growth lowland rainforest adjacent to the Yasuní Biosphere Reserve. The yearly rainfall follows a bimodal pattern, totaling c. 3000 mm y⁻¹; mean temperatures exceed 25°C; the relative humidity equals c. 80% (source: Dirección de Aviación Civil, Coca Airport, 0°27′8″S, 76°59′2″W). The soils are alluvial and clayey (Baldock 1982), and the topography is flat. The type of forest is known as “terra firme” (Jacobs 1981, p. 114). For the mature forest, ~728 trees ha⁻¹ (dbh > 20 cm) and ~288 species ha⁻¹ were observed. Average overall canopy height was estimated to be ~16 m (Salvador-Van Eysenrode et al. 1999b).

We demarcated a permanent sample plot of 13.5 ha on a plateau surrounded by swamps and an oxbow lake. In the plot, 24 gaps formed between October 1996 and March 1998 were dated (monthly resolution) and marked at their center; the positions of the centers were recorded up to the nearest meter (Salvador-Van Eysenrode et al. 1998). To assess gap area, we traced radii between the center stake and the stems of the first trees surrounding the gaps (dbh > 20 cm), and added the areas of the polygons (Runkle 1981). Gaps were only included in the study if the vertical ground projection of the canopy opening exceeded a predefined minimum gap area of 4 m² (area sensu Brokaw 1982a). All saplings (height: 1–4 m) of woody plants (stems of self-supported life-forms) were marked, encoded, and identified. Plant identification was supported with local names, collections, and photographs of all plants. Plant collections were archived at the USFQ herbarium (international code: QUSF).

We determined the compositional diversity (Roberts and Gilliam 1995) in each gap at the time of formation or shortly thereafter (maximally 6 months). We quantified species richness using the number of species (S). Species evenness was measured by means of the Gini evenness index (G′) (Weiner and Solbrig 1984, Rousseau and Van Hecke 1999):

\[
G' = 1 - \left( \frac{S+1}{S} - \frac{2}{S} \sum_{i=1}^{S} (S+1-i)p_i \right) \tag{1}
\]

where \(p_i\) equals the probability of occurrence of the \(i\)th species, and where \(G' = 1\) for perfect evenness (\(p_1 = p_2 = \ldots = p_S = 1\)). The average of the distances (\(d_i\)) measured between the center of every gap and the \(g–1\) other gap centers provided a measure of gap isolation (I):

\[
I = \frac{1}{g-1} \sum_{i=1}^{g-1} d_i \tag{2}
\]
with \( g \) equal to the number of gaps considered. Species composition similarity was assessed with the Sørensen coefficient, i.e.,
\[
S_{\text{Sør}} = 2 \left( \frac{S_c}{S_a + S_b} \right)
\]
where \( S_a \) and \( S_b \) are the number of species in gap communities \( a \) and \( b \), respectively, and \( S_c \) the number of species in common, i.e., observed in both gaps; \( S_{\text{Sør}} = 1 \) for perfect similarity. Using the same absence/presence data, we tested association between gaps (stand similarity sensu Causton 1988, p. 71–97) using \( (24 \times 23)/2 = 276 \) pairwise \( \chi^2 \) tests (\( df = 1 \)) based on \( 2 \times 2 \) contingency tables.

We analyzed gap similarity using MVSP Plus v. 2.1 (Kovach 1986, p. 30–36) by an agglomerative hierarchical cluster analysis using the Sørensen coefficient and the farthest neighbor or complete linkage cluster method. We selected this method to avoid chaining (with every fusion, one single gap is added to the previously formed cluster containing all other gaps) and inversion effects (gap fusion sequence should be characterized by decreasing similarity levels; with inversion, similarity levels are not monotonously decreasing) in the dendrogram (Clifford and Stephenson 1975, p. 99–124). The value of \( S_{\text{Sør}} \) of the first fusion of two gaps, i.e., the degree of similarity of the two most similar gaps, was used as an index of overall similarity. If this fusion occurs at \( S_{\text{Sør}} = \omega \) with \( 0 \leq \omega < 1 \), then the following inequality applies for all fusions:
\[
\omega \geq 2 \left( \frac{S_c}{S_a + S_b} \right) = \left( \frac{2S_c}{2S_a + S_b} \right)
\]
with \( S'_a = S_a - S_c \) and \( S'_b = S_b - S_c \). Using \( S' = S'_a + S'_b = S_c \).

