

# Catastrophic natural origin of a species-poor tree community in the world's richest forest

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(Accepted 21 February 2005)

**Abstract:** Upper Amazonian tree communities are famous for their very high alpha-diversity. This paper describes an anomalous forest just 6 km south of the equator in lowland Ecuador that is structurally mature, surrounded by hyperdiverse forest, but strikingly poor in species. To investigate the anomaly, a 1-ha tree inventory and soil analysis were carried out and compared with 15 similar surveys of upland forest in the same region. The anomalous forest contains only 102 tree species ha<sup>-1</sup>, compared with a regional mean of 239 ± 28 species ha<sup>-1</sup>. It is structurally indistinguishable from richer forests, and closest in composition to upland forest, but lacks the uplands' typically rich understorey tree community. Three hypotheses for its origin are examined: recovery from anthropogenic disturbance, unique soil conditions and recovery from a large-scale natural catastrophe. The third hypothesis is the best supported. Mineralogical, geological and remote-sensing evidence, and <sup>14</sup>C-dating suggest that the forest grows on a vast debris plain left by a catastrophic flooding event roughly 500 y ago. The forest's low diversity today is most likely due to the failure of a full complement of the region's tree species – especially understorey taxa – to recolonize the outwash plain in the time since the disaster.

**Key Words:** Amazon, disturbance, Ecuador, El Reventador, history, natural disaster, trees, tree diversity, volcano

## INTRODUCTION

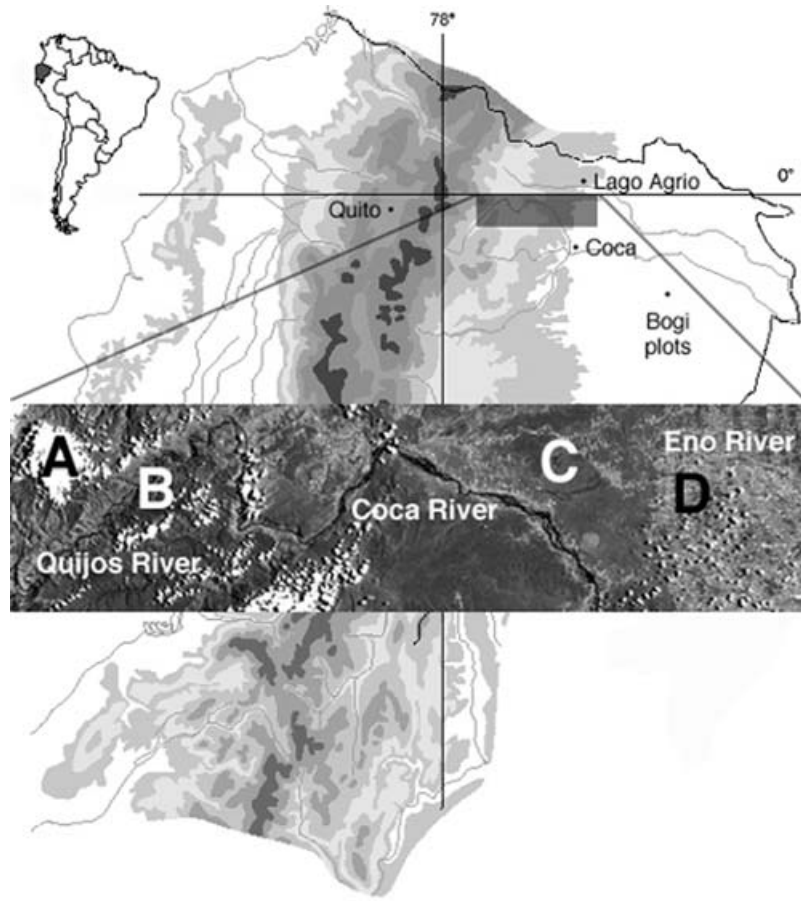
The ten most diverse 1-ha tree plots inventoried to date are in Amazonian rain forest within five degrees of the equator (ter Steege *et al.* 2003). These plots have received a disproportionate amount of attention from tropical ecologists, in part because no satisfying hypothesis yet explains why they contain so many tree species (Balslev *et al.* 1987, Gentry 1988, Pitman 2000, Pitman *et al.* 2002a, Romero-Saltos *et al.* 2001, Romoleroux *et al.* 1997, ter Steege *et al.* 2000, Valencia *et al.* 1994, Vásquez-Martínez & Phillips 2000).

In this paper we describe inventory results from a remarkably species-poor tree community growing just 6 km from the equator in Amazonian Ecuador. The

anomalous plot is in mature, undisturbed, lowland *terra firme* forest on a plain surrounded by hilly, extremely diverse, well-studied forests. Our goal is to understand why this plot contains so few tree species, as part of the larger project of understanding why most tree plots near the equator contain so many. As in Pitman *et al.* (2002a), we approach these questions by first comparing the composition and structure of the species-poor forest to those of species-rich forests growing in the same vicinity, and then examining, and where possible testing, specific explanations for the difference in diversity.

The project is not only a step towards a better understanding of floristic patterns in this corner of the Amazon basin, but also a cautionary note on the role of geographic anomalies in patterns of large-scale diversity. As more and more researchers coax macro-ecological patterns out of the meagre scattering of biological inventories across the tropics, the sometimes significant medium-scale variation that gets lost in the big picture (or distorts it) is worth noting.

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**Figure 1.** The geographic context of the study site near the Eno River, Ecuador. Letters indicate the locations of (A) the El Reventador Volcano at 3562 m, (B) the Cascada San Rafael, where remnants of a debris dam are evident, (C) scars where a massive washout flood 500 y bp is believed to have jumped from the Coca River to the Eno River (the dark line under the C), and (D) the Eno tree plot at 350 m, near the town of Yurimaguas. The satellite image is a 100 × 25-km segment of a Landsat taken on 11 September 2001. Base maps courtesy of Flemming Nørgaard.