Equation (4) can be simplified into
\[
S_c \leq \frac{\omega}{2 - \omega} S'
\]
Equation (5) gives information about the ratio \( S_c / S' \) (i.e., about the relative number of common species with regard to the total number of species present in two gaps compared). In the case of \( \omega = 1 \), the gaps are identical, and \( S_c = S' \) (all species are common species). In the case of \( \omega = 0 \), \( S_c = 0 \), indicating no similarity or common species between the gaps.

Using MVSP Plus v. 2.1 (Kovach 1986), gap size, richness, evenness, isolation, and average species similarity were analyzed in a standardized centered principal components analysis (PCA, based on a correlation matrix; see Kovach 1986, p. 25–27) to assess their interaction.

The relationship between gap area and species richness was examined with a species-gap area curve, which ranks gaps in increasing size order and shows the relative contribution of new species with each added gap.

Finally, we constructed three expected distributions of species abundance based on the MacArthur’s broken-stick, the log-normal, and the log-series models, respectively (Ludwig and Reynolds 1988, p. 71–84; Magurran 1988, p. 9–45; Waite 2000, p. 52–82). These models are strongly advocated as providing the only sound basis for the examination of species or community diversity (Magurran 1988, p. 9–45). If a simple distribution can be found which fits the observed pattern of species abundance, then—in theory—it should be possible to objectively describe and compare community samples. This approach has the advantage of using all the data collected, not only information on the number of species but also on their abundance. And, if species abundance is related to resource availability, then the fitted model may provide information about the way in which key community resources are partitioned between species (Waite 2000, p. 52–82). The log-series predicts that the rarest species should occur most frequently in a sample, whereas the log-normal predicts that species of intermediate abundance should be most common (Gotelli and Graves 1996, p. 47–63). The majority of communities studied by ecologists are found to display a log-normal distribution (Magurran 1988, p. 9–45).

The broken-stick model reflects a much more equitable state than those suggested by the log-normal and log-series models (Magurran 1988, p. 9–45). Every model was generated for an equal number of species and individuals as observed in the field. These models were used to explore the structure of the sapling community of all gaps pooled. The sapling communities were assumed to constitute an even-aged cohort. The closeness of the observed to the expected distribution was assessed by means of the \( \chi^2 \) statistic (goodness-of-fit). Classes were pooled to obtain expected frequencies exceeding five, as recommended by Poole (1974, p. 101–125) and Ludwig and Reynolds (1988, p. 19–40).

**Results**

In the 24 initial gap communities (total gap area 2,148 m²), 310 species, and 1,448 individuals were recorded. Information on gap size and number of species and individuals is shown in Table 1. Table 2 shows the genera (and family) of species with individuals in more than 20% of the gaps.

The species-gap area curve (Figure 1) reveals an initial steep increase due to a majority (91.6%) of gap sizes <150 m².

**Table 1. Gap size and sapling density data (Tiputini Biodiversity Station, Amazonian Ecuador).**

<table>
<thead>
<tr>
<th>Gap size (m²)</th>
<th>Species (m⁻² gap⁻¹)</th>
<th>Individuals (m⁻² gap⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum</td>
<td>23</td>
<td>0.13</td>
</tr>
<tr>
<td>Median</td>
<td>73</td>
<td>0.47</td>
</tr>
<tr>
<td>Maximum</td>
<td>310</td>
<td>2.42</td>
</tr>
<tr>
<td>Mean (± SD)</td>
<td>89.50 (± 76.75)</td>
<td>0.62 (± 0.48)</td>
</tr>
</tbody>
</table>

*Forest Science 49(6) 2003 911*
Gaps ≤ 50 m² (10 gaps, and representing 14.9% of the total gap area) contained 30.3% of the total number of species. In total, 86.1% of all the species were found in the group of “small” gaps, which are the most common, considering 150 m² as a breakpoint to discriminate small from large gaps (Brokaw 1982b). Steep species-area curves for gap plots were also reported by Busing and White (1997).

All gaps together presented a species distribution skewed to the right. The majority of species was represented by two individuals, decreasingly followed by one, three, four individuals up to 128 individuals, the latter abundance observed for Faramea sp. (Rubiaceae). About one-third of the number of species was represented by one or two individuals, and half of the number of species was represented by less than four individuals (Figure 2). Six gaps contained only one single species represented by more than 10 individuals, and an average of 5.9 individuals per species was found.

The observed species abundance distribution deviated significantly from the expected distributions based on the log-normal (χ² = 41.38, df = 3, P < 0.001), and the broken-stick (χ² = 59.01, df = 4, P < 0.001) models, but was not significantly different from the expected distribution based on the log-series model (χ² = 3.91, df = 2, P > 0.1, Figure 2), which enabled us to speculate about the factors governing the structure of the initial gap community (Waite 2000, p. 52–82).

The average species similarity of each gap compared to all other gaps was 17.3% (SD ± 7.1%, Figure 3), and no influence of gap size on average species similarity was evident (rₛ = 0.22, P = 0.28). However, gap size was found to be significantly correlated with species richness (rₛ = 0.45, P = 0.02), with gap isolation (rₛ = 0.41, P = 0.04), and with species evenness (rₛ = −0.39, P = 0.05). Species richness was significantly correlated with average species similarity (rₛ = 0.61, P = 0.001).

Associations between gaps were found for gap pairs having more (or less) species in common than would be present in case of randomness (Causton 1988, p. 71–97). From the 276 values, 33.7% indicated significant association at the P = 0.05 level (χ² > 3.841); 10.1% of the values were

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### Table 2. Initial gap community species (Tiputini Biodiversity Station, Amazonian Ecuador).

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td>Tapirira</td>
<td>2</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Annona</td>
<td>1</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Guatteria</td>
<td>1</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Rollinia</td>
<td>1</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Xilopia</td>
<td>1</td>
</tr>
<tr>
<td>Arceae</td>
<td>Bactris</td>
<td>1</td>
</tr>
<tr>
<td>Arceae</td>
<td>Socratea</td>
<td>1</td>
</tr>
<tr>
<td>Bombacaceae</td>
<td>Quarariea</td>
<td>4</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>Dacryodes</td>
<td>1</td>
</tr>
<tr>
<td>Caesalpinaceae</td>
<td>Brownea</td>
<td>4</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Acalipha</td>
<td>2</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Mabea</td>
<td>1</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Pausandra</td>
<td>1</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Myroxylon</td>
<td>1</td>
</tr>
<tr>
<td>Flacourtaceae</td>
<td>Caesaria</td>
<td>1</td>
</tr>
<tr>
<td>Lauraceae</td>
<td>Nectandra</td>
<td>1</td>
</tr>
<tr>
<td>Lauraceae</td>
<td>Ocotea</td>
<td>4</td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td>Grias</td>
<td>1</td>
</tr>
<tr>
<td>Melastomataceae</td>
<td>Miconia</td>
<td>1</td>
</tr>
<tr>
<td>Meliaceae</td>
<td>Guarea</td>
<td>3</td>
</tr>
<tr>
<td>Mimosaceae</td>
<td>Inga</td>
<td>6</td>
</tr>
<tr>
<td>Monimiaceae</td>
<td>Siparsena</td>
<td>1</td>
</tr>
<tr>
<td>Moraceae</td>
<td>Brosmium</td>
<td>1</td>
</tr>
<tr>
<td>Moraceae</td>
<td>Ficus</td>
<td>4</td>
</tr>
<tr>
<td>Myrtaceae</td>
<td>Eugenia</td>
<td>2</td>
</tr>
<tr>
<td>Olacaceae</td>
<td>Heisteria</td>
<td>1</td>
</tr>
<tr>
<td>Piperaceae</td>
<td>Piper</td>
<td>2</td>
</tr>
<tr>
<td>Polygonaceae</td>
<td>Triplaris</td>
<td>1</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Faramea</td>
<td>1</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Palicourea</td>
<td>2</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Pentagonia</td>
<td>1</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Psychotria</td>
<td>2</td>
</tr>
<tr>
<td>Sapindaceae</td>
<td>Paulinia</td>
<td>1</td>
</tr>
<tr>
<td>Tiliaceae</td>
<td>Apeiba</td>
<td>1</td>
</tr>
</tbody>
</table>