## STUDY SITE

The tree plot (hereafter referred to as the Eno plot) was established in mature, closed-canopy humid forest at 350 m elevation in Amazonian Ecuador, 13 km southwest of the city of Lago Agrio, 10 km east of the Andean foothills, and just a few km south of the Eno River (00°04.956' S 076°57.110' W; Figure 1). The site is reached by following an unpaved road west from the town of El Eno, past the small community of Yurimaguas.

We were drawn to forests around the Eno River because of their anomalous soils and topography, which are immediately obvious to travellers on the main highway between the cities of Lago Agrio and Coca. Unlike the sharply dissected or rolling hills of red clay to the north and south, the >100-km<sup>2</sup> plain on which the plot was established is perfectly level and has dark brown, sandy soils. In our limited exploration of the feature, we found no streams or rivers draining it, apart from the Eno,

a meandering low-gradient river that runs along its northern edge. Residents told us that the soils never hold standing water, even after heavy rainfall. We have been unable so far to map the extent of the plain, in part because it is not easily distinguished from surrounding forest in Landsat images.

The tree plot is in a ~25-ha forest remnant in an area that has been severely fragmented by agricultural expansion. Sierra (2000), studying 1996 satellite images of a ~4500-km<sup>2</sup> area that includes the Eno plot, estimated that 46% of the original forest had been cut by that year (mostly in the preceding 25 y), while roughly half of the remaining forest was in fragments smaller than 10 000 ha. The situation is worse in the immediate vicinity of the Eno plot, because the dark soils and flat landscape make this attractive land for farmers. In a Landsat image taken on 11 September 2001, standing forest covers only 10–20% of a ~25-km<sup>2</sup> area containing the Eno plot. The remaining forest is an archipelago of small fragments.

## METHODS

### Field work in the Eno plot

In December 2000, we established a square, 1-ha tree plot in a forest fragment bordered by pastures. The nearest border of the plot was approximately 10 m from the closest forest edge. Within the plot all living, free-standing trees  $\geq 10$  cm dbh (including 'woody' monocots like palms and bamboos) were measured for circumference at breast height (c. 1.3 m). Where buttresses, stilt roots, or other trunk irregularities were present at breast height, we measured above them. Tree diameters were later calculated from the circumferences by assuming stems to be cylindrical. All trees  $\geq 10$  cm dbh were also estimated for height, and labelled with a numbered aluminium tag.

In June and July 2001, all tagged trees were field-identified or collected by CC. Voucher specimens were subsequently identified by comparing them with specialist-identified specimens in the National Herbarium of Ecuador (QCNE) and the Alfredo Paredes Herbarium (QAP) of the Universidad Central del Ecuador and following the taxonomic nomenclature of Jørgensen & León-Yáñez (1999). The 137 voucher specimens are currently deposited in QAP, under Carlos Cerón series 44073–44258. Two living trees that had broken canopies and no leaves were neither collected nor identified to morphospecies, but they were counted and measured. The full dataset is publicly available at [www.salvias.net](http://www.salvias.net).

Two soil samples were collected at the same location in the plot, one from just below the organic layer and the other from a depth of 50 cm. Samples were analysed separately at the soils laboratory of the Universidad Central del Ecuador for pH, per cent organic matter, total N, and the proportion of sand, silt and clay.

### Analyses

Characteristics of the Eno tree community (diversity, forest structure, community structure, etc.) were compared to those of tree communities in 15 1-ha *terra firme* plots established previously in eastern Ecuador. Locations and characteristics of these plots have been reported in detail elsewhere (Pitman *et al.* 2001); all are within 150 km of the Eno plot. To compare species composition, we calculated the Sørensen's similarity index of the Eno plot with 24 other plots in eastern Ecuador: the 15 *terra firme* plots mentioned above, as well as five 1-ha floodplain plots, three 1-ha swamp plots and one 2-ha swamp plot (N. Pitman *et al.*, unpubl. data).

Sørensen's is one of the most frequently used indices in the study of tropical vegetation, but as typically presented it is not a reliable measure of compositional difference.

Because the index is not independent of diversity, only compositionally identical samples of the same diversity can attain its maximum (1), while compositionally identical samples that have different diversities will measure closer to its minimum (0) if the difference in species number is greater than 3:1. This makes Sørensen's index a bad choice for researchers comparing samples whose number of species varies even slightly. Burnham's (2004) analysis of liana communities in two different forest types illustrates the problem. Samples from different forest types scored lower on the Sørensen index than samples from the same forest type, but because the two forest types differ in diversity it is not possible to say whether these results indicate high liana species turnover between upland and floodplain forests, or whether they are an artefact of the difference in diversity between the two forest types.

To avoid this problem, we standardized all of our Sørensen's index scores by dividing the observed similarity of two plots by the maximum possible similarity of those two plots, given their difference in diversity. Sørensen's index is calculated as:

$$\frac{2(\text{no. spp. shared by the two plots})}{(\text{no. spp. in plot A} + \text{no. spp. in plot B})}$$

The standardized Sørensen's index is calculated as Sørensen's index divided by the maximum possible similarity between the two plots:

$$\text{Sorensen's index} / \left( \frac{2(\text{no. of spp. in the less diverse plot})}{(\text{no. spp. in plot A} + \text{no. spp. in plot B})} \right)$$

The advantage of this standardized form is that all plot comparisons, regardless of the plots' diversity, are measured on the same scale, from 0 to 1. A drawback to the standardized form of the index is that it scores a plot with one species and a plot with 300 species as compositionally identical if that one species is shared by the two plots. On the other hand, this seems only fair, since the plot with one species is as compositionally similar to the richer plot as it could possibly be, given its diversity.

We used a database describing morphological, ecological and other attributes of tree species native to eastern Ecuador, compiled from florulas and taxonomic treatments (see Pitman 2000, Pitman *et al.* 2001), to compare attributes of 81 species in the Eno plot with those of 638 species known to occur in eastern Ecuador but not collected in the Eno plot. Analyses were via t-tests of means (for continuous variables) or chi-squared tests of frequencies (for categorical variables). The attributes were: (1) the number of species belonging to the species'

**Table 1.** Attributes of the Eno River tree plot compared to those of 15 other upland plots in eastern Ecuador. Asterisks indicate Eno plot values that are significantly different from the 15-plot mean at the 0.05 level. Soil data are from superficial samples collected just below the organic layer.