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Figure 1. Cumulative species-gap area curve for the 24 gaps surveyed at the Tiputini Biodiversity Station. Gap sequence is presented in ascending size order. Gap sizes are typical below 150 m² and ~30% of the total number of species is found in gaps smaller than 50 m². Total number of species equals 310.

![Figure 1](https://example.com/f1.png)

Figure 2. Observed, and expected species abundance distribution according to the log-series model for the saplings of all gaps pooled. The log-series model was found to be a good fit (χ² = 3.91) to the underlying species abundance distribution of the initial gap communities found at the Tiputini Biodiversity Station.
significant at the $P=0.001$ level ($\chi^2 > 10.828$). All significant associations indicated positive association (i.e., more species are in common than expected with random conditions).

Using the number of significant associations as a guideline, we found that associations were not evenly spread over the gaps—some gaps clearly showed higher similarity than others, and no coupling with gap area was evident. These results put the relative low similarity values in perspective: although the similarity between gap pairs can be denoted as "low" (~17%), one out of three pairwise comparisons provided a significant association.

The cluster analysis revealed the presence—as quantified by Sørensen similarity—of four groups (Figure 4, gaps labeled with gap size rank with $G_1 =$ smallest and $G_24 =$ largest gap size), containing respectively 7, 10, 1, and 6 gaps. The cluster with one single gap consisted of the gap showing the lowest similarity with all other gaps (number 5, Figure 3). This gap also did not have a single significant association at the $P = 0.05$ level with any other gap (data not shown). The dendrogram (Figure 4) did not show chaining or inversion effects, as could be expected using the complete linkage method. Clustering in four groups becomes clear at $S_{or} = 0.10$, indicating high dissimilarity between gaps/clusters. The first fusion (or pairing) occurred at $S_{or} = 0.42$, which leads—using Equation (5)—to the conclusion that 26.6% or less of the species are in common between the groups/clusters compared in the dendrogram. We observed no grouping of equal-sized gaps (large gaps are interspersed with small gaps in the clusters, Figure 4). No effect of isolation or spatial similarity gradient was found (Figure 4), as quantified by the average isolation of the fusions of two individual gaps (no cluster fusion considered), which equals 196.6 m (CV = 0.82).

The first three axes of the PCA yielded 91.6% of the total variance (eigenvalues: $\lambda_1 = 2.17$, $\lambda_2 = 1.61$, and $\lambda_3 = 0.79$; Figure 5). Principal component 1 was dominated by gap size and was followed by species evenness. However, the component loadings of species richness and species similarity were also very close to that of gap size, which suggested no clear separation between gap size, species evenness, species richness and average species similarity on this axis. This made the ecological interpretation of this axis complex. Principal component 2 was clearly dominated by gap isolation, followed by species richness, which enabled a vague discrimination between isolated gaps with a low number of species, and clustered or spatially aggregated gaps containing more species. In principal component 3, gap size dominated again and was followed by species similarity and species evenness. This relationship could be an indirect result of the additive effect of gap size on the number of species, which also

![Figure 3. Average similarity (Sørensen coefficient, ± SD) of the species composition of each individual gap compared to all other gaps surveyed at the Tiputini Biodiversity Station. The overall mean is indicated by a dashed line. Gap sizes range from 23 up to 310 m².](https://academic.oup.com/forestscience/article-lookup/doi/10.1093/forestscience/49.6.909)

![Figure 4. Cluster analysis dendrogram based on Sørensen similarity and the farthest neighbor method. Gaps are labeled in ascending size order, with $G_1 =$ smallest and $G_{24} =$ largest gap size. The 24 gaps can be subdivided in four clusters: {G7,G9,G13,G18,G21,G24}, {G5}, {G3,G11,G12,G14,G15,G16,G17,G19,G20,G22}, and {G1,G2,G4,G6,G8,G10,G23}.](https://academic.oup.com/forestscience/article-lookup/doi/10.1093/forestscience/49.6.909)

![Figure 5. Representation of the results of the principal components analysis (PCA) for the 24 gaps surveyed at the Tiputini Biodiversity Station. The component loadings of gap size (m²), number of species ($S$), evenness ($G'$), isolation ($I$), and species similarity ($S_{or}$) in the first three axes (PC1, PC2, and PC3) of the centered, standardized PCA are shown.](https://academic.oup.com/forestscience/article-lookup/doi/10.1093/forestscience/49.6.909)
increased the probability to encounter a species with a higher abundance. The latter increased the probability of species similarity, but reduced species evenness.

Discussion

Many rare species and a few common species were characteristic when analyzed for all gaps separately, as well as for the species abundance distribution of the initial gap communities pooled. If compared to nongap areas, the high richness observed in gaps is generally caused by higher stem densities: on a per-stem basis, gap and nongap areas are often considered equally rich (Hubbell et al. 1999, Brokaw and Busing 2000). This per-stem basis comparison of richness of gaps relative to nongap patches is still subject to debate (Chazdon et al. 1999). Considering the high species richness of our data set, the general shape of this abundance distribution initially suggested an underlying log-normal pattern (Sugihara 1980, May 1981). However, the observed distribution was not significantly different from the log-series pattern (as it was from the log-normal model), which reflects the evenness component less than the log-normal. A log-series distribution would result from a process where species would arrive at an unsaturated habitat at random intervals of time, and each species would consequently partition a constant fraction of the remaining resources (Gotelli and Graves 1996, p. 47–63).

The small number of abundant species and the large number of species represented by only a few or by one single individual, as predicted by the log-series model, suggested that such a distribution would result from situations where one or only a few factors dominated the ecology of the community (Magurran 1988, p. 17–19). Consequently, this distribution was expected to characterize small, stressed or pioneer communities (Gotelli and Graves 1996, p. 47–63), which probably applied for gap sapling communities.

The extent to which an initial gap community should be considered “small” is a debatable issue. Gap environments can be assumed to be a source of stress for the gap communities and these communities can be considered “pioneer” in the sense of being the first communities of the forest cycle and containing pioneer species next to the advanced regeneration. In this case, these arguments could support the evidence that a log-normal process may be influencing the species abundance distribution when the community is at early gap stage. Considering the primary processes occurring in gaps, it also seems that the requirements to obtain a log-series distribution can be met. Firstly, gap formation in space and time is hard to predict (Brokaw and Busing 2000, Salvador-Van Eysenrode et al. 2000), as well as the arrival of species at a gap (Hubbell et al. 1999). This suggests that the presence of any species in a gap is a stochastic event (Brokaw and Busing 2000), where, among others, species arrival occurs at random time intervals. Moreover, it seems reasonable that 2-D space is the main limiting resource for plant establishment in a gap, and that each species occupies a theoretically constant fraction of the remaining available gap-space (Fagerström 1988). Later, when forest communities enter the building phase, more factors are influencing, e.g., recruitment limitation and survival (Raich and Christensen 1989, Richards 1996, p. 49–69, Brokaw and Busing 2000), and these factors could also introduce shifts in the species abundance distribution. Although the log-series model of species abundance distribution can be used to explain in which way initial gap communities are shaped, the conclusions remain speculative. Tropical rain forests are reported to have more species than those present in the current data set [Hubbell et al. (1999) report for their Panama plot that gaps typically include saplings of only about 2.3% of the canopy species in the forest], and the natural conditions of gap communities are complex and involve many other factors than those on which the presented models are based. Because a perfect fit between a natural and a predicted situation is rare, conclusions can only be drawn from approximations, and an analysis of the shift of the species abundance through time would provide more insight.