Attributes	Eno plot	Ecuador mean $\pm$ SD	Ecuador range
<b>Diversity</b>			
Number of species	102*	239 $\pm$ 28	18–295
Number of genera	67*	129 $\pm$ 9	114–142
Number of families	38*	47 $\pm$ 4	41–57
<b>Physical structure</b>			
Number of stems $\geq$ 10 cm dbh	623	654 $\pm$ 71	542–790
Number of stems $\geq$ 50 cm dbh	25	22 $\pm$ 7	10–38
Basal area (m <sup>2</sup> )	34.7	30.2 $\pm$ 6.2	18.9–38.5
Mean dbh (cm)	21.5	20.6 $\pm$ 1.6	17.9–24.3
<b>Community structure</b>			
Number of singletons	44*	128 $\pm$ 22	80–165
% of species that are singletons	43.1*	53.1 $\pm$ 4.2	42.6–59.1
% stems <i>Iriartea deltoidea</i>	25.0*	7.4 $\pm$ 2.9	3.2–12.2
% stems most common species	25.0*	7.7 $\pm$ 2.9	3.2–12.2
% stems Cecropiaceae	6.4*	3.4 $\pm$ 1.0	2.1–5.5
<b>Soils</b>			
pH	6.4*	4.5 $\pm$ 0.8	3.7–6.1
% organic matter	8.95*	4.16 $\pm$ 1.20	1.94–5.36
% total N	0.45*	0.21 $\pm$ 0.06	0.10–.27
% sand	66*	24 $\pm$ 13	11–51
% silt	30*	27 $\pm$ 7	17–41
% clay	4*	49 $\pm$ 13	26–68

family and the species' genus worldwide; (2) the maximum height achieved by the species; (3) latitudinal, longitudinal and elevational ranges; (4) the maximum floral dimension; (5) the length and width of fruits and seeds; (6) dispersal syndrome; (7) the length of leaves or leaflets; (8) leaves deciduous or evergreen; and (9) leaves compound or simple. Because not all attributes were available for all species, comparisons were usually made with subsets of the Eno and non-Eno species pools.

## RESULTS

### Physical structure

The forest in the Eno plot is structurally indistinguishable from primary forests elsewhere in eastern Ecuador, in stem number, basal area, mean dbh, and the number of very large trees (Table 1). The forest has a tall, closed canopy at 25–30 m, overtopped with nine emergents exceeding 40 m. Median tree height was 15 m and median dbh 18 cm, and nine trees measured  $\geq$  70 cm dbh.

### Diversity

Tree diversity in the Eno plot is strikingly lower at all taxonomic levels than in other *terra firme* plots in eastern Ecuador (Table 1). Species diversity at Eno is 43% that of the regional mean and 54% that of the regional minimum.

The most diverse families in the Eno plot were Fabaceae *sensu lato* (17 species), Meliaceae (9), Cecropiaceae (8) and Rubiaceae and Lauraceae (both 5). Every family except Cecropiaceae showed significantly lower species diversity in the Eno plot than in previously established plots. Several families that are typically diverse in eastern Ecuadorian tree plots were especially poorly represented in or absent from the Eno plot, including Sapotaceae (3 spp. in Eno vs. a regional mean of 12), Annonaceae (1 vs. 9), Burseraceae (0 vs. 8), Myrtaceae (1 vs. 7), Melastomataceae (1 vs. 4) and Chrysobalanaceae (0 vs. 3). Similar patterns were apparent at the generic level.

### Composition and abundance

The Eno tree community is closest in composition to *terra firme* plots, with which it scores an average standardized Sørensen's index of 0.32 (range 0.21–0.42). This is within the range of standardized Sørensen's scores of pairwise comparisons of the 15 *terra firme* plots (range 0.22–0.58), but lower than the average (0.40). The Eno plot is less similar in composition with floodplain plots (average 0.22) and swamp plots (average 0.08).

Early successional species are nearly twice as abundant at Eno than in any of the previously established upland plots. The pioneer family Cecropiaceae accounts for 6.4% of all the trees at Eno, compared with a mean 3.4% of trees in previously established plots. Several other light-demanding species are also abundant, including *Jacaratia spinosa* (Caricaceae), *Urera caracasana* (Urticaceae), *Heliocarpus americanus* (Tiliaceae) and *Croton sampatik* (Euphorbiaceae). By contrast, the understorey treelet guild, typically an important component of tree diversity in western Amazonia, is practically absent and represented only by a scattering of species in the genera *Grias*, *Pentagonia*, *Chrysochlamys*, *Capparis* and *Sorocea*. Regionally important understorey species in *Rinorea*, *Matisia*, Nyctaginaceae, Melastomataceae, Myrtaceae and Rubiaceae are missing or rare.

Most of the species in the Eno plot are typical of *terra firme* forests, and most of the common species are well-represented in other *terra firme* forests of eastern Ecuador. The most common species in the Eno plot, the palm *Iriartea deltoidea*, is a near-ubiquitous dominant of Ecuadorian *terra firme* forests (Pitman *et al.* 2001). The second most abundant tree species in the Eno plot, *Metteniusa tessmanniana*, is not as common in the surrounding lowlands as any of the other top species in the Eno plot,

but its abundance is not atypical. It is one of the most common species in a tree plot at 1200 m on the slopes of nearby Sumaco Volcano, very common in the Puyo area, at about 1000 m elevation (D. Neill, pers. comm.), and 'common in the midstory' in the province of Pastaza at 350 m (label data from W. Palacios collection no. 10264).

Only 28 of the 150 species which Pitman *et al.* (2001) hypothesized to be dominant in eastern Ecuadorian *terra firme* forests are present in the Eno plot, but they account for 51% of the individual trees there. Most of the ten most important species reported by Pitman *et al.* (2001) are absent from the Eno plot, including otherwise ubiquitous taxa like *Matisia malacocalyx sensu lato* (Bombacaceae), *Siparuna decipiens* (Monimiaceae) and *Rinorea apiculata* (Violaceae; N. Pitman *et al.*, unpubl. data). Their absence is especially striking because all three species are well-represented in a tree plot just 10 km to the north, in hilly forest along the Aguarico River (C. Cerón, N. Pitman & W. Sarabia, unpubl. data).

Common species are more abundant and rare species fewer in the Eno plot than elsewhere in Ecuador (Table 1). A quarter of the trees in the Eno plot belong to the most common species, *Iriarteia deltoidea*. The five most common species in the plot, including *Metteniusa tessmanniana* (Icacinaceae), *Guarea macrophylla* (Meliaceae), *Grias neuberthii* (Lecythidaceae) and *Jacaratia spinosa* (Caricaceae), account for more than half of the trees, and the 20 most common species account for 75% of the trees.

### Species attributes

Species in the Eno plot are indistinguishable from the broader tree flora of eastern Ecuador for all but one attribute in our database. Trees at Eno have significantly larger leaves than trees elsewhere in eastern Ecuador; this is explained by the strong element of successional taxa.

### Soils

The soils collected at the Eno plot are less acidic and richer in nitrogen and organic matter than soils from previously established plots (Table 1). They contain almost no clay (4%), which typically accounts for 50% of soils in eastern Ecuador, and are almost two-thirds sand. They are also young and undeveloped. There is essentially no difference in pH or the proportion of clay, silt and sand between the superficial sample and the sample taken at 50 cm depth.

## DISCUSSION

The forest we surveyed near the Eno River is a departure from all other forests inventoried to date in upper Amazonia. It is relatively depauperate at all taxonomic levels,

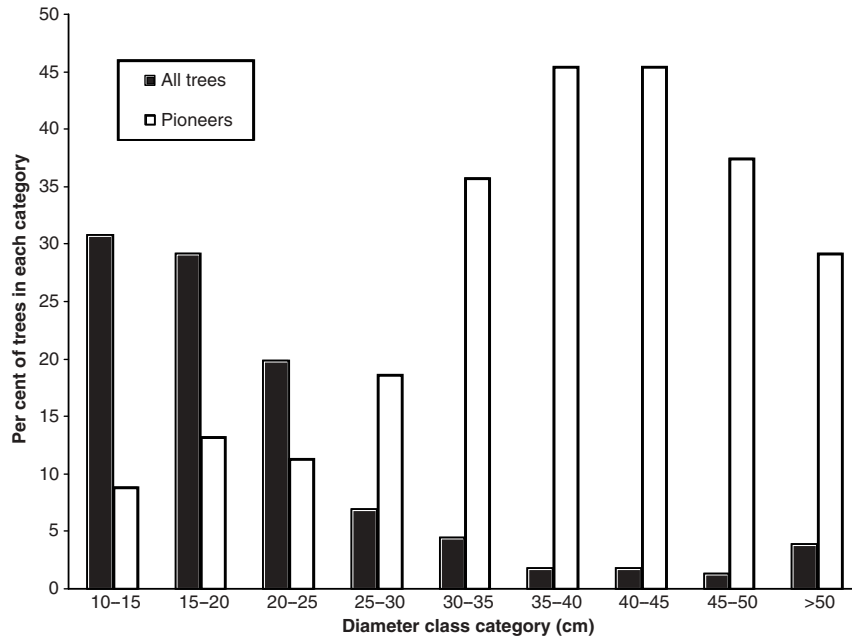
dominated by a few very common species, and almost completely lacking in understorey tree species. When stem densities are standardized, the Eno forest is less diverse than forests in Belize, 1830 km to the north, at 16°34' N (Fisher's alpha of 34.7 at Eno vs. 41.8 in the Bladen Nature Reserve, Belize; Brewer & Webb 2002). And despite these anomalies, the Eno forest is structurally mature and indistinguishable in structure from the hyperdiverse forests that surround it.

### Hypotheses for low diversity

The discussion of why the Eno plot is so poor in species should start with the admission that ecologists still have no general explanation for why tropical tree diversity varies from place to place (see Pitman *et al.* 2002a, ter Steege *et al.* 2003, and references therein). Previous discussions of especially species-poor stands of rich tropical forests have focused on (1) monodominance, in which a single species or a suite of closely related species dominates the community to the exclusion of most others (Connell & Lowman 1989, Hart 1990, Hart *et al.* 1989, Henkel 2003); (2) secondary successional forests, recovering from recent natural (e.g. Garwood *et al.* 1979) or anthropogenic (e.g. Ferreira & Prance 1999) disturbance; (3) forests growing on 'islands' of unique soil conditions (Ruokolainen & Tuomisto 1998, Vásquez-Martínez 1997); and (4) primary successional forests along rivers (Pitman *et al.* 1999, Terborgh & Petren 1991), or on the bare slopes left by landslides or volcanic ash falls (Garwood *et al.* 1979). Monodominance is not relevant to the Eno plot, because the dominant species is not a caesalpinoid legume (as in the classic cases of upland monodominance in the tropics), is a frequent dominant across eastern Ecuador, and accounts for only 25% of the plot's trees; the other three ideas are discussed below.

*Recovery from anthropogenic disturbance.* This is a tempting explanation, because the Eno plot contains a larger-than-usual component of secondary species, and forests in this area of Ecuador have been occupied by humans for at least 500 y (de Velasco 1981) and severely fragmented in recent years (Sierra 2000). Furthermore, the dark colour of the Eno soils is reminiscent of anthropogenic soils around long-inhabited sites in Amazonian Brazil (so-called 'terra preta do índio', see Lima *et al.* 2002 and references therein). Thus both twentieth century and much older human disturbance could potentially be responsible for the peculiar features of the Eno tree community.