From the correlation analysis, it can be concluded that gap size has an influence on richness, evenness, and also on isolation. Large gaps (>150 m², \( n = 2 \)) had, in general, more species than smaller gaps (\( S = 61 \) and \( S = 59 \) for gaps with size 300 m² and 310 m², respectively). However, some of the small gaps (\( S = 69, S = 66 \) and \( S = 66 \) for gaps with size 71 m², 81 m², and 110 m², respectively) also had more species than the largest gaps, which explains the weakness of this correlation. Although low, the inverse correlation between gap size and evenness suggested a contribution of gap size to the dominance of certain species in gaps. If all species in our data set would have been represented by a single individual, then evenness would have been “perfect” (\( G^* = 1 \)), and the correlation between gap size and richness would have been higher. Moreover, the probability to find species represented by more than one individual (which reduces evenness when a majority is single-represented) also slightly increased with gap size. The correlation found between gap size and isolation may be stochastic, and intrinsic to the gap size distribution, where gaps tend to be rather small (Hartshorn 1990). Moreover, the likelihood of gaps to be formed in the neighborhood of previously formed gaps, as shown elsewhere (Salvador-Van Eysenrode et al. 2000), should be considered. It is difficult to base conclusions merely on a low correlation between gap size and “average” isolation. Species richness and average species similarity showed the highest correlation, a logical result due to the presence of the number of species itself in the calculation of the similarity index. However, the general average similarity of all gaps together was rather low, as was to be expected from the species abundance distribution in each gap, making gaps almost “unique” in terms of their species composition. This low average similarity was confirmed by the cluster analysis which did not provide clear gap grouping at high similarity levels and did not suggest that dissimilarity was induced by spatial remoteness or a difference in gap size. The association analysis showed, however, that one out of three gap pairs contained more species in common than would be expected under random assumptions, which mortgages somewhat the “uniqueness” of gaps. This low abundance makes species, and...
consequently forest diversity, prone to extinction. This low abundance is not taken into account by the \( \chi^2 \) statistic, since absence/presence data are used as an input in the contingency table.

The PCA analysis also reflected the correlation results. In the first principal component, the unclear dominance of gap size, species richness, and average species similarity showed the interaction among these variables, as well as the polarization between gap size and species evenness. However, this indicated that the larger the gap area would be, the more species would be found, which in turn would increase the probability of finding species represented by more than one individual. This would consequently increase the chance of similarity, but would reduce species evenness. The dominance of isolation in the second principal component confirmed the independency of this variable, although it was casually correlated with gap size. Finally, the third principal component showed a dominance of gap size followed by average similarity, but the component loadings of the two variables were more separated than in the first axis. Moreover, this component accounted for only 15.9% of the total variance. Gaps contained a high number of species represented mostly by one or a few individuals, which made them highly dissimilar. Gap size had an effect on sapling richness, although low, and this is a consequence of the dominance by single-represented species. Gap isolation appeared to be independent of all other variables, at least in the way it has been assessed in this study (unbiased way as based on gap interdistance).