Indeed, there is good evidence that the Eno plain was densely populated 500 y ago; however, those same data strongly suggest that those settlements were not the cause of the Eno tree plot's low diversity (see archaeological



**Figure 2.** Frequency distribution of diameter size classes and importance of pioneer species in the Eno plot. Dark bars give the per cent of all stems in each dbh size class. Lighter bars give the per cent of stems in that size class accounted for by pioneer (early successional) species.

data below). Several other independent lines of evidence suggest that the plot has not suffered important anthropogenic disturbance since its establishment. First, despite the relative abundance of successional species, 87% of all species and 85% of all trees are mature forest taxa. The four most common species are large-seeded, hardwooded, shade-tolerant species typical of mature forest. Second, structural characteristics of the Eno plot are essentially identical to those of other undisturbed forests in the region. Third, the pioneer taxa are much better represented in large size classes than in smaller size classes (i.e. pioneer trees in the plot are relatively old), implying that whatever accounts for the abundance of pioneers in the Eno plot is not related to the recent fragmentation of surrounding forests (Figure 2). Fourth, the pioneer guild in the Eno plot is much more diverse than that of the secondary forests that grow up after large-scale anthropogenic disturbance in eastern Ecuador, which are generally dominated by *Cecropia sciadophylla* (N. Pitman, *pers. obs.*). Finally, mineralogical analyses of surface soils on the Eno plain demonstrate that these are not carbon-rich soils created by a long history of human occupation (see below). Anthropogenic disturbance has surely affected the tree community in the Eno plot, as it is now affecting tree plots in the most remote corners of the Amazon basin (Phillips *et al.* 2004), but it cannot be the primary cause for its low diversity.

**Unique soils.** Tropical tree communities growing on islands of geographically atypical soils often have lower

diversity and different species assemblages than the surrounding forest (see for example Ruokolainen & Tuomisto 1998, ter Steege *et al.* 2000). It is possible that variation in fertility leads to variation in species dominance and diversity (see for example Huston 1994). Alternatively, the small size and isolation of unique soil patches may depress diversity (ter Steege *et al.* 2000).

Soils in the Eno plot are much sandier and much less acidic, on average, than those in surrounding forests, and some evidence suggests that the forest's peculiar composition and diversity are related to its edaphic condition. For example, five of the nine *terra firme* plots most similar in species composition to the Eno plot (Bogi plots A–E) are located in an edaphically similar area of Yasuní National Park, roughly 90 km to the SE of the Eno site (for a detailed description of the area, see DiFiore 1997). The terrain in those Bogi plots could not be more different from that in the Eno plot – it is characterized by tall, knife-edged ridges – but soils at the two sites are rather similar. The three sandiest and the four least acidic soil samples from the 15 *terra firme* plots come from the Bogi plots. In general, we found a weak positive relationship between the acidity of a plot's soils and its compositional similarity to the Eno plot, with forests more similar in composition growing on less acidic soils. We also found a non-significant trend towards lower diversity on less acidic soils (Spearman's  $\rho = -0.51$ ,  $P = 0.07$ ).

These results suggest that the very sandy, almost neutral soils of the Eno plot probably contribute in some degree to its peculiar composition and diversity. Quantifying

the degree is not possible at present, given that so few specifics are available regarding relationships between soil characters and tree communities. But three lines of evidence suggest that soils are only a small part of the reason for the low diversity. First, the Eno plot's predicted diversity based on its pH (see above) is still more than twice its observed diversity. Second, a 1-ha plot established in hilly terrain just 10 km north of the Eno plot, has very similar sandy, well-drained, nearly neutral soils but contains more than twice as many tree species (C. Cerón *et al.*, unpubl. data). Third, the next section provides convincing evidence that it was the way in which these soils were deposited, and not the soils themselves, that is primarily responsible for the low diversity.

*Primary succession following catastrophic disturbance.* As part of an archaeological inventory of the Eno plain, Thurber & Arellano (unpubl. data) dug soil pits at five sites, 9–20 km E and ESE of the Eno tree plot. In those pits, the sandy soil we found in the Eno plot formed a superficial layer 4–38 cm thick, and rested on top of a palaeosol which contained ceramic artefacts. Charcoal fragments collected in association with the artefacts at one site (Luz de America 1, ~20 km ESE of the Eno plot) yielded a  $^{14}\text{C}$  date of  $520 \pm 40$  y bp in 2002 (Beta Analytical, Inc., Miami, Florida), suggesting that the surface soil of the Eno plain has been deposited relatively recently.

The same study analysed the mineralogy of the sandy surface soil at the laboratory of the Escuela Politecnica Nacional, Departamento de Geología y Riesgos Geológicos (Quito, Ecuador), and found it to be fluvially deposited material of volcanic origin. The dominant mineralogical components of the sand were plagioclase, quartz, hornblende, pyroxene, and lithic fragments; fine-grained sediments, which would indicate aerial deposition, are mostly absent. These results are similar to those from mineralogical analyses of rock samples collected from the volcanic edifice of the nearby El Reventador Volcano (INECEL 1988). The 3562-m El Reventador, one of the most active volcanoes in the eastern Andes and just 80 km to the west of the Eno tree plot, is the most likely origin of the sand. The volcano has erupted at least 12 times over the last 100 y, sometimes for 6 y continuously, and has been active since the Pliocene (Nieto *et al.* 1991). Two other volcanoes stand upstream from the Eno plot (Cayambe and Antisana), but neither has been active in the last 500 y. Nearby Sumaco Volcano can also be discounted as a source of the material, since Sumaco debris flows are rich in nepheline (a sodium-rich mineral) not present in the Eno soils, and drain into the Napo River, not the Coca.

We hypothesize that the plain on which the Eno forest grows today was formed by a catastrophic breakout flood *c.* 500 y bp that originated near the El Reventador Volcano, swept down the Quijos and Coca rivers, and

washed out across the Eno area, destroying the existing vegetation and burying several hundred or thousand square kilometres of forest, crops and human settlements under a layer of debris and volcanic sands. The most plausible cause of the flood is the catastrophic failure of a natural dam in the Quijos and Coca rivers, which run past El Reventador and could easily be blocked by volcanic activity or landslides (Nieto *et al.* 1991).

The formation and failure of natural dams are relatively common phenomena in mountainous areas worldwide, where large landslides or glaciers temporarily impound rivers, and then fail in spectacularly violent outbursts of stored water (Costa & Schuster 1988). The best-documented tropical example is from Papua New Guinea, where an earthquake-triggered landslide in 1985 temporarily dammed the Bairaman River to create a temporary lake that swelled to 3 km long and 200 m deep. When the dam failed 16 mo later, the accumulated water coursed down the dry river bed at  $5.5 \text{ m s}^{-1}$  in a debris flow so massive that 39 km downriver the river level peaked at 20 m above normal (King *et al.* 1989).

There is evidence that recent eruptions of El Reventador and associated debris flows and landslides have created similar temporary lakes on the Quijos River. Varved lacustrine deposits have been described on the canyon walls of the Quijos River to the south of El Reventador, and remnants of a debris dam can be observed just upstream of Cascada San Rafael (M. Thurber, *pers. obs.*). When these temporary debris dams were breached catastrophically by the impounded water of the Quijos Rivers, debris flows would have travelled downstream into the narrow channel of the Coca River, in the area of Codo Sinclair. The headwaters of the Eno river are near the north bank of the Coca River, where it exits a narrow gorge and emerges into the lowlands. We hypothesize that the debris flows jumped the low divide separating the Coca and Eno rivers and buried the floodplains of the Eno River. Satellite images of the region show long, thin scars emanating eastwards from this gorge. A similar scar a few kilometres down river points directly at the Eno River (visible as a dark east–west line in Figure 1, just below the letter B).

Wood from volcanic landslide deposits near El Reventador has been  $^{14}\text{C}$ -dated to 600 y bp, and wood from silt and sand lacustrine deposits in the same area has been dated to 500 y bp (in Figure 1, the sampled deposits are on the north bank of the Quijos River, SE of El Reventador, INECEL 1988). These dates, presumably associated with a lake-forming event, correlate well with the  $^{14}\text{C}$  date from the palaeosol under the Eno plain.

We expect that similar events have been frequent in forests at the base of the Andes throughout the last glacial cycle, because the region combines steep terrain, frequent earthquakes and volcanic eruptions, expanding and retreating glaciers, and high levels of rainfall (Espinosa *et al.* 1991, Pitman *et al.* 2002b). A well-documented

event like the one we describe above occurred in the same vicinity following an earthquake in 1987, when earthquake-triggered landslides temporarily dammed the Quijos and nearby rivers. Subsequent breaching of the dams resulted in a flash flood 20 m high (Nieto *et al.* 1991), which destroyed large patches of riparian forest downstream (Pitman *et al.* 2002b). That flood did not deposit large amounts of sediment in lowland *terra firme* forest, but a larger event of the same kind could have.

By this line of speculation, the Eno forest is relatively poor in species because it is young, primary successional forest composed of species capable of rapidly colonizing a barren landscape. It may be no accident that the four most common species in the Eno plot have large seeds that are dispersed long distances by large animals, while a large number of the 'missing' taxa there are smaller-seeded understorey species with presumably slower dispersal rates. Charles-Dominique *et al.* (2003) have recently estimated the maximum colonization rate of an understorey palm in French Guiana at  $2.3 \text{ m y}^{-1}$ . If some understorey trees in eastern Ecuador are currently re-colonizing the Eno forest at equivalent rates, then they have travelled less than 1.4 km since the putative breakout flood – far too little to have reached the Eno forest.

Another possibility is that the large-seeded species now dominant in the Eno plot germinated *in situ* following the flood event. Given that the layer of sand deposited in many places is only a few centimetres thick, large-seeded species that produce tall seedlings could have potentially germinated in the washout plain immediately after the event, and grown to maturity under a closed canopy of *Cecropia* and other pioneer species.

Whatever the mechanism, the forests on the Eno plain have grown to structural maturity in <500 y. That diversity, and compositional maturity, lag so much farther behind implies that building community complexity in an Amazonian forest is a long process of slow-motion invasions, as individual species re-colonize at a snail's pace over the space of centuries. In the case of the Eno forest and many others in fragmented areas of Amazonia, that return will never be complete until healthy populations of animal dispersers also recover.

### Human history

The flooding event hypothesized above was so destructive and so recent that a record of it is likely to exist in some form of human history. For example, stories in which catastrophic floods leave the world treeless and covered with mud feature prominently in the oral tradition of the Cofán (R. Borman, *pers. comm.*), an indigenous group known to have inhabited the area since at least 1536 AD (de Velasco 1981). Given the limited archaeological

exploration of the region, the fact that human artefacts were found in all five excavations of the palaeosoil beneath the Eno plain suggests that a large human population was buried by the debris flood (M. Thurber & J. Arellano, unpubl. data). This raises the possibility that more extensive archaeological work in the area could uncover a Pompeii-like record of indigenous life in eastern Ecuador just a few years before the arrival of European explorers.

There is also a possibility that some aspect of the catastrophe or its aftermath was recorded in written historical accounts by eyewitnesses. If our dating of the event at  $520 \pm 40 \text{ y bp}$  is correct, giving a range of dates from 1442 to 1522 AD, then the first non-indigenous explorers of western Amazonia, the Gonzalo Pizarro and Francisco de Orellana expeditions in 1541 AD, must have passed through or very close to the area affected by the catastrophic flooding (de Carvajal 1992).

### Natural disasters elsewhere in the tropics

The recovery of Amazonian plant and animal communities following large-scale natural disturbance remains poorly studied. That is not for want of natural cataclysms in the region, which include, apart from the phenomena described in this article, meteorite impacts (Campbell *et al.* 1989), earthquake-triggered landslides (Garwood *et al.* 1979), vast windthrows (Nelson *et al.* 1994), large-scale flooding events (Campbell & Frailey 1984, Colinvaux *et al.* 1988), abrupt course changes of major rivers, and forest fires (Barlow & Peres 2004). In closing, it is instructive to ask whether plant ecologists today are capable of distinguishing an Amazonian forest untouched by major disturbances in thousands of years from a several-hundred-year-old forest recovering from a massive natural disaster – like, for example, the asteroid explosion that annihilated 215 000 ha of Siberian forest in 1908 (Farinella *et al.* 2001). The answer is probably not. In our case, the best biological indicator of the historical disturbance suffered by the Eno tree plot – apart from its anomalously low diversity – is the conspicuous absence of a mature community of understorey trees.