The species composition of particular gaps often shows more similarity to that of adjacent, undisturbed forest patches, than to similar gap types in different locations; this suggests that seedlings present at the time of gap formation dominate the regeneration community (Raich and Christensen 1989). However, this does not imply that gaps are not important in maintaining forest diversity: gaps constitute another stage of the forest cycle than mature patches. The impact on forest diversity evolution will consequently be different. Mature forest patches can be considered as representing the diversity “of the present,” while gaps represent the diversity “of the future,” or the “potential diversity.” Assuming the intermediate disturbance hypothesis, the low similarity between gaps is needed to enable maintenance of the high biodiversity status. The similarity between the gap composition and that of the surrounding forest, as observed by Raich and Christensen (1989), should be put in perspective. For the Tiputini Biodiversity Station, lower similarities between nongap forest sites and gaps among gap sites was observed (Salvador-Van Eysenrode, unpubl. results). It should raise concern if overall gap diversity was exceeded by the diversity of the mature forest: in the long run this could imply richness decline, if not compensated by gap-to-gap differences. Moreover, the intermediate disturbance hypothesis predicts not simply that species richness in any one gap will be greater than in the same area of the mature forest, but that gaps collectively will be richer than the matrix, because gaps provide more diverse conditions and resources (Chazdon et al. 1999).

A comparison with the milestone paper of Hubbell et al. (1999) is appealing. This study tested the intermediate disturbance hypothesis for a 50 ha plot of old growth tropical moist forest on Barro Colorado Island (Panama). The plot contained over 1,200 gaps, with variation over a 46 fold size range from 25 m\(^2\) to the largest gap of 1150 m\(^2\). Quadrats containing light gaps had substantially more species than did quadrats in nongap, mature forest sites, as predicted by the intermediate disturbance hypothesis. Species richness, expressed on a per stem basis, was not significantly different, so that the main effect of gaps on species richness was considered a simple area effect by Hubbell et al. (1999). Recruitment limitation (i.e., the failure of a species to recruit in all sites favorable for its growth and survival, was considered the major factor determining local species richness and composition. Many sites are won by default by species that are not absolutely the best competitor for the sites. Strong recruitment limitation does not prevent ultimate competitive exclusion, but can slow down the rate so that the elimination of inferior competitors can be nearly infinitely delayed (Hubbell et al. 1999, Tilman 1999). This reassesses the role of gaps in maintaining species richness, and thus depreciates the importance of gap diversity survey as executed for this article. However, this daring statement is subject to debate (Chazdon et al. 1999, Kobe 1999). It was concluded from the Barro Colorado study that gaps do promote tree diversity, but mainly by increasing community-wide seedling establishment. A virtually no gap-to-gap predictability of the species richness in gaps was observed (Hubbell et al. 1999), which confirms the uniqueness of gaps as found also for the Tiputini Biodiversity Station.

Our findings can be used to assess the impact of artificial gap creation, which is destructive for saplings and seedlings (Skole and Tucker 1993, Nepstad et al. 1999). As a consequence of gap uniqueness, it is expected that if more gaps are created in a forest, more sapling species would be destroyed, and the probability of finding another individual of a given species in another gap would be very low. Moreover, the larger the gaps created, the more species affected, independently of how isolated gaps are. Thus, from the point of view of artificial gap creation, not only the saplings, but also “diversity” as an intrinsic ecosystem property is threatened. As gap creation drives the forest cycle, then controlling the destruction of saplings during artificial gap opening in combination with exploiting the constructive effects of gap creation, can be a useful tool for forest management and conservation (Hartshorn 1990). With regard to species diversity, where a gap occurs (or is created) is apparently more important than in which way, due to the advanced regeneration and the availability of seed (Raich and Christensen 1989, Brokaw and Busing 2000). The uniqueness of gaps in terms of sapling composition, as shown by the current study and as expressed by low species abundance and low community similarity, outlines their vulnerability and conservation value, while their role in maintaining forest diversity remains debatable (Chazdon et al. 1999, Hubbell 1999, Hubbell et al. 1999, Kobe 1999). However, the stochastic availability of gaps, and
the limited recruitment of juveniles, means that gaps are filled mostly by chance occupants rather than by the best adapted species; this chance survival can maintain tree diversity (Brokaw and Busing 2000).

**Literature Cited**