### ACKNOWLEDGEMENTS

We thank Jorge Vera and Jairo Zambrano for seeking out this patch of forest, laying out the plot, and measuring the trees. Fieldwork was supported by grants from the Andrew W. Mellon Foundation to J. Terborgh and the Center for Tropical Conservation at Duke University. The Landsat image in Figure 1 is courtesy of the Environmental and Conservation Programs at the Field Museum. The base maps in Figure 1 are courtesy of Flemming Nørgaard of

Aarhus University. Careful readings by an anonymous reviewer helped improve the manuscript in revision.

## LITERATURE CITED

- BALSLEV, H., LUTEYN, J., ØLLGAARD, B. & HOLM-NIELSEN, L. B. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica* 92:37–57.
- BARLOW, J. & PERES, C. A. 2004. Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 359:367–380.
- BREWER, S. W. & WEBB, M. A. H. 2002. A seasonal evergreen forest in Belize: unusually high tree species richness for northern Central America. *Botanical Journal of the Linnean Society* 138:275–296.
- BURNHAM, R. J. 2004. Alpha and beta diversity of lianas in Yasuni, Ecuador. *Forest Ecology and Management* 190:43–55.
- CAMPBELL, K. E. J. & FRAILEY, D. 1984. Holocene flooding and species diversity in southwestern Amazonia, South America. *Quaternary Research* 21:369–375.
- CAMPBELL, K. E., GRIEVE, R. A. F., PACHECO, J. & GARVIN, J. B. 1989. A newly discovered probable impact structure in Amazonian Bolivia. *National Geographic Research* 5:495–499.
- CHARLES-DOMINIQUE, P., CHAVE, J., DUBOIS, M. A., DE GRANVILLE, J. J., RIERA, B. & VEZZOLI, C. 2003. Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. *Global Ecology and Biogeography* 12:237–248.
- COLINVAUX, P. A., FROST, M., FROST, I., LIU, K. B. & STEINITZ-KANNAN, M. 1988. Three pollen diagrams of forest disturbance in the western Amazon Basin, Ecuador. *Review of Palaeobotany and Palynology* 55:73–82.
- CONNELL, J. H. & LOWMAN, M. D. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. *The American Naturalist* 134:88–119.
- COSTA, J. E. & SCHUSTER, R. L. 1988. The formation and failure of natural dams. *Geological Society of America Bulletin* 100:1054–1068.
- DE CARVAJAL, G. 1992. *Relación del nuevo descubrimiento del Río Grande de las Amazonas (1541–1542)*. Gobierno del Ecuador, Comisión Nacional Permanente de Conmemoraciones Cívicas, Quito.
- DE VELASCO, J. 1981. *Historia del Reino de Quito en la América Meridional*. Biblioteca Ayacucho, Caracas.
- DIFIORE, A. F. 1997. *Ecology and behavior of lowland Woolly Monkeys (Lagothrix lagotricha poeppigii, Atelinae) in eastern Ecuador*. Ph.D., University of California-Davis, Davis, USA.
- ESPINOSA, A. F., HALL, M. L. & YEPES, H. 1991. Tectonics and seismicity. Pp. 29–41 in Schuster, R. L. (ed.). *The March 5, 1987, Ecuador earthquakes: mass wasting and socioeconomic effects*. Natural Disaster Studies, Vol. 5. National Academy Press, Washington, DC.
- FARINELLA, P., FOSCHINI, L., FROESCHLE, C., GONCZI, R., JOPEK, T. J., LONGO, G. & MICHEL, P. 2001. Probable asteroidal origin of the Tunguska Cosmic Body. *Astronomy and Astrophysics* 377:1081–1097.
- FERREIRA, L. V. & PRANCE, G. T. 1999. Ecosystem recovery in *terra firme* forests after cutting and burning: a comparison on species richness, floristic composition and forest structure in the Jau National Park, Amazonia. *Botanical Journal of the Linnean Society* 130:97–110.
- GARWOOD, N. C., JANOS, D. P. & BROKAW, N. 1979. Earthquake-caused landslides: major disturbance to tropical forests. *Science* 205:997–999.
- GENTRY, A. H. 1988. Tree species richness of upper Amazonian forest. *Proceedings of the National Academy of Sciences of the United States of America* 85:156–159.
- HART, T. B. 1990. Monospecific dominance in tropical rain forests. *Trends in Ecology and Evolution* 5:6–11.
- HART, T. B., HART, J. A. & MURPHY, P. G. 1989. Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *The American Naturalist* 133:613–633.
- HENKEL, T. W. 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpinaceae) from Guyana. *Journal of Tropical Ecology* 19:417–437.
- HUSTON, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge. 681 pp.
- INECEL. 1988. *Estudio vulcanológico de El Reventador*. Instituto Ecuatoriano de Electrificación (INECEL), Quito. 116 pp.
- JØRGENSEN, P. M. & LEÓN-YÁNEZ, S. 1999. *Catalogue of the vascular plants of Ecuador*. Missouri Botanical Garden, St. Louis. 1181 pp.
- KING, J., LOVEDAY, I. & SCHUSTER, R. L. 1989. The 1985 Bairaman landslide dam and resulting debris flow, Papua New Guinea. *Quarterly Journal of Engineering Geology* 22:257–270.
- LIMA, H. N., SCHAEFER, C. E. R., MELLO, J. W. V., GILKES, R. J. & KER, J. C. 2002. Pedogenesis and pre-Colombian land use of “Terra Preta Anthrosols” (“Indian black earth”) of Western Amazonia. *Geoderma* 110:1–17.
- NELSON, B. W., KAPOS, V., ADAMS, J. B., OLIVEIRA, W. J., BRAUN, O. P. G. & DO AMARAL, I. L. 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75:853–858.
- NIETO, A. S., SCHUSTER, R. L. & PLAZA-NIETO, G. 1991. Mass wasting and flooding. Pp. 51–82 in Schuster, R. L. (ed.). *The March 5, 1987, Ecuador earthquakes: mass wasting and socioeconomic effects*. Natural Disaster Studies, Vol. 5. National Academy Press, Washington, DC.
- PHILLIPS, O. L., BAKER, T. R., ARROYO, L., HIGUCHI, N., KILLEEN, T. J., LAURANCE, W. F., LEWIS, S. L., LLOYD, J., MALHI, Y., MONTEAGUDO, A., NEILL, D. A., VARGAS, P. N., SILVA, J. N. M., TERBORGH, J., MARTINEZ, R. V., ALEXIADES, M., ALMEIDA, S., BROWN, S., CHAVE, J., COMISKEY, J. A., CZIMCZIK, C. I., DI FIORE, A., ERWIN, T., KUEBLER, C., LAURANCE, S. G., NASCIMENTO, H. E. M., OLIVIER, J., PALACIOS, W., PATINO, S., PITMAN, N. C. A., QUESADA, C. A., SALIDAS, M., LEZAMA, A. T. & VINCETI, B. 2004. Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 359:381–407.
- PITMAN, N. C. A. 2000. *A large-scale inventory of two Amazonian tree communities*. Ph.D. dissertation, Duke University.
- PITMAN, N. C. A., TERBORGH, J., SILMAN, M. R. & NÚÑEZ V., P. 1999. Tree species distributions in an upper Amazonian forest. *Ecology* 80:2651–2661.

- PITMAN, N. C. A., TERBORGH, J. W., SILMAN, M. R., NÚÑEZ, V. P., NEILL, D. A., CERÓN, C. E., PALACIOS, W. A. & AULESTIA, M. 2001. Dominance and distribution of tree species in upper Amazonian *terra firme* forests. *Ecology* 82:2101–2117.
- PITMAN, N. C. A., TERBORGH, J. W., SILMAN, M. R., NUNEZ, P., NEILL, D. A., CERON, C. E., PALACIOS, W. A. & AULESTIA, M. 2002a. A comparison of tree species diversity in two upper Amazonian forests. *Ecology* 83:3210–3224.
- PITMAN, N., MOSKOVITS, D. K., ALVERSON, W. S. & BORMAN A., R. (eds.) 2002b. *Ecuador: Serranías Cofán - Bermejo, Sinangoe*. The Field Museum of Natural History, Chicago. 226 pp.
- ROMERO-SALTOS, H., VALENCIA, R. & MACÍA, M. J. 2001. Patrones de diversidad, distribución y rareza de plantas leñosas en el Parque Nacional Yasuní y la Reserva Étnica Huaorani, Amazonía ecuatoriana. Pp. 131–162 in Duivenvoorden, J., Balslev, H., Cavelier, J., Grández, G., Tuomisto, H. & Valencia, R. (eds.). *Evaluación de los recursos no-maderables en la Amazonía Nor-occidental*. IBED, Universiteit van Amsterdam, Amsterdam.
- ROMOLEROUX, K., FOSTER, R., VALENCIA, R., CONDIT, R., BALSLEV, H. & LOSOS, E. 1997. Árboles y arbustos (dap  $\geq$  1 cm) encontrados en dos hectáreas de un bosque de la Amazonía ecuatoriana. Pp. 189–215 in Valencia, R. & Balslev, H. (eds.). *Estudios sobre diversidad y ecología de plantas*. Pontificia Universidad Católica del Ecuador, Quito.
- RUOKOLAINEN, K. & TUOMISTO, H. 1998. Vegetación natural de la zona de Iquitos. Pp. 253–365 in Kalliola, R. & Flores-Paitán, S. (eds.). *Geocología y desarrollo Amazónico: estudio integrado en la zona de Iquitos, Perú*. Annales Universitatis Turkuensis Ser A II 114, Turku, Finland.
- SIERRA, R. 2000. Dynamics and patterns of deforestation in the western Amazon: the Nape deforestation front, 1986–1996. *Applied Geography* 20:1–16.
- TER STEEGE, H., SABATIER, D., CASTELLANOS, H., VAN ANDEL, T., DUIVENVOORDEN, J., DE OLIVEIRA, A. A., EK, R., LILWAH, R., MAAS, P. & MORI, S. 2000. An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology* 16:801–828.
- TER STEEGE, H., PITMAN, N., SABATIER, D., CASTELLANOS, H., VAN DER HOUT, P., DALY, D. C., SILVEIRA, M., PHILLIPS, O., VASQUEZ, R., VAN ANDEL, T., DUIVENVOORDEN, J., DE OLIVEIRA, A. A., EK, R., LILWAH, R., THOMAS, R., VAN ESSEN, J., BAIDER, C., MAAS, P., MORI, S., TERBORGH, J., VARGAS, P. N., MOGOLLON, H. & MORAWETZ, W. 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation* 12:2255–2277.
- TERBORGH, J. & PETREN, K. 1991. Development of habitat structure through succession in an Amazonian floodplain forest. Pp. 28–46 in Bell, S., McCoy, E. D. & Mushinsky, H. R. (eds.). *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, New York.
- VALENCIA, R., BALSLEV, H. & PAZ Y MIÑO C., G. 1994. High tree alpha-diversity in Amazonian Ecuador. *Biodiversity and Conservation* 3:21–28.
- VÁSQUEZ-MARTÍNEZ, R. 1997. *Flórula de las Reservas Biológicas de Iquitos, Perú*. Missouri Botanical Garden, St. Louis. 1046 pp.
- VÁSQUEZ-MARTÍNEZ, R. & PHILLIPS, O. L. 2000. Allpahuayo: floristics, structure, and dynamics of a high-diversity forest in Amazonian Peru. *Annals of the Missouri Botanical Garden* 87:499–527.